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Ecology and behaviour of bottlenose dolphins (*Tursiops truncatus*) in a coastal area subject to shellfish farming

Séverine Methion

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DE L'UNIVERSITÉ DE BORDEAUX

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Présentée par Séverine METHION

Pour obtenir le grade de Docteur de l'Université de Bordeaux

Ecology and behaviour of bottlenose dolphins
(*Tursiops truncatus*) in a coastal area subject to
shellfish farming

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Devant le jury composé de :

Antoine GRÉMARE, Professeur, Université de Bordeaux

Vincent RIDOUX, Professeur, Université de La Rochelle

Christophe GUINET, Directeur de recherche, CEBC-CNRS

Graham PIERCE, Professeur, Universidade de Aveiro

Thierry CORRÈGE, Professeur, Université de Bordeaux

Bruno DÍAZ LÓPEZ, Docteur, BDRI

Président, Examineur

Examineur

Rapporteur

Rapporteur

Directeur de thèse

Co-directeur de thèse

Ecology and behaviour of bottlenose dolphins (*Tursiops truncatus*) in a coastal area subject to shellfish farming

Abstract. Studying the ecology of cetaceans living under the pressure of anthropogenic activities is essential for their conservation. Yet, there is a paucity of information on cetaceans and shellfish farming. Using a long-term and year-round dataset, this study investigates the ecology and the behaviour of a coastal cetacean, the bottlenose dolphin (*Tursiops truncatus*), in an important area for shellfish farming (Ría de Arousa, North-West Spain). A resident population of bottlenose dolphins was present year-round in this area. Their seasonal abundance varied from 56 to 144 individuals and their apparent survival was high. Of the investigated environmental factors, depth and shellfish farms were influencing dolphins habitat use, and chlorophyll-a and dissolved oxygen were influencing their spatio-temporal aggregation patterns. Foraging behaviour was mainly determined by the sea surface temperature, time of day, and whether the dolphins were foraging within shellfish farm areas. Dolphins were predicted to be more likely found foraging inside these areas than outside (57% vs. 43%). Findings of this study also revealed variation in foraging behaviour among dolphins, with some individuals foraging more frequently than others within the shellfish farms. In turn, individuals that frequently foraged within shellfish farms had weaker associations compared to others. This study generates key insights into the ecology and the behaviour of a coastal cetacean living under the pressure of the shellfish farming industry. It further provides valuable information on conservation priorities for coastal cetaceans living under such pressures, as well as regulations for the shellfish farming industry.

Key-words: bottlenose dolphin, cetacean, ecology, behaviour, aquaculture, conservation.

Écologie et comportement du grand dauphin (*Tursiops truncatus*) dans un écosystème côtier sous l'influence de la conchyliculture

Résumé. L'étude de l'écologie des cétacés vivant sous la pression d'activités anthropiques est essentielle pour leur conservation. Cependant, il existe peu d'informations sur les cétacés et la conchyliculture. À l'aide d'un ensemble de données collectées à long terme, cette étude examine l'écologie et le comportement d'un cétacé côtier, le grand dauphin (*Tursiops truncatus*), vivant dans une zone importante pour la conchyliculture (Ría d'Arousa, Nord-Ouest de l'Espagne). Le grand dauphin était présent à l'année dans cette région. Leur abondance saisonnière variait de 56 à 144 individus et leur survie apparente était élevée. Parmi les facteurs environnementaux étudiés, la profondeur et la présence de fermes conchylicoles influaient sur leur utilisation de l'habitat, et la chlorophylle-a et l'oxygène dissous influaient sur leurs modes d'agrégation spatio-temporelle. Leur comportement alimentaire dépendait principalement de la température de la surface de la mer, de l'heure de la journée et du fait que les dauphins s'alimentent dans les zones conchylicoles, les dauphins ayant une probabilité plus élevée de se nourrir à l'intérieur de ces zones, qu'à l'extérieur (57%-43%). Certains individus s'alimentaient plus fréquemment que d'autres autour des fermes conchylicoles. À leur tour, les individus qui se nourrissaient fréquemment autour des fermes avaient des associations plus faibles que les autres. Cette étude génère des informations clés sur l'écologie et le comportement d'un cétacé vivant sous la pression de l'industrie conchylicole, sur les priorités de conservation des cétacés vivant sous de telles pressions, ainsi que sur les réglementations applicables au secteur de la conchyliculture.

Mots-clés: grand dauphin, cétacé, écologie, comportement, aquaculture, conservation.

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Table of content

ACKNOWLEDGEMENTS	V
SCIENTIFIC PRODUCTION	VII
TABLE OF CONTENT	XI
LIST OF FIGURES	XVII
LIST OF TABLES.....	XXI
LIST OF ABBREVIATIONS	XXIII
RÉSUMÉ SUBSTANTIEL	XXV
CHAPTER 1. GENERAL INTRODUCTION	1
1.1 Anthropogenic activities and marine top predators	2
1.1.1 Anthropogenic activities in marine coastal ecosystems	2
1.1.2 Top predators in marine coastal ecosystems.....	4
1.1.3 Impact of anthropogenic activities on cetaceans	6
1.2 Studying cetacean ecology and behaviour.....	11
1.2.1 Abundance estimates	12
1.2.2 Distribution and habitat use	16
1.2.3 Behavioural pattern	18
1.2.4 Social behaviour	20
1.3 Marine aquaculture and cetaceans	23
1.3.1 Marine aquaculture: an industry in worldwide expansion	23
1.3.2 Impacts of marine aquaculture in the environment.....	25
1.3.3 Interaction between marine aquaculture and cetaceans.....	30
1.4 Objectives and outlines of the thesis	35
1.4.1 Background context	35
1.4.2 Objectives.....	39
1.4.3 Thesis structure.....	41
CHAPTER 2. GENERAL METHODS.....	43
2.1 Study area: the Ría de Arousa (Galicia, Spain)	44
2.1.1 Environmental characteristics of the study area	44
2.1.2 Human activities: importance of shellfish aquaculture	47

2.2	The common bottlenose dolphin (<i>Tursiops truncatus</i>).....	52
2.2.1	Systematic and general appearance	52
2.2.2	Life history	53
2.2.3	Distribution	53
2.2.4	Diet and foraging behaviour	54
2.2.5	Predators.....	56
2.2.6	Social ecology.....	56
2.2.7	Threats	57
2.2.8	Conservation	59
2.2.9	Bottlenose dolphins in Galician waters	60
2.3	Data collection and analysis.....	63
2.3.1	Data collection from boat-based surveys.....	63
2.3.2	Mark-recapture analysis	72
2.3.3	Data obtained from external repositories.....	77
2.3.4	Data obtained from GIS	79
CHAPTER 3. ABUNDANCE AND DEMOGRAPHIC PARAMETERS OF BOTTLENOSE DOLPHINS IN A HIGHLY AFFECTED COASTAL ECOSYSTEM.....		83
3.1	Abstract	84
3.2	Introduction	85
3.3	Methods	88
3.3.1	Study area	88
3.3.2	Data collection	88
3.3.3	Relative frequency of occurrence.....	90
3.3.4	Analysis of photographs.....	90
3.3.5	Mark-recapture abundance models.....	92
3.3.6	Total population size.....	95
3.4	Results	97
3.4.1	Survey effort, group size and datasets	97
3.4.2	Relative frequency of occurrence.....	100
3.4.3	Photographic identification data	100
3.4.4	Robust design model selection.....	100
3.4.5	Abundance estimation	103
3.4.6	Survival rates, temporal emigration patterns and capture probabilities	103
3.5	Discussion.....	105

CHAPTER 4. DOLPHIN GROUP DYNAMICS AS AN INDICATOR OF ENVIRONMENTAL CHANGE

109

4.1	Abstract	110
4.2	Introduction	111
4.3	Methods	114
4.3.1	Study area	114
4.3.2	Data collection	115
4.3.3	Environmental data.....	116
4.3.4	Data analysis and modelling framework	117
4.4	Results	120
4.4.1	Survey effort and bottlenose dolphin group dynamics	120
4.4.2	Effects of environmental conditions on the bottlenose dolphin group size	123
4.5	Discussion.....	126
CHAPTER 5. THE IMPACT OF SHELLFISH FARMING ON COMMON BOTTLENOSE DOLPHINS' USE OF HABITAT		129
5.1	Abstract	130
5.2	Introduction	131
5.3	Methods	133
5.3.1	Study area	133
5.3.2	Data collection	135
5.3.3	Data analysis and modelling framework	137
5.4	Results	140
5.4.1	Survey effort and presence of common bottlenose dolphins	140
5.4.2	Models output: environmental (persistent and non-persistent), geographical, and anthropogenic variables.....	143
5.5	Discussion.....	149
CHAPTER 6. NATURAL AND ANTHROPOGENIC DRIVERS OF FORAGING BEHAVIOUR IN BOTTLENOSE DOLPHINS: INFLUENCE OF SHELLFISH AQUACULTURE.....		153
6.1	Abstract	154
6.2	Introduction	155
6.3	Methods	158
6.3.1	Study area	158
6.3.2	Data collection	159

6.3.3	Data selection	163
6.3.4	Data analysis	163
6.4	Results	165
6.4.1	Survey effort, group size, and behavioural samples	165
6.4.2	Behavioural budget.....	166
6.4.3	Factors influencing bottlenose dolphin foraging behaviour.....	167
6.5	Discussion.....	170
CHAPTER 7. INDIVIDUAL FORAGING VARIATION DRIVES SOCIAL ORGANIZATION IN BOTTLENOSE DOLPHINS.....		173
7.1	Abstract	174
7.2	Introduction	175
7.3	Methods	179
7.3.1	Study area	179
7.3.2	Data collection	180
7.3.3	Individual foraging variation and spatial distribution	181
7.3.4	Defining association and estimating affiliation indices.....	181
7.3.5	Analysis of affiliation patterns	182
7.3.6	Network metrics and social structure	183
7.4	Results	185
7.4.1	Individual foraging variation and spatial distribution	185
7.4.2	Association patterns, network metrics, and social structure	185
7.5	Discussion.....	189
CHAPTER 8. GENERAL DISCUSSION.....		195
8.1	Overview	196
8.2	Ecology and behaviour of bottlenose dolphins in Galician waters.....	197
8.3	Influence of shellfish aquaculture on bottlenose dolphin ecology and behaviour	205
8.4	Implication for the conservation of bottlenose dolphins	208
8.4.1	Recommendations for the conservation of bottlenose dolphins.....	208
8.4.2	Recommendations for the shellfish farming industry.....	210
8.5	Limitations and suggestions for future studies	213
8.6	Conclusions	216
REFERENCES.....		217
ANNEXES		261

Annex 1. Infanticide attacks and associated epimeletic behaviour in bottlenose dolphins.....	262
Annex 2. Habitat use and relative density in harbour porpoises.	284
Annex 3. Supervision of Bachelor and Master students.....	310

List of figures

Figure 1.1. Global map of cumulative impacts of human activities on marine ecosystems (source: Halpern et al. 2008b).	2
Figure 1.2. The structure and functioning of marine ecosystems lead to the ecological production of ecosystem services (source: Barbier 2017).	3
Figure 1.3. Flow diagram expressing trophic flows and levels in the Ionian Sea (source: Pirrodi et al. 2011).	5
Figure 1.4. Global patterns of human threats for land (brown) and marine (blue) mammals (source: Schipper et al. 2008).	6
Figure 1.5. Photographs of (a) an Indo-Pacific humpback dolphin with propeller cuts on the peduncle, and (b) an Indo-Pacific bottlenose dolphin with a propeller cut on the dorsal fin (Persian Gulf) (source: Bruno Díaz López, BDRI).	7
Figure 1.6. Photographs of bottlenose dolphins carrying plastic on their rostrum (Galicia, Spain) (source: Bruno Díaz López, BDRI).	8
Figure 1.7. Sighting rates for (a) Minke whale, <i>Balaenoptera acutorostrata</i> , and (b) harbour porpoise before, during, and after military sonar exercises (Scotland) (source: Parsons et al. 2000).	9
Figure 1.8. Temporal trend of social patterns in bottlenose dolphin, associated to a temporal switch to the food sources provided by finfish aquaculture (Italy). HWI: Half Weight Index (associations between individuals). Seasons: seasons of the year, from January 2005 to December 2013 (source: Díaz López 2019).	10
Figure 1.9. Time-series data for (a) monthly Southern Oscillation Index values and (b) seasonal abundance estimates for bottlenose dolphins (Western Australia) (source: Sprogis et al. 2018).	14
Figure 1.10. Exposure of (a) white-sided dolphins, <i>Lagenorhynchus acutus</i> , to pelagic trawls and (b) bottlenose dolphins to gillnets in Irish and UK waters. Green indicates lower exposure and red indicates higher exposure (source: Breen et al. 2016).	17
Figure 1.11. Proposed marine protected area for killer whale for a priority feeding area in Washington state, USA, and British Columbia, Canada (source: Ashe et al. 2010).	19
Figure 1.12. Hinde's (1976) framework. Circles represent independent factors that may operate at different levels of the framework (adapted from Whitehead 2008).	21
Figure 1.13. World capture fisheries and aquaculture production (source: FAO 2018).	23
Figure 1.14. Aquaculture production of main groups of food fish species (source: FAO 2018).	25
Figure 1.15. Ecological effects of farming shellfish (source: Keeley et al. 2009).	27
Figure 1.16. Attraction (A) and repulsion (R) mechanisms of mobile wild species by fish farming cages (source: Callier et al. 2017).	30

Figure 1.17. Bottlenose dolphins incidentally catch in lines from a finfish cage (a, c), in anti-predator net from a finfish farm (d), and exhibiting a dorsal fin cut probably due to a boat strike (Sardinia, Italy) (source: Bruno Díaz López, BDRI).	32
Figure 1.18. Percentage of bottlenose dolphin observations before and during the implementation of oyster farms, and after their removal in Shark Bay (Australia) (source: Watson-Capps & Mann 2005).	33
Figure 1.19. Bottlenose dolphins between shellfish farms in Galicia, North-West Spain (source: Bruno Díaz López, BDRI).	36
Figure 1.20. Illustration of harpoons used for killing bottlenose dolphins in Galicia (source: Valdes Hansen 2004).	38
Figure 1.21. Flowchart of the PhD strategy.	42
Figure 2.1. Map of the Southern Galician coast (North-West Spain).	44
Figure 2.2. Satellite image of sea surface temperature during an upwelling event along the Galician coast (source: Álvarez et al. 2005).	45
Figure 2.3. Map of the study area, the Ría de Arousa (North-West Spain).	47
Figure 2.4. Filter feeders' biomasses and carrying capacity of shellfish aquaculture in coastal ecosystems around the world. ECC: ecological carrying capacity; PCC: production carrying capacity (source: Outeiro et al. 2018).	48
Figure 2.5. Flowchart diagram of mussel aquaculture production on floating rafts (source: FAO 2014).	49
Figure 2.6. Photographs of (a) a floating platform for shellfish cultivation and (b) underwater view of a shellfish platform with ropes where mussels are growing in the Ría de Arousa (source: Séverine Methion).	50
Figure 2.7. Aerial view of shellfish cultivation in the Ría de Arousa (source: Bruno Díaz López).	50
Figure 2.8. A common bottlenose dolphin, <i>Tursiops truncatus</i> (source: NOAA fisheries, www.fisheries.noaa.gov , accessed 1 July 2019).	52
Figure 2.9. Geographic range of the common bottlenose dolphin (source: Wells et al. 2019).	54
Figure 2.10. Bottlenose dolphins interacting with a fishing boat in Galicia (source: Bruno Díaz López, BDRI).	56
Figure 2.11. Associations between bottlenose dolphins during different feeding activities in Sardinia (Italy) (source: Díaz López & Shirai 2008).	57
Figure 2.12. Mean PCBs concentrations in bottlenose dolphins in European waters.	59
Figure 2.13. Overall sightings rates of cetaceans along the Galician coast from 2003 to 2007.	60
Figure 2.14. Most common prey species of bottlenose dolphins in Galician waters.	61
Figure 2.15. Research vessel used for the data collection (source: Séverine Methion, BDRI).	64
Figure 2.16. Observers onboard the research vessel, scanning the sea surface in search of bottlenose dolphins (source: Séverine Methion, BDRI).	65

Figure 2.17. Photograph of (a) an adult with a new-born and (b) an adult with an immature bottlenose dolphin.	71
Figure 2.18. Ventral side of a male (left) and a female (right) bottlenose dolphin.	72
Figure 2.19. Photograph of the dorsal fin of two individual bottlenose dolphins. The arrows present the notches used for photo-identification analysis.	73
Figure 2.20. Photographs of (a) unmarked, (b) poorly marked, (c) marked, and (d) well marked bottlenose dolphins.....	76
Figure 2.21. Screen capture of the dorsal fin of two individual bottlenose dolphins matched with the software Darwin.....	77
Figure 2.22. Map of the study area with the 11 oceanographic stations.	78
Figure 2.23. Map of the study area with a grid of 1 nm.	80
Figure 2.24. Minimum convex polygons and centroids for two individual bottlenose dolphins.	81
Figure 3.1. Map of the study area (Ría de Arousa and surrounding waters, North-West Spain) including the 50 and 100 isobaths. Bottlenose dolphin encounters are indicated by filled circles.	99
Figure 4.1. The Ría de Arousa (North-West Spain) where bottlenose dolphin distribution and abundance surveys were conducted from 2014 to 2018.	117
Figure 4.2. Bottlenose dolphins encounters in the Ría de Arousa, from 2014 to 2018.....	120
Figure 4.3. Averaged predictions of the number of bottlenose dolphins in each group for each significant covariate in the final model.....	124
Figure 4.4. Monthly average of (a) fluorescence (mg/m^3) and (b) dissolved oxygen (mL/L) in the Ría de Arousa, from 2014 to 2018.	125
Figure 5.1. Geographical location of the Ría of Arousa (Galicia, NW Spain) including 50 and 100 isobaths with index map of the Iberian Peninsula. Survey effort is indicated by grey track lines. Dolphin encounters are indicated by small circles. Filled polygons indicate location of mussel aquaculture zones.....	134
Figure 5.2. Common bottlenose dolphin presence modelled as a smooth function of depth. The AIC of the best permanent environment model was 230 (corresponding $R^2 = 0.2$) and $P < 0.01$. Shaded areas represent 95% CIs. A rug plot with the actual data values is also shown.	146
Figure 5.3. Common bottlenose dolphin presence modelled as a smooth function of longitude (UTM X, grid 29N). The AIC of the best geographic model was 229 (corresponding $R^2 = 0.19$) and $P < 0.01$. Shaded areas represent 95% CIs. A rug plot with the actual data values is also shown.....	147
Figure 5.4. Common bottlenose dolphin presence modelled as a smooth function of distance to mussel farms. The AIC of the best anthropogenic model was 237 (corresponding $R^2 = 0.14$) and $P < 0.05$. Shaded areas represent 95% CIs. A rug plot with the actual data values is also shown.....	148

Figure 6.1. Map of the study area (Ría de Arousa, North-West Spain) with survey tracks, bottlenose dolphin encounters (indicated by filled circles), and polygons representing the shellfish farm areas.	159
Figure 6.2. Map of the study area with grid representing bottlenose dolphin foraging budget and polygons representing the shellfish farm areas.	165
Figure 6.3. Bottlenose dolphin behavioural budget inside and outside shellfish farm areas..	167
Figure 6.4. Averaged predictions of bottlenose dolphin foraging behaviour for each covariate present in the confidence set of models and their 95% confidence limits when all other variables are fixed on their mean value.....	168
Figure 7.1. Map of the study area (Ría de Arousa, North-West Spain) showing the minimum convex polygon centroids for each of the 66 bottlenose dolphins studied. Polygons represent shellfish farm areas.	179
Figure 7.2. Scatter plot with fitted line and Spearman rho coefficient between farm foraging rate (x-axis) and each affiliation (mean GAI and max GAI) and network metrics (Strength, Eigenvector Centrality, Clustering Coefficient, Reach, and Affinity) (y-axis). Histograms with rug plot are provided for each variable. Significance codes: * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$	187
Figure 7.3. Social network of bottlenose dolphins in the Ría de Arousa (North-West Spain). Each individual is represented by a node. Only edges with GAI greater than 0.02 are displayed. Node sizes represent the farm foraging rate of the individuals, and edge width is proportional to the strength of the affiliations.	188
Figure 8.1. Spatial distribution of bottlenose dolphins in Galician waters.....	197
Figure 8.2. Mean bottlenose dolphin group size in various locations around the world.	201
Figure 8.3. Social network of dolphins from Laguna (Brazil) defined by their foraging tactic (source: Daura-Jorge et al. 2012).....	204
Figure 8.4. Existing SACs and proposed expansions in the Ría de Arousa.	210

List of tables

Table 1.1. Conservation status of cetaceans (adapted from IUCN red list, www.iucnredlist.org , accessed 1 July 2019).	13
Table 2.1. List of variables collected every 20 minutes during each boat survey.....	66
Table 2.2. List of variables recorded during a sighting of bottlenose dolphin.....	67
Table 2.3. Description of the behavioural event observed in bottlenose dolphins in the Ría de Arousa (North-West Spain).	69
Table 2.4. Description of the behavioural states observed in bottlenose dolphins in the Ría de Arousa (North-West Spain).	70
Table 2.5. Age classification of bottlenose dolphins.....	71
Table 2.6. Sex classification of bottlenose dolphins.	72
Table 2.7. Photograph grading for the identification if individual bottlenose dolphin.	74
Table 2.8. Overall quality score for each photograph.	74
Table 2.9. Distinctiveness category for individual bottlenose dolphins.....	75
Table 3.1. Annual observation effort, robust design periods, bottlenose dolphin encounters, encounter ratio, and the number of bottlenose dolphins identified included in the mark–recapture analysis.....	98
Table 3.2. Capture–recapture models fitted to the capture histories of bottlenose dolphins to estimate parameters for population size (\hat{N}), apparent survival (ϕ), emigration probabilities (γ'' , γ') and capture probability (p).	102
Table 3.3. Seasonal abundance estimates of bottlenose dolphins in the study area.....	103
Table 3.4. Mean seasonal temporary emigration rates for the best fitting Markovian model.	104
Table 4.1. Yearly variation in bottlenose dolphin group size and associated environmental factors, between 2014 and 2018, in the Ría de Arousa.	122
Table 4.2. Seasonal variation in bottlenose dolphin group size and associated environmental factors, between 2014 and 2018, in the Ría de Arousa.	122
Table 5.1. The seasonal observation effort, bottlenose dolphin encounters, and number of 20 min samples collected in relation to the two years of research.	141
Table 5.2. Frequency of occurrence of common bottlenose dolphins (ER) with respect to whether or not dolphins were present inside the mussel aquaculture zones.	142
Table 5.3. Mean number of dolphins \pm standard error with respect to whether or not bottlenose dolphins were present inside the mussel aquaculture zones.	143
Table 5.4. Summary of the variables retained by the final selected models (persistent environment, geographical, and anthropogenic models) for presence and absence of common bottlenose dolphins.	144

Table 6.1. Description of the behavioural states observed in bottlenose dolphins in the Ría de Arousa (North-West Spain).	161
Table 6.2. Summary of the 6 best-supported models of bottlenose dolphin foraging behaviour.	169
Table 6.3. Model-averaged relative variable importance (RVI) estimated by a generalized additive model to determine the effects of shellfish farms (SF), sea surface temperature (SST), time (T), slope gradient (S), wind speed (W), group size (G), tidal cycle (TC), and sea surface salinity (SSS) on bottlenose dolphin foraging behaviour (n = 574).	169
Table 7.1. Significance of predictor variables on association indices using multiple regression quadratic assignment procedures (N = 66 individuals).	186

List of abbreviations

ACCOBAMS	Agreement on the Conservation of Cetaceans of the Black Sea, Mediterranean Sea and contiguous Atlantic Area
ACF	Auto-Correlation Functions
ADD	Acoustic Deterrent Device
AHD	Acoustic Harrassment Device
AIC	Akaike Information Criterion
AICc	Akaike Information Criterion corrected for small sample size
AR	Artificial Reef
ASCOBANS	Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas
BDRI	Bottlenose Dolphin Research Institute
CARTs	Classification And Regression Trees
CI	Confidence Interval
CITES	Convention on International Trade of Endangered Species
cm	centimetre
CMS	Convention on Migratory Species
CV	Coefficient of Variation
DCP	Dispositif de Concentration de Poisson
ENACW	Eastern North Atlantic Central Water
ER	Encounter Ratio
FAD	Fish Aggregating Device
FAO	Food and Agriculture Organisation
GAI	Generalized Affiliation Index
GAM	Generalised Additive Model
GCV	General Cross Validation
GIS	Geographic Information System
GLM	Generalised Linear Model
GPS	Global Positioning System
HWI	Half-Weight Index
IDW	Inverse Distance Weighted

IUCN	International Union for Conservation of Nature
kg	kilogram
km	kilometre
kn	knot
L	Litre
LRT	Likelihood Ratio Test
m	metre
mg	milligram
mL	millilitre
MRQAP	Multiple Regression Quadratic Assignment Procedure
nm	nautical mile
OLS	Ordinary Least Squares
OQS	Overall Quality Score
PCB	PolyChlorinated Biphenyl
PIM	Parameter Index Matrix
PSU	Practical Salinity Unit
s	second
SAC	Special Area of Conservation
SCI	Site of Community Importance
SD	Standard Deviation
SE	Standard Error
SIG	Système d'Information Géographique
SLR	Single Lens Reflex
SSS	Sea Surface Salinity
SST	Sea Surface Temperature
UTC	Coordinated Universal Time
UTM	Universal Transverse Mercator
VIF	Variance Inflation Factor
WGS	World Geodesic System
ZSC	Zone Spéciale de Conservation
°C	degree Celsius

Résumé substantiel

Introduction

De nombreuses espèces de cétacés ont une distribution côtière (Jefferson & Hung 2004 ; López et al. 2004 ; Díaz López 2019). Ainsi, ces cétacés sont directement ou indirectement exposés à de multiples activités anthropiques (par exemple, pêche, aquaculture, trafic maritime, fragmentation et perte de l'habitat, et pollution), ce qui peut entraîner des changements de répartition, d'utilisation de l'habitat, d'abondance, de comportement, de structure sociale et, dans des situations extrêmes, peut provoquer l'extinction de certaines populations de cétacés (Nowacek et al. 2001 ; Dans et al. 2003 ; McLeod et al. 2005 ; Watson-Capps & Mann 2005 ; Hoffmann et al. 2010 ; Wein & Pierce 2012 ; Taylor et al. 2017 ; Díaz López 2019).

Afin d'identifier et de surveiller l'influence potentielle des activités anthropiques sur les populations de cétacés, il est essentiel d'obtenir des données de base sur leur écologie (Whitehead et al. 2000). Premièrement, la connaissance des paramètres de population est cruciale afin d'évaluer l'état d'une population (c'est-à-dire, une estimation de son abondance) et pour mieux cerner les changements et les tendances de la population (Boyd et al. 2010). Deuxièmement, il est nécessaire de comprendre l'utilisation de l'habitat par les populations de cétacés afin d'identifier les zones d'habitat clés et afin d'élaborer des mesures de conservation appropriées (Ingram & Rogan 2002). De plus, l'évaluation du comportement des populations de cétacés dans leur habitat est essentielle pour leur protection, leur gestion et pour la conservation des zones critiques d'habitat (Bailey & Thompson 2006). De même, étudier l'organisation sociale d'une population est important pour mieux comprendre la nature, la qualité et la structure temporelle des relations individuelles ainsi que les processus évolutifs qui façonnent leur système social (Wells et al. 1987). Enfin, déterminer l'influence de facteurs écologiques et anthropiques sur l'abondance d'une population, leur utilisation de l'habitat, leur comportement et leur organisation sociale peut approfondir notre compréhension de l'écologie des cétacés en vue de l'élaboration de stratégies de conservation et de gestion (Chilvers & Corkeron 2001 ; Lusseau & Higham 2004 ; Bejder et al. 2006 ; Díaz López 2019).

La distribution de nombreuses espèces de cétagés, étant côtière, se chevauche avec celle de l'aquaculture marine. L'aquaculture marine (c'est à dire, l'élevage d'espèces végétales et animales dans la mer) est l'un des secteurs de production alimentaire à la croissance la plus rapide au monde (FAO 2014). La conchyliculture, qui est la culture de mollusques, est le secteur principal de l'aquaculture marine, représentant 59 % de la production totale et, comme les autres formes d'aquaculture, est en expansion (FAO 2018). L'infrastructure physique des fermes aquacoles (bouées, cordes, ancres, cages ou filets) fournit un substrat à des organismes sessiles appartenant à un large éventail de taxons (notamment, macro-algues, bryozoaires, mollusques, tuniciers et cnidaires) (Willemsen 2005). Le plancton s'accumule autour des fermes qui regroupent des poissons sauvages se nourrissant de ces ressources (Díaz López et al. 2008a ; Fernández-Jover et al. 2016). De même, les organismes sessiles et les communautés associées, y compris les amphipodes, les petits poissons et les gastéropodes, fournissent également des ressources trophiques supplémentaires aux poissons, qui peuvent ensuite être transférés vers des niveaux trophiques supérieurs (Lacoste & Gaertner-Mazouni 2015). Les structures des fermes et les organismes associés agissent donc comme des dispositifs de concentration de poisson (DCP) (Callier et al. 2017). À leur tour, de nombreuses espèces de grands prédateurs sont attirées par la présence de poissons autour de la ferme (par exemple, Díaz López 2017) (Figure i).

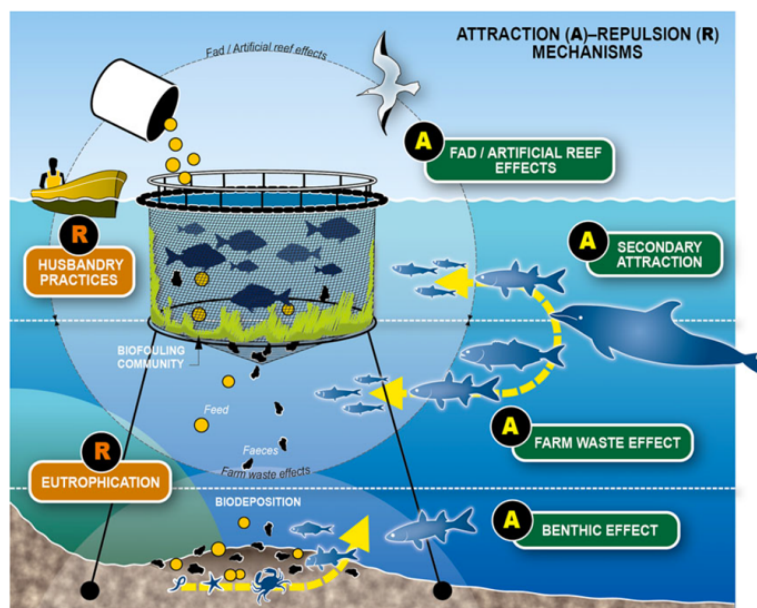


Figure i. Mécanismes d'attraction (A) et de répulsion (R) d'espèces sauvages mobiles autour de cage piscicole (source : Callier et al. 2017).

Les cétacés peuvent éviter ou être attirés par les fermes aquacoles (piscicoles et conchylicoles), en fonction de la méthode de culture employée, des conditions environnementales et de l'écologie d'une espèce donnée (Watson-Capps & Mann 2005 ; Ribeiro et al. 2007 ; Díaz López 2019). Cette interaction peut, à son tour, influencer l'écologie des cétacés (par exemple, leur abondance, utilisation de l'habitat, comportement alimentaire, et organisation sociale) (Watson-Capps & Mann 2005 ; Díaz López 2019). Par conséquent, étudier l'écologie et le comportement des cétacés vivant dans des zones fortement industrialisées, notamment pour l'aquaculture, est essentiel pour la conservation des cétacés et pour une gestion efficace de ces industries.

Plusieurs études suggèrent que l'échelle tridimensionnelle des fermes aquacoles réduit les zones côtières utilisées par les cétacés pour des activités biologiques et sociales potentiellement importantes. Plusieurs espèces de dauphins, à divers endroits dans le monde, semblent éviter les zones occupées par la conchyliculture, indiquant un impact potentiellement important de cette industrie sur les cétacés (par exemple, grands dauphins de l'océan Indien, *Tursiops aduncus*, en Australie : Watson-Capps & Mann 2005 ; dauphins obscurs, *Lagenorhynchus obscurus*, en Nouvelle-Zélande : Markovitz et al. 2004 ; Pearson 2009 ; Pearson et al. 2012 ; dauphins du Chili, *Cephalorhynchus eutropia*, au Chili : Ribeiro et al. 2007). Würsig & Gailey (2002) ont suggéré que cela pourrait être dû à la structure physique des fermes qui empêche les dauphins d'agréger leurs proies. De même, les marsouins communs (*Phocoena phocoena*) évitent les fermes piscicoles lors du nettoyage de cages (Haarr et al. 2009) et les orques (*Orcinus orca*) ont été déplacés de leur habitat en raison de l'utilisation de pinger (« acoustic harrassment devices ») autour des fermes à saumons (Morton & Symonds 2002).

À l'inverse, certaines espèces de cétacés peuvent être attirées par les fermes aquacoles marines en raison de la disponibilité accrue de nourriture dans ces zones (Díaz López 2019). Comme indiqué précédemment, l'accumulation d'éléments nutritifs autour des fermes marines peut conduire à une concentration de poissons sauvages, qui sont ensuite disponibles pour les dauphins (Díaz López 2006a). Une série d'études menées en Sardaigne (Italie) a révélé que les grands dauphins (*Tursiops truncatus*) sont attirés par les cages piscicoles en raison de la présence de poissons sauvages et d'élevage (Díaz López 2006a, 2009). En effet, la présence de grands dauphins a augmenté dans les zones côtières après la mise en place d'un élevage de

poissons (Díaz López et al. 2005) et à proximité immédiate des exploitations (Bonizzoni et al. 2014). Au contraire, la répartition spatiale et l'utilisation de l'habitat du dauphin du Chili n'étaient pas influencées par la présence de cages piscicoles (Ribeiro et al. 2007).

L'attrait pour les fermes aquacoles marines induit des changements de l'abondance, du comportement et de la socialité des cétacés. Une étude longitudinale a révélé une tendance à la hausse de la densité des grands dauphins en raison de la présence d'un élevage de poissons (Díaz López 2017, 2019). Dans plusieurs régions, la plupart du temps, les dauphins présents autour des fermes marines sont à la recherche de nourriture (Ribeiro et al. 2007 ; Díaz López 2012). Cependant, les zones d'aquaculture marine ne sont pas associées à d'autres activités importantes telles que la socialisation ou le repos (Ribeiro et al. 2007 ; Díaz López 2012). Des études menées sur les grands dauphins autour d'exploitations piscicoles ont montré que seuls certains dauphins présentent une grande fidélité pour les zones de pisciculture marine (Díaz López 2012 ; Díaz López et al. 2013). Ces grands dauphins développent des stratégies alimentaires spécialisées pour se nourrir de poissons sauvages présents autour des élevages de poissons et de poissons d'élevage (Díaz López 2006a, 2009). Par ailleurs, l'interaction sociale entre les individus est affectée par la présence de fermes aquacoles. Différentes études ont montré que les exploitations aquacoles affectent le niveau d'association entre les dauphins (Díaz López & Shirai 2008 ; Pace et al. 2011). Par conséquent, étudier le lien entre l'aquaculture marine et le comportement des cétacés peut fournir des données de base importantes, à partir desquelles des stratégies de gestion et de conservation efficaces peuvent être conçues.

Contexte de la thèse

La plupart de la littérature s'est concentrée sur les cétacés et la pisciculture (Díaz López et al. 2005 ; Díaz López 2006a, 2006b, 2009, 2012, 2017, 2019 ; Díaz López et Shirai 2007, 2008 ; Díaz López et al. 2008a ; Haarr et al. 2009 ; Pace et al. 2011 ; Bonizzoni et al. 2014) et il y a peu de données sur les cétacés et la conchyliculture (mais voir Markovitz et al. 2004 ; Watson-Capps & Mann 2005 ; Ribeiro et al. 2007 ; et Pearson et al. 2012). Cela est particulièrement vrai pour le grand dauphin et la conchyliculture, pour lesquels aucune étude spécifique n'a été réalisée.

Ayant une distribution côtière, les grands dauphins sont particulièrement susceptibles d'interagir avec les activités humaines (Würsig & Gailey 2002 ; Bearzi et al. 2009 ; Díaz López 2019). Les grands dauphins présentent une grande plasticité comportementale et écologique qui leur permet de tirer profit d'activités humaines telles que la pêche au filet maillant et au chalut, et l'aquaculture, pour bénéficier de la disponibilité de ressources alimentaires (Fertl & Leatherwood 1997 ; Chilvers & Corkeron 2001 ; Díaz López 2006b, 2012). Les grands dauphins de l'Atlantique sont répertoriés dans plusieurs accords et directives en matière de conservation (par exemple, la convention de Bonn, www.cms.int consulté le 15 Avril 2019 ; la convention de Berne, www.coe.int consulté le 15 Avril 2019 ; ASCOBANS, www.ascobans.org consulté le 15 Avril 2019 ; ACCOBAMS, www.accobams.org consulté le 15 Avril 2019 ; les annexes II et IV de la directive Habitats de l'Union européenne, directive 92/43/EEC du conseil, www.ec.europa.eu consulté le 15 Avril 2019). L'étude de l'écologie de ce grand prédateur marin est donc essentielle pour identifier les effets potentiels de pressions anthropiques et naturelles, afin de prendre des mesures de conservation et de gestion appropriées.

La conchyliculture est pratiquée dans les eaux galiciennes (Nord-Ouest de l'Espagne) depuis la fin des années 1940 (Miguez et al. 2009) et s'est développée au fil des années, faisant de cette région le leader européen de ce secteur (FAO 2014). La Ría d'Arousa (Galice, Espagne), étant l'une des zones les plus importantes du monde pour la conchyliculture et où les grands dauphins sont présents (López et al. 2004), offre des conditions adéquates pour étudier l'influence potentielle de la conchyliculture sur l'écologie du grand dauphin. Bien que les grands dauphins soient les cétacés côtiers les plus répandus dans les eaux côtières galiciennes (López et al. 2004), il existe un manque de connaissances sur l'écologie et le comportement des grands dauphins dans les eaux galiciennes et sur la surveillance comportementale et écologique rigoureuse de cette espèce. La plupart des études sur les grands dauphins dans les eaux galiciennes ont été réalisées à partir de données provenant d'individus échoués et de données d'observation provenant de plateformes terrestres ou opportunistes (bateaux de pêche) (López et al. 2002, 2004 ; Pierce et al. 2010 ; Fernández et al. 2011a, b, 2013 ; Spyrakos et al. 2011 ; Méndez-Fernández et al. 2012, 2013, 2014a, 2014b ; Louis et al. 2014 ; Nykänen et al. 2019). Pierce et al. (2010) ont par conséquent indiqué que des études spécifiques par bateau étaient nécessaires pour permettre l'identification de zones critiques d'habitat (telles que les aires

d'alimentation) des grands dauphins et que de futures études devraient être axées sur l'interaction des grands dauphins avec les activités humaines.

Objectifs de la thèse

L'objectif général de cette thèse est donc de combler une lacune de connaissances sur l'écologie et le comportement d'un grand prédateur marin, le grand dauphin, vivant sous la pression de l'industrie conchylicole. Cette thèse va permettre de fournir des informations de base sur l'abondance et le comportement des grands dauphins dans une zone soumise à une pression anthropique importante. En décrivant et en comprenant l'utilisation de l'habitat, le comportement et l'organisation sociale des grands dauphins en relation avec la conchyliculture, ce travail vise à étudier l'influence potentielle de cette industrie sur ce prédateur marin. Le résultat proposé de ce travail est triple : (i) fournir des données de base, qui pourront être utilisées pour informer les agences de gestion sur l'état de conservation des grands dauphins dans une zone fortement anthropisée, (ii) étudier l'influence potentielle de la conchyliculture sur l'écologie et le comportement des grands dauphins, et (iii) suggérer des mesures de gestion et de conservation appropriées pour les grands dauphins, ainsi que des réglementations pour le secteur de la conchyliculture.

Méthodes

L'étude a été réalisée le long de la côte Nord-Ouest de la péninsule ibérique (Galice, Espagne), en particulier dans la plus grande des rías (anciennes vallées tectoniques envahies par la mer) galiciennes, la Ría d'Arousa (240 km²) (Prego et al. 1999 ; Evans & Prego 2003) (**Figure ii**). Dans cette région, les vents favorables au phénomène d'upwelling prédominent d'avril à octobre (Álvarez et al. 2011). Au cours des épisodes d'upwelling, des eaux froides et riches en éléments nutritifs (Eastern North Atlantic Central Waters, ENACW) se déplacent vers la côte et les eaux de surface se déplacent vers le large (Fraga 1981 ; Alvarez et al. 2005). Les épisodes d'upwelling entraînent un enrichissement en éléments nutritifs des eaux côtières, permettant ainsi une productivité primaire élevée et faisant de cette zone l'une des régions océaniques les plus productives du monde (Figueiras et al. 2002). En raison de cette productivité primaire élevée le long de cette côte, la Galice est une zone importante pour la pêche et la conchyliculture, et plus particulièrement pour la production de moules et d'huîtres (Prego et al. 1999). En Galice,

les coquillages sont élevés sur des plates-formes flottantes rectangulaires (appelées « batea »), contrairement à d'autres systèmes de production (par exemple, tables d'élevages, filières, bouchots) (Perez Camacho et al. 1991). Les radeaux se maintiennent à flot grâce à un système de dispositifs flottants et restent en place au moyen de chaînes liées à un bloc de béton posé au fond de la mer. Les radeaux sont configurés en forme de rectangle, généralement en bois, et les bivalves sont cultivés sur des cordes attachées aux platesformes. Dans la Ría d'Arousa, il y a environ 2300 radeaux (environ 2100 pour la production de moules et 200 pour la production d'huîtres) couvrant environ 17 % (41 km²) de la surface totale de la ría (Figueiras et al. 2002) (**Figure ii**). Le grand dauphin est l'espèce de cétacé la plus fréquemment observée dans les eaux côtières galiciennes, en particulier dans les rías galiciennes (Fernández-Cordeiro et al. 1997 ; López et al. 2004 ; Pierce et al. 2010).

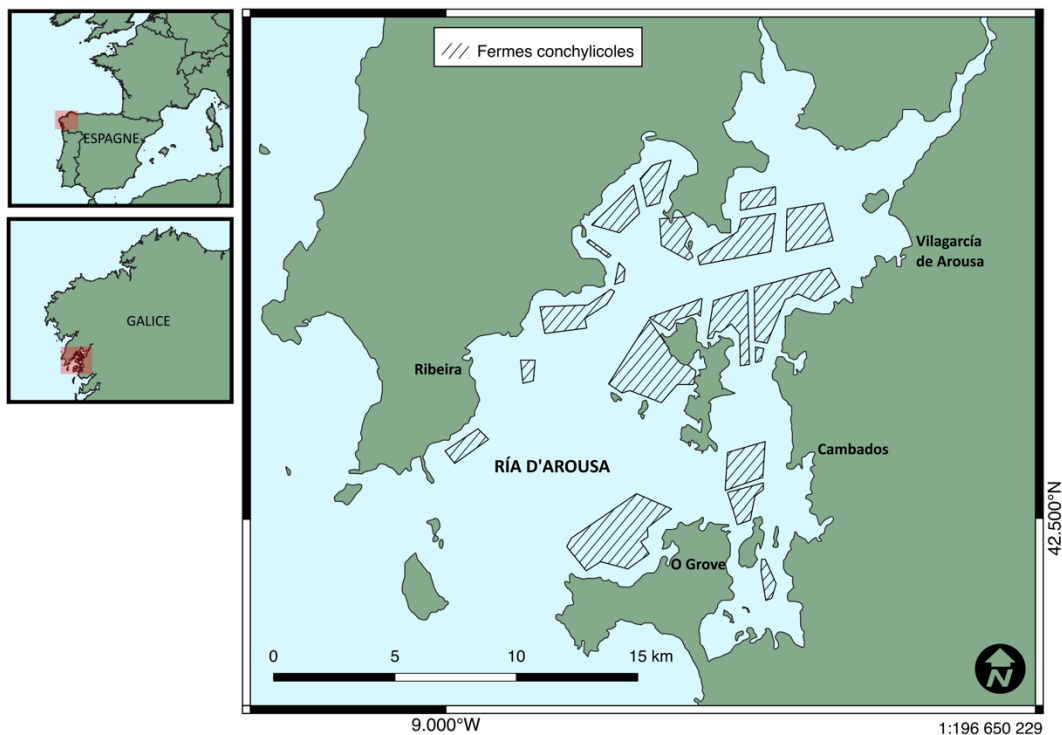


Figure ii. La Ría d'Arousa (Nord-Ouest de l'Espagne). Les polygones rayés représentent les zones conchylicoles.

Les travaux de cette thèse sont principalement basés sur des données collectées de 2014 à 2018 par le Bottlenose Dolphin Research Institute (ci-après BDRI). Afin de répondre aux objectifs, des relevés systématiques par bateau ont été menés mensuellement avec le bateau de recherche du BDRI, de mars 2014 à novembre 2018 dans la Ría d'Arousa. Lors de chaque

sortie, des données environnementales (position GPS, température de surface de la mer, salinité de surface de la mer, vitesse et direction du vent, profondeur), des données de présence/absence de grands dauphins, des données individuelles et comportementales (nombre d'individus, sexe et âge des individus, comportement), et des données photographiques ont été collectées. Des données supplémentaires ont été obtenues à partir d'analyses de photo-identification, de bases de données externes (fluorescence, oxygène dissous, niveau de marée), et d'analyse SIG (distance à la côte, pente), puis ont été associées aux données recueillies à bord. Les données ont ensuite été analysées à l'aide de méthodes et de logiciels différents, en fonction de l'objectif de chaque étude présentée dans cette thèse.

Résultats

Estimation de l'abondance des grands dauphins dans la Ría d'Arousa

La première étude de cette thèse présente les premières estimations robustes de l'abondance et des paramètres démographiques du grand dauphin dans la Ría d'Arousa. L'objectif de cette étude était d'estimer l'abondance, la survie apparente et les taux d'émigration temporaire des grands dauphins dans la zone conchylicole la plus importante d'Europe en utilisant un plan d'échantillonnage systématique par photo-identification et des modèles de marquage-recapture. L'abondance saisonnière, la survie apparente et les taux d'émigration temporaire des grands dauphins ont été estimés à l'aide du modèle robuste de Pollock (Pollock 1982). Des données d'identification photographique ont été collectées de 2014 à 2016 dans la Ría d'Arousa. Les grands dauphins étaient présents toute l'année et présentaient un degré élevé d'occurrence dans la zone d'étude. L'abondance locale des grands dauphins variait de 56 à 144 individus (**Table i**). Le taux de survie apparent était élevé et constant, indiquant une absence de mortalité et pas d'émigration permanente pendant la période d'étude. Les taux d'émigration temporaire variaient selon les saisons et étaient plus bas de l'automne à l'hiver, ce qui suggère que les grands dauphins avaient une forte probabilité de revenir pendant la période hivernale. Les changements d'abondance et les taux d'émigration observés reflètent probablement les fluctuations saisonnières de l'abondance des proies des grands dauphins dans cette zone. Ces résultats fournissent des informations de base importantes dans une zone soumise à une pression anthropique importante et pour de futures comparaisons avec d'autres populations de grands dauphins sous la pression d'activités humaines, telles que la pêche et l'aquaculture.

Table i. Estimation de l'abondance saisonnière des grands dauphins dans la Ría d'Arousa. \hat{N} , estimation de la population marquée ; $\hat{\theta}$, proportion d'individu adulte marqué ; \hat{N}_t , taille totale de la population ; s.e., erreur type ; IC, intervalle de confiance.

<i>Année</i>	<i>Saison</i>	Nombre de dauphins identifiés	\hat{N}	s.e.	$\hat{\theta}$	\hat{N}_t	95 % IC
2014	Printemps	73	76	2.8	0.68	111	107–125
	Été	100	85	3.0	0.69	123	118–138
	Automne	37	50	1.8	0.89	56	55–66
2015	Hiver	115	122	6.7	0.85	144	133–166
	Printemps	46	46	1.8	0.81	57	56–67
	Été	82	68	1.2	0.88	77	76–84
2016	Automne	40	61	3.5	0.92	66	62–78
	Hiver	84	87	3.3	0.75	116	110–130
	Printemps	114	110	4.0	0.79	139	133–153

Influence de paramètres environnementaux sur la taille du groupe de grands dauphins

La deuxième étude présentée dans cette thèse avait pour objectif principal d'étudier l'influence de multiples facteurs environnementaux (température de l'eau, salinité de l'eau, concentration en chlorophylle-a et oxygène dissous) sur la taille du groupe de grands dauphins. Les prédateurs marins étant souvent de grande taille et ayant une longue espérance de vie, les caractéristiques de leurs populations peuvent potentiellement servir à comprendre les effets de changement environnementaux sur une gamme d'échelles spatiales et temporelles. Les cétacés forment souvent des groupes pour accroître l'accès aux ressources alimentaires. L'abondance et la répartition de leurs proies étant influencées par les conditions environnementales, la variation environnementale pourrait être une cause de la variation intra-spécifique de la taille de groupe. L'hypothèse selon laquelle les conditions environnementales influencent la taille de groupe des grands dauphins a été testée. En utilisant des données collectées à long terme (cinq ans) et tout au long de l'année, les résultats ont indiqué que les conditions environnementales (la concentration en chlorophylle-a et oxygène dissous) influencent la taille de groupe des grands dauphins (**Figure iii**). Le lien observé entre ces variables environnementales et la taille du

groupe des dauphins peut être associé à des changements en disponibilité des ressources alimentaires pour les dauphins. Cette étude fournit des informations importantes sur l'influence des changements environnementaux à petite échelle dans les écosystèmes côtiers sur la dynamique des groupes de dauphins. Cette étude suggère également que la dynamique d'un groupe de dauphins pourrait constituer un indicateur utile des changements environnementaux dans les écosystèmes côtiers. Les résultats soulignent l'importance de considérer l'interaction de multiples variables environnementales à de petites échelles temporelles et spatiales dans les études écologiques. Ces résultats fournissent des informations importantes sur la vulnérabilité potentielle de cette espèce face aux changements environnementaux dans un écosystème côtier. Des études complémentaires, menées à différentes échelles spatiales et temporelles, permettraient de comprendre l'influence de conditions environnementales sur les paramètres démographiques des populations de dauphins à une plus grande échelle.

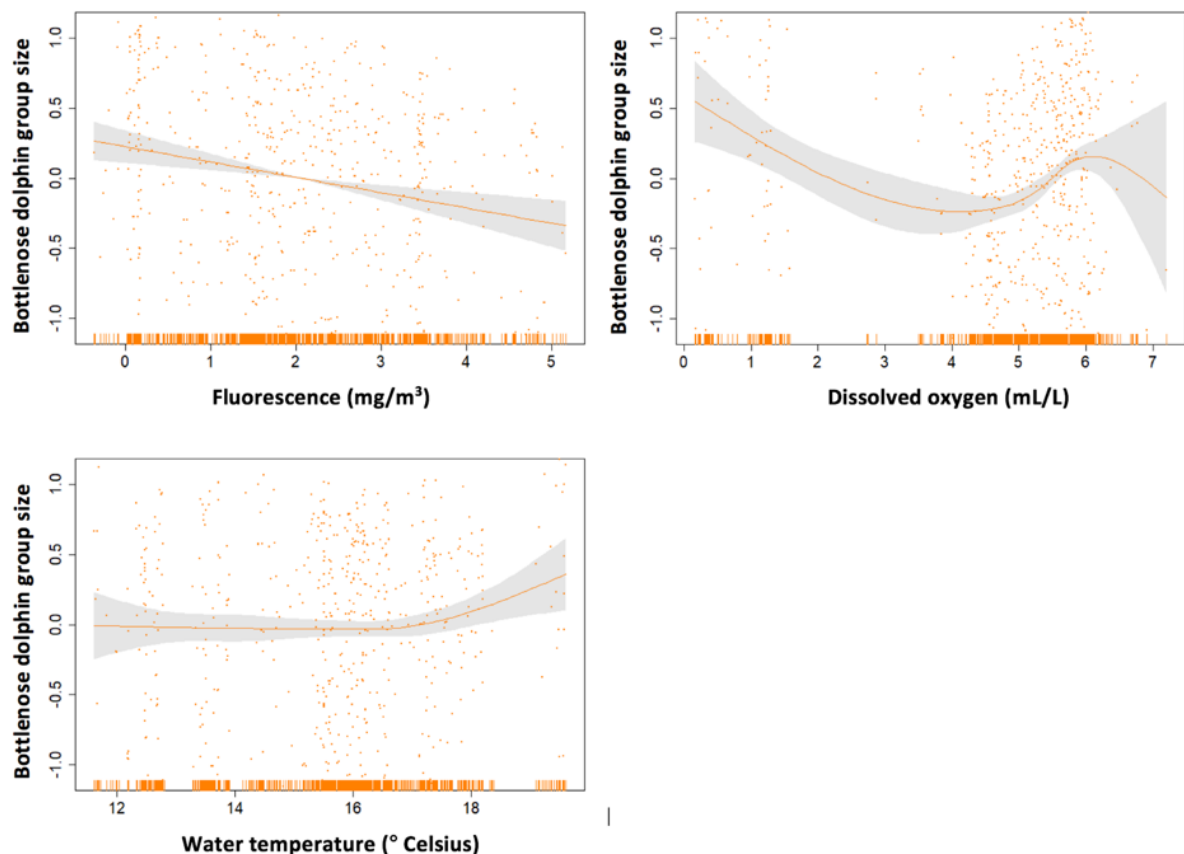


Figure iii. Prévisions moyennes du nombre de grands dauphins dans chaque groupe pour chaque covariable significative dans le modèle final. Les limites de confiance à 95 % sont représentées lorsque toutes les autres variables sont fixées sur leur valeur moyenne.

Influence de la conchyliculture sur l'utilisation de l'habitat par les grands dauphins

L'objectif de la troisième étude de cette thèse était d'étudier la distribution spatio-temporelle des grands dauphins dans la Ría d'Arousa et d'identifier les facteurs environnementaux et anthropiques à l'origine de l'utilisation de l'habitat par les grands dauphins. L'hypothèse selon laquelle la conchyliculture, qui induit une fragmentation de l'habitat dans l'écosystème, pourrait attirer les grands dauphins et, ainsi, influencer leur utilisation de l'habitat, a été testée. Au cours d'une période de 22 mois, 154 sorties en bateau ont été effectuées et 353 groupes de grands dauphins ont été observés (**Figure iv**). Les résultats de cette étude démontrent que les zones conchylicoles sont fréquemment utilisées par les grands dauphins. Parmi les facteurs étudiés, les fermes conchylicoles semblaient avoir un effet évident, avec une augmentation du nombre d'observation de grands dauphins entre les fermes et dans les eaux proches des zones d'aquaculture. Ces observations contrastent avec des études précédentes où la présence et la répartition d'espèces de cétacés diminuaient en association avec la présence de fermes conchylicoles, source de perte d'habitat. Ces différences suggèrent que les interactions entre les fermes conchylicoles et les cétacés dépendent de la méthode de culture et de l'espèce de cétacé impliquée. La relation entre la présence de dauphins et les zones conchylicoles est vraisemblablement le résultat de vastes concentrations de poissons autour des fermes, qui fournissent une grande densité de proies de haute qualité pour les dauphins. Cette étude fournit de nouvelles informations sur la compréhension de l'influence de la conchyliculture sur les dauphins côtiers et soutient ainsi la conception de politiques visant à mettre en œuvre des principes de gestion des écosystèmes.

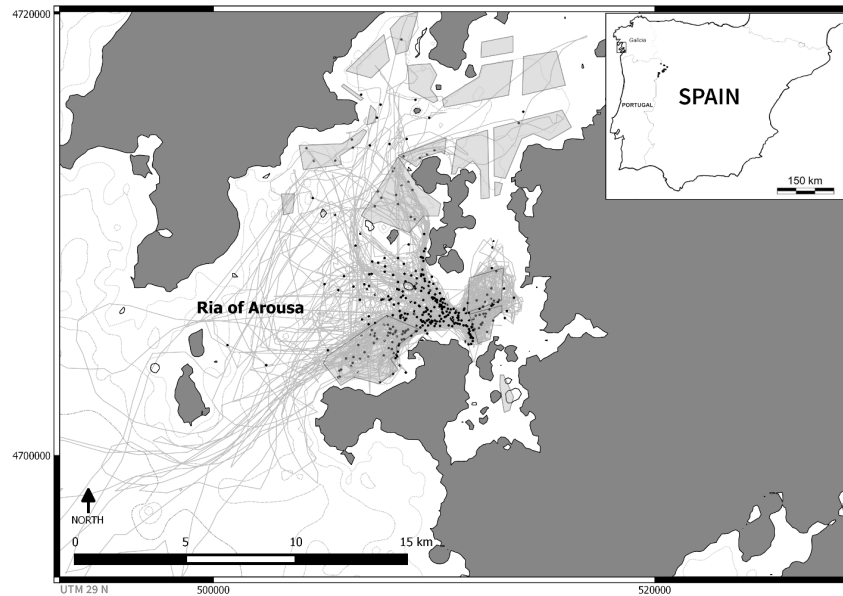


Figure iv. Situation géographique de la Ría d’Arousa. L’effort de recherche est indiqué par des lignes grises. Les rencontres avec les dauphins sont indiquées par de petits cercles. Les polygones pleins indiquent l’emplacement des zones de conchyliculture.

Comportement alimentaire des grands dauphins : influence de la conchyliculture

La quatrième étude de cette thèse avait pour objectif principal de déterminer si la conchyliculture influence le comportement du grand dauphin. L’identification d’habitats clés, tels que les aires d’alimentation dans les zones industrialisées, est essentielle à la conservation des espèces. Par conséquent, la compréhension des variables qui influencent le comportement d’alimentation d’une espèce est importante pour sa conservation, en particulier pour les mammifères à longue espérance de vie tels que les cétacés. Les objectifs de cette étude étaient (a) d’identifier et de quantifier les facteurs environnementaux et anthropiques qui influencent le comportement alimentaire du grand dauphin, et (b) d’étudier si la présence de fermes conchyliques influence le comportement de cette espèce. L’hypothèse selon laquelle les fermes conchyliques, augmentant l’abondance de poissons par rapport aux zones adjacentes, pourraient constituer un important lieu d’alimentation pour les grands dauphins a été testée. Pour ce faire, des observations comportementales ont été menées dans la Ría d’Arousa. Une approche de modélisation multiple a mis en évidence l’importance des zones conchyliques en tant que lieu d’alimentation pour les grands dauphins. Les dauphins étaient plus susceptibles de se nourrir entre les fermes conchyliques qu’à l’extérieur (57 % contre 43 %) (**Figure v**). La variabilité du comportement des grands dauphins est probablement due aux interactions de

facteurs environnementaux et anthropiques avec la disponibilité de proies et les besoins physiologiques des dauphins. Cependant, bien que les zones conchylicoles fournissent une grande densité de proies aux dauphins, elles pourraient également constituer une menace (collisions avec des navires, enchevêtrement avec des cordes, perte d'habitat, bruit et pollution de l'eau). Du point de vue de la conservation, l'industrie conchylicole devrait prendre en compte la présence de dauphins qui s'alimentent autour des fermes et minimiser les risques que cette industrie pourrait présenter pour ces cétacés côtiers.

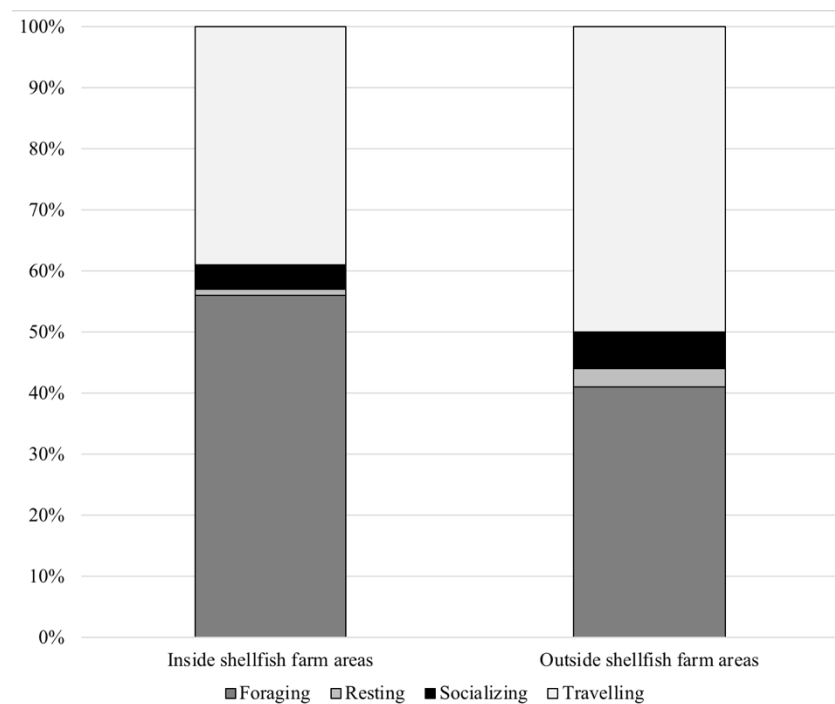


Figure v. Budget comportemental du grand dauphin à l'intérieur et à l'extérieur des zones conchylicoles.

Influence de la conchyliculture sur l'organisation sociale des grands dauphins

Dans la dernière étude de cette thèse, la variation inter-individuelle du comportement alimentaire chez le grand dauphin et l'influence potentielle de cette variation comportementale sur leur organisation sociale ont été étudiées. Identifier des variations comportementales au sein d'une population et évaluer leur relation avec la structure sociale est essentiel pour accroître les connaissances sur l'évolution des systèmes sociaux. Cette étude avait pour objectif de déterminer si la fréquence à laquelle les grands dauphins s'alimentent autour des fermes conchylicoles variait entre individus et de déterminer si cette variation était liée à leur organisation sociale. L'hypothèse selon laquelle la concentration des ressources

alimentaires associée à la conchyliculture pourrait induire des variations comportementales, avec certains individus s'alimentant plus régulièrement dans les fermes conchylicoles que d'autres, a été testée. Par la suite, une autre hypothèse affirmant que cette variation comportementale pourrait influencer sur l'organisation sociale des grands dauphins, avec des associations plus faibles entre les individus montrant des préférences pour s'alimenter dans autour des fermes conchylicoles, a également été testée. À travers ce cadre, l'objectif était de comprendre si les variations comportementales entre individus influencent l'organisation sociale chez un grand prédateur marin. Nous avons utilisé des indices d'affiliation généralisés et une analyse de réseau social appliquée aux données collectées au cours de quatre années de recherche consécutives dans une zone côtière soumise à une pression anthropique importante. Les résultats ont révélé des variations inter-individuelles dans le comportement alimentaire chez les grands dauphins, qui à leur tour, conditionnent leur organisation sociale (**Figure vi**). Les résultats ont indiqué que les individus qui s'alimentent fréquemment entre les fermes conchylicoles ont des associations plus faibles que les autres. Ces grands dauphins bénéficient d'une source de nourriture fiable et facile à localiser, ce qui peut augmenter leur apport énergétique et favoriser une compétition inter-individuelle. En revanche, les individus qui s'alimentent moins souvent autour des fermes conchylicoles occupaient une position centrale dans le réseau social et manifestaient de fortes associations. Ces dauphins peuvent tirer parti d'une coopération accrue et d'une réduction de la compétition intragroupe, renforçant ainsi l'apprentissage et le partage d'informations, étant donné que ces individus peuvent être confrontés à une distribution inégale et irrégulière de leurs proies. Les résultats dénotent également que les grands dauphins préféraient s'affilier à des individus ayant des stratégies alimentaires similaires (homophilie), ce qui pourrait, avec le temps, favoriser la ségrégation de la population en groupes distincts sur le plan comportemental. Ces résultats fournissent des informations importantes sur l'évolution des systèmes sociaux des grands dauphins.

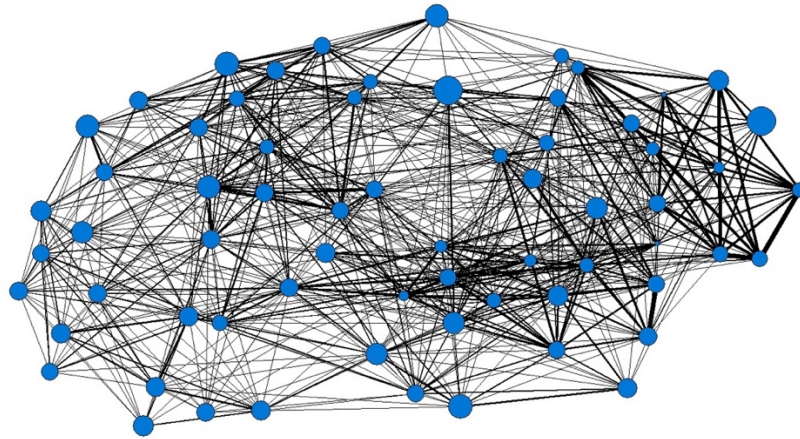


Figure vi. Réseau social des grands dauphins de la Ría d'Arousa. Chaque individu est représenté par un nœud. La taille des nœuds représente le nombre de fois qu'un individu a été observé s'alimentant autour des fermes conchylicoles par rapport au nombre total de fois que cet individu a été observé s'alimentant. La largeur des liens est proportionnelle à la force des affiliations.

Discussion

Implications pour la conservation du grand dauphin

Les résultats de cette thèse démontrent que les grands dauphins présentent un degré élevé de résidence dans la Ría d'Arousa, utilisent cette zone toute l'année, utilisent la zone avec leurs petits et, utilisent la zone comme aire d'alimentation. Les grands dauphins et leur habitat devraient donc être protégés, comme l'exige la directive Habitat de l'Union européenne.

Il existe actuellement une zone spéciale de conservation (ZSC) couvrant environ 11,5 % (28 km² sur 240 km²) de la Ría d'Arousa et le grand dauphin est inclus en tant que caractéristique (<http://natura2000.eea.europa.eu>, consulté le 10 août 2019) (**Figure vii**). Le site a été proposé comme site d'intérêt communautaire (SIC) en 1997, confirmé en tant que SIC en 2003 et désigné ZSC en 2014 (www.xunta.gal, consulté le 10 août 2019). Par conséquent, une évaluation périodique de la population aurait dû être effectuée tous les 6 ans. Pourtant, aucune estimation de l'abondance n'a encore été donnée pour le grand dauphin dans la région. Les résultats présentés dans cette thèse fournissent donc la première estimation robuste de l'abondance des grands dauphins dans la région. Les autorités de gestion devraient maintenant utiliser ces informations pour mettre à jour leur programme de surveillance.

Comme le soulignent les résultats de cette thèse, les grands dauphins s'alimentent dans différentes parties de la Ría d'Arousa. En protégeant une population spécifique, l'aire protégée optimale couvrirait la zone utilisée annuellement par cette population (Whitehead et al. 2000). La ZSC actuelle présente dans certaines parties de la Ría d'Arousa devrait donc être étendue (**Figure vii**) et devrait être spécifiquement désignée pour la conservation des grands dauphins. Une première expansion de la ZSC pourrait concerner les zones où le budget d'alimentation des grands dauphins est supérieur à 80% (**Figure vii a, b**). Une deuxième expansion pourrait concerner les zones où le budget d'alimentation des grands dauphins est supérieur à 40% (**Figure vii a, c**). Idéalement, le ZSC devrait être étendu à toute la Ría de Arousa (**Figure vii d**). Un plan de gestion et de surveillance à long terme, contribuant à l'état de conservation des grands dauphins et de leur habitat, devrait également être mis en place. Les dispositions destinées à protéger les grands dauphins pourraient aider d'autres cétacés dans cette zone, y compris le marsouin commun (Díaz López & Methion 2018a : annexe 5), qui figure également dans la directive Habitat de l'Union Européenne.

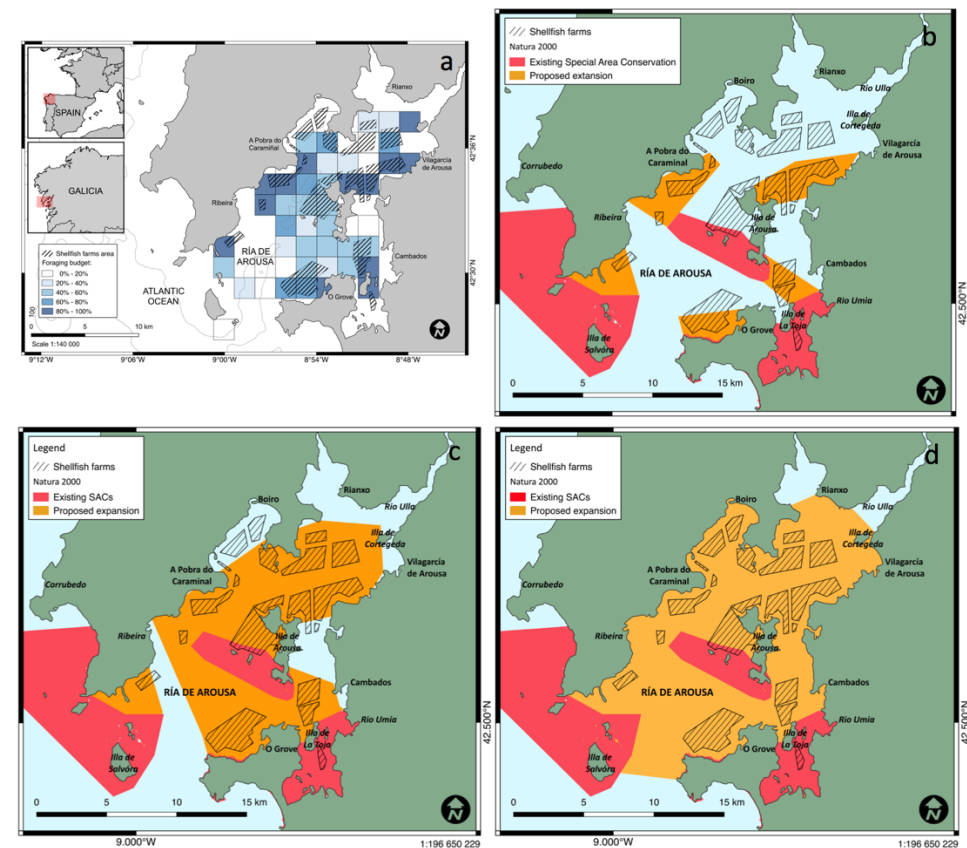


Figure vii. ZSCs existantes (rouge) et extension proposée (orange), en plusieurs étapes, dans la Ría d'Arousa.

Recommandations pour l'industrie conchylicole

Cette étude fournit de nouvelles informations sur l'influence de la conchyliculture sur les cétacés et soutient donc la conception de politiques visant à appliquer les principes de gestion des écosystèmes.

Les résultats de cette étude montrent que les grands dauphins s'alimentent régulièrement autour des fermes conchylicoles. Des études antérieures ont montré que les interactions entre les dauphins et l'aquaculture marine peuvent causer des dommages à la fois au secteur de l'aquaculture (endommagement de l'équipement, déprédation du poisson d'élevage) et aux dauphins (enchevêtrement fatal, perte et dégradation de l'habitat, introduction de maladies) (Würsig & Gailey 2002 ; Díaz López 2012). Alors que les dauphins autour des fermes piscicoles peuvent se nourrir de poissons sauvages et d'élevage, causant souvent des dommages à l'équipement et aux poissons d'élevage (Díaz López 2006a), les dauphins autour des fermes conchylicoles ne se nourrissent que de proies sauvages, n'affectant donc pas le produit aquacole, ni l'équipement (producteur local de moules dans la Ría d'Arousa, communication personnelle). En outre, la présence de grands dauphins autour des fermes conchylicoles pourrait éloigner des espèces de poissons (par exemple, les dorades) qui pourraient potentiellement endommager le produit aquacole (Díaz López & Methion 2018b). Par conséquent, les tentatives visant à dissuader les grands dauphins, au moyen de filets anti-prédateurs ou de pingons (« acoustic harrassment devices »), ne sont pas nécessaires pour la conchyliculture.

En revanche, la conchyliculture peut constituer une menace directe pour les cétacés côtiers de plusieurs manières : (a) une mortalité accrue à la suite de collisions fatales avec des bateaux travaillant dans la zone (Ribeiro et al. 2007) ou d'enchevêtrement avec des cordes ; (b) une perte d'habitat (Watson-Capps & Mann 2005) ; c) une augmentation de la pollution sonore due au nombre élevé de bateaux dans la zone ; et d) une pollution de l'eau due à l'utilisation de peintures antifouling contenant des biocides (composés toxiques : plomb, arsenic, mercure, cuivre, oxyde cuivreux, composés organostanniques tels que les tributylétains) sur les radeaux flottants et les bateaux (Terlizzi et al. 2001). Certains auteurs ont affirmé que l'accumulation de biocides pouvait entraîner la mortalité des cétacés en supprimant leur système immunitaire (Kannan et al. 1996). L'industrie conchylicole devrait donc prendre en compte la présence de

cétacés s'alimentant dans les zones conchylicoles et minimiser les risques que cette industrie pourrait présenter pour ces cétacés côtiers. Les mesures de gestion relatives aux menaces du secteur conchylicole énumérées dans la présente étude devraient être mises en œuvre conformément aux obligations légales de l'Union européenne en vertu de la directive Habitats visant à protéger les grands dauphins. Nous proposons ici une liste de recommandations de gestion visant à réduire les risques associés à la conchyliculture pour les cétacés :

- Établir une limite de vitesse pour les bateaux opérant dans les zones de conchyliculture.

Une vitesse < 10 nœuds est suggérée pour réduire le risque de décès et de blessures graves des cétacés résultant de collisions avec des bateaux (conformément à la loi sur la protection des mammifères marins, www.fws.gov, consultée le 10 août 2019). Cette mesure laisserait plus de temps aux cétacés pour prendre des mesures d'évitement et pourrait également réduire le bruit sous-marin.

- Contrôler l'utilisation de peintures antifouling contenant des biocides utilisés pour les radeaux flottants et les bateaux de travail.

Cette mesure pourrait minimiser les impacts potentiels de cette industrie sur la santé et, à terme, la survie des cétacés.

- Réaliser des études d'impact environnemental.

La mise en place de fermes conchylicoles dans des zones d'importance écologique particulière pour toutes espèces de cétacés devrait être réglementée. Avant de mettre en place des exploitations conchylicoles, cette industrie devrait évaluer la présence potentielle de cétacés, collecter des données de base sur leur écologie, étudier les impacts potentiels sur les cétacés et prendre en considération les résultats de cette thèse afin de mettre en œuvre un plan de gestion. Après la mise en place de fermes conchylicoles, un plan de surveillance permanent, axé sur la conservation des espèces de cétacés locales, devrait être mis en place pour évaluer l'efficacité du plan de gestion en déterminant si les objectifs de conservation sont atteints à long terme.

Conclusions

Les résultats de cette thèse fournissent des informations de base importantes sur l'écologie et le comportement d'un grand prédateur marin vivant dans une zone côtière sous la pression de l'industrie conchylicole. Plus précisément, cette thèse fournit des informations précieuses sur l'abondance, les paramètres démographiques, la répartition, l'utilisation de l'habitat, le comportement alimentaire et l'organisation sociale des grands dauphins en Galice. De plus, les résultats permettent de mieux comprendre l'influence des changements induits par la conchyliculture dans le milieu marin sur l'utilisation de l'habitat du grand dauphin, sur son comportement alimentaire et sur son système social. Globalement, cette étude améliore les connaissances disponibles sur la variation comportementale constatée parmi les populations de grand dauphin et constitue un modèle pour de futures études. Cette thèse contribue également à la littérature traitant des conséquences environnementales de la conchyliculture, en particulier des effets sur les cétacés côtiers, qui ont rarement été évalués. Dans l'ensemble, les résultats de cette thèse améliorent la base scientifique pour la prise de décision sur la conservation et la gestion des grands dauphins vivant sous la pression de la conchyliculture dans les eaux côtières.

Chapter 1. General introduction

This first chapter introduces the themes for the main data chapters. First, the literature on the impact of human activities on marine coastal ecosystems is examined, with particular emphasis on the influence of anthropogenic activities on cetaceans. In the second part of this chapter, the methods commonly used for studying coastal cetacean ecology are reviewed. In the third part, the importance of the marine aquaculture industry, and the impacts of this industry on marine ecosystems are reviewed, with particular emphasis on the interaction between marine aquaculture and cetaceans. Lastly, the rationale, objectives, and structure of the thesis are presented.

1.1 Anthropogenic activities and marine top predators

1.1.1 Anthropogenic activities in marine coastal ecosystems

Marine coastal environments encompass a broad range of habitat types and are one of the most productive ecosystems in the world sustaining a large variety of marine species (Costanza et al. 1995; Crain 2009). In these environments, land runoff and seasonal coastal upwelling can lead to high concentration of nutrients, particularly nitrogen and phosphorus, giving rise to a high concentration of phytoplankton (Nixon et al. 1986; Cloern & Jassby 2008). This high primary production sustains a broad variety of consumers from higher trophic levels (Ray 1988). Yet, anthropogenic activities are responsible for significant modifications at an unprecedented rate and scale over the last few decades, leading to marine coastal environments becoming some of the most vulnerable and severely degraded ecosystems (Crain et al. 2008; Halpern et al. 2008a) (**Figure 1.1**).

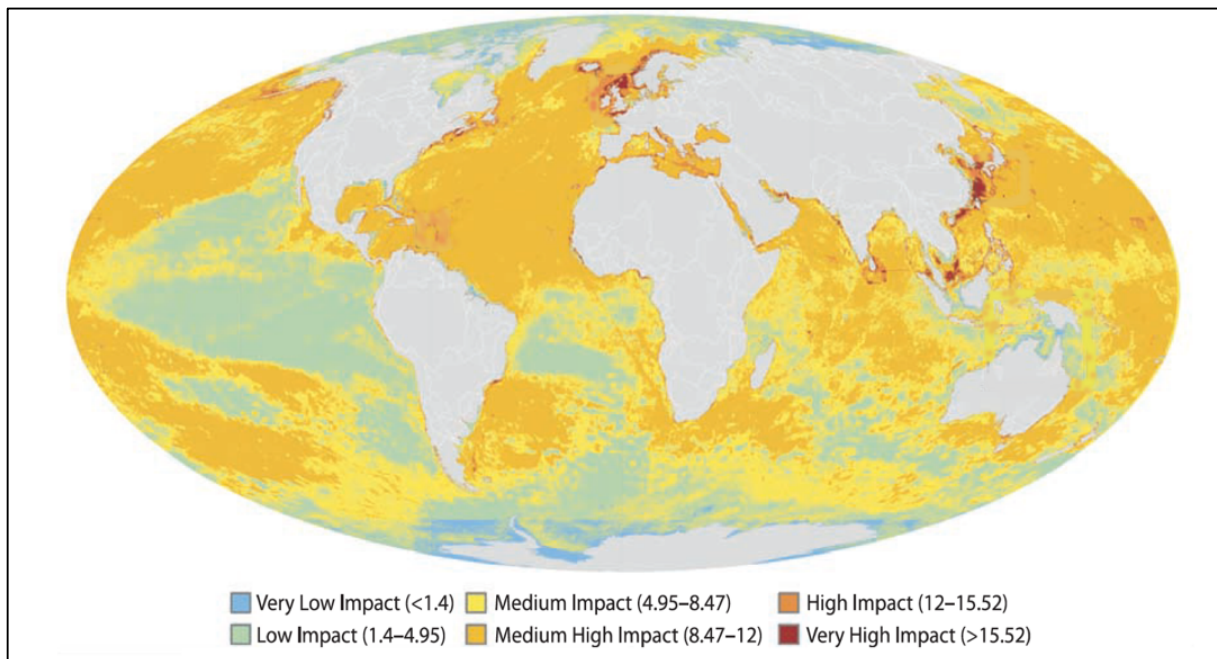


Figure 1.1. Global map of cumulative impacts of human activities on marine ecosystems (source: Halpern et al. 2008b).

Marine coastal ecosystems provide humans with valuable social, economic, and biological services (e.g. food resources, transportation, tourism) (Granek et al. 2010) (Figure 1.2). With more than one third of the human population living within 100 km from the coastline and continuing to grow and to migrate to the coasts, demand for ocean space and resources is expanding, increasing pressures from a wide range of anthropogenic activities (Food and Agriculture Organization, FAO 2018). These ecosystems are threatened by multiple anthropogenic activities from both land and sea such as agriculture, aquaculture, fisheries, tourism, shipping, transport, and urbanisation (Crain et al. 2008, 2009; Halpern et al. 2008a). These human activities lead to drastic changes in the ecosystems such as overexploitation, habitat and biodiversity loss, introduction of exotic species, environmental degradation, and global warming (Halpern et al. 2008a). Human stressors threaten the sustainability and existence of marine biodiversity and the suite of benefits these ecosystems provide (Myers & Worm 2003; Worm et al. 2006). The magnitude and impact of each stressor in coastal zones and communities differ, depending on the type and characteristic of each stressor and local environmental conditions (Halpern et al. 2008b). Therefore, to holistically understand ecosystem responses to anthropogenic threats, it is necessary to know how threats affect different components within ecosystems (Maxwell et al. 2013).

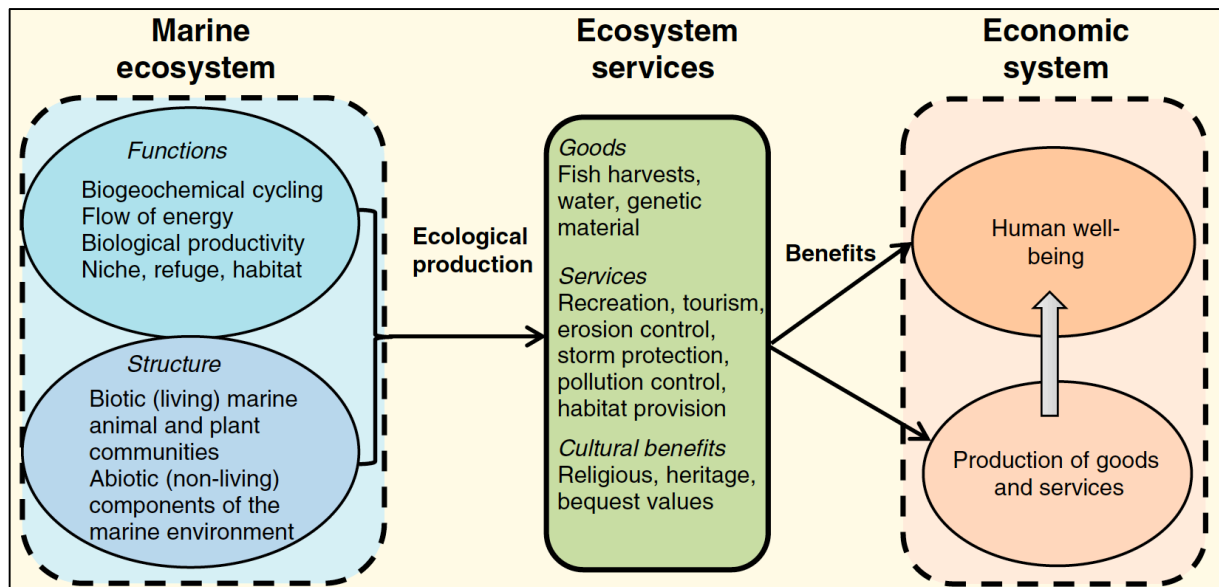


Figure 1.2. The structure and functioning of marine ecosystems lead to the ecological production of ecosystem services (source: Barbier 2017).

When populations are under the pressure of human activities, they can react in different ways: moving towards another place (migration), adapt to the novel environment (phenotypically or genetically), or become extinct (if a species is not able to move, or to adapt, either phenotypically or genetically) (Sih et al. 2011). As species within an ecosystem interact together, anthropogenic disturbances lead to changes in the structure and function of ecosystems (Elmqvist et al. 2003). Response of species to anthropogenic threats depends on a species ecology and on the level of anthropogenic impact (Isaac et al. 2004). From an evolutionary point of view, species with r-selected life histories (short time until sexual maturity, short gestation, many offspring, and short parental care) have more potential for adaptation compared to species with K-selected life histories (long period until sexual maturity, long gestation, few offspring, and long parental care) (e.g. Chiu & Kuo 2012; Legder et al. 2013). Given their lower potential to adapt, K-selected species, such as marine top predators, cannot respond as quickly to changes occurring in their environment and are therefore vulnerable to human activities.

1.1.2 Top predators in marine coastal ecosystems

Top predators (e.g. cetaceans, pinnipeds, seabirds, and some large predatory fish), also named 'upper-trophic-level predators' or 'apex predators', are a principal component of marine coastal ecosystems (Boyd & Murray 2001). Top predators play a key role in maintaining a functioning ecosystem, balancing marine food-webs through top-down influences on ecosystem structure (Bowen 1997; Croll et al. 1998; Cox et al. 2002; Myers et al. 2007; Heithaus et al. 2008; Kiszka et al. 2015) (**Figure 1.3**). They are supported by the productivity of primary and secondary consumers, thus integrating a range of processes across the lower levels of the trophic food web (Katona & Whitehead 1988; Frederiksen et al. 2006; Díaz López et al. 2008a). They also play an important role in shaping the behaviour and life history traits of prey species (Bond et al. 2019) and competitors, in nutrient storage and recycling, and in modifying benthic habitats (Katona & Whitehead 1988). Apart from their ecological importance, a number of marine top predators are also of high economic importance, some of them providing commercial and/or cultural value (e.g. Beaumont et al. 2008; Mustika et al. 2012). Marine top predators provide resilience and health to marine coastal ecosystems, and are a key element of spatial and ecosystem-based management (Maxwell et al. 2013). Because top predators are

often large and long-lived, characteristics of their populations can potentially serve to integrate the cumulative effects of ecosystem change over a range of spatial and temporal scales (Iverson et al. 2006). As such, they can serve as indicators of ecosystem health (Bowen et al. 2006). Therefore, protecting the environment marine top predators live in can indirectly protect other species within the ecosystem (Hooker & Gerber 2004).

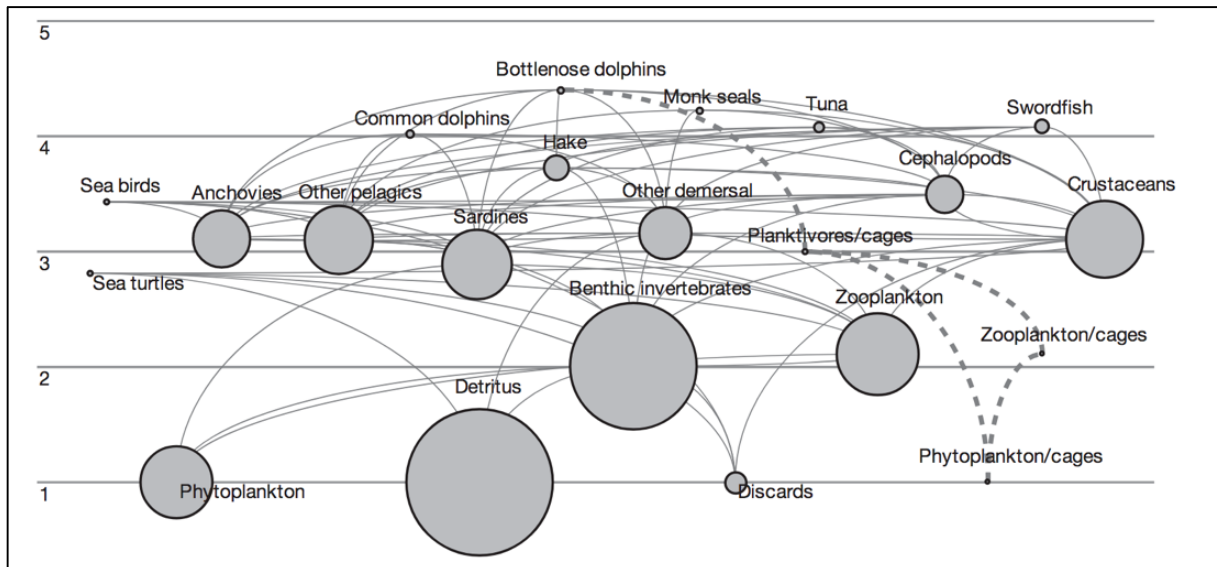


Figure 1.3. Flow diagram expressing trophic flows and levels in the Ionian Sea (source: Pirrodi et al. 2011).

Marine top predators are exposed to multiple anthropogenic stressors such as direct catches, habitat loss, global warming, and marine traffic (Maxwell et al. 2013) (**Figure 1.4**). As a result, human activities, through direct physiological and indirect ecological pathways, are causing shifts in the distribution, abundance, and behaviour of marine top predators, and are increasing the likelihood of local extinction (Walther et al. 2002; Ward & Myers 2005; Butchart et al. 2010; Hoffmann et al. 2010). Changes in marine top predators' abundance and distribution can result in alterations in ecosystems function and structure through trophic cascades, which in turn, affect other species and habitats, and ecosystem processes (Norse & Crowder 2005; Casini et al. 2009; Estes et al. 2011). Such changes can also enhance human impacts such as increasing an ecosystem's susceptibility to invasive species or biodiversity loss (Chapin et al. 2000).

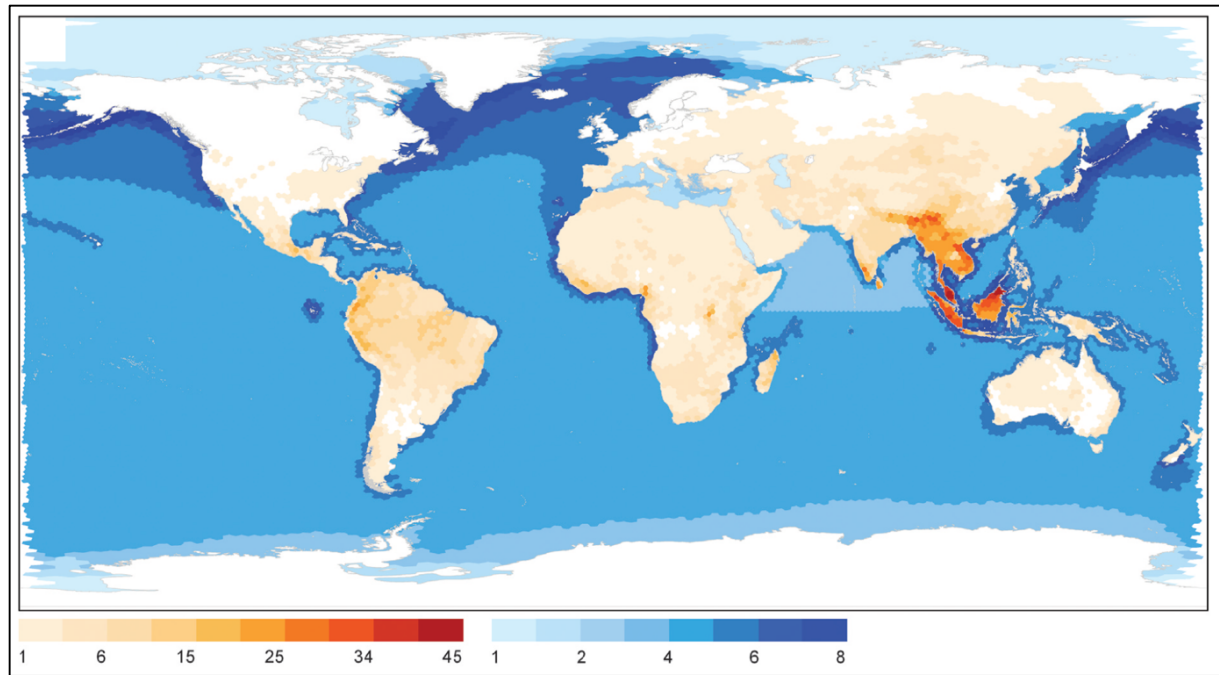


Figure 1.4. Global patterns of human threats for land (brown) and marine (blue) mammals (source: Schipper et al. 2008).

1.1.3 Impact of anthropogenic activities on cetaceans

Numerous cetacean species have a coastal distribution and thus overlap with a wide range of anthropogenic activities (e.g. Jefferson & Hung 2004; López et al. 2004; Díaz López 2019). Cetaceans are directly or indirectly exposed to multiple human activities (e.g. commercial fisheries, direct catches, aquaculture, marine traffic, habitat fragmentation, loss and pollution, and global climate change) which in turn may cause shifts in the distribution, habitat use, abundance, behaviour, social structure, and in extreme situations, may cause extinction (e.g. Nowacek et al. 2001; Dans et al. 2003; MacLeod et al. 2005; Watson-Capps & Mann 2005; Hoffmann et al. 2010; Weir & Pierce 2013; Taylor et al. 2017; Díaz López 2019).

Many cetacean species have experienced severe population depletion because of directed takes (i.e. deliberate killing of cetaceans and live captures for exhibition in aquariums) (Bearzi et al. 2004; Weir & Pierce 2013). Up to the twentieth century, the whaling industry was a major source of income for many countries of the world and led to the reduction of diverse cetacean species (e.g. Atlantic grey whale, *Eschrichtius robustus*: Swartz 2018; North Atlantic right whale, *Eubalaena glacialis*, in the Eastern Atlantic Ocean: Aguilar 1986). Moreover, to reduce the effect of predation, culling was implemented in the past and caused major depletion of some

coastal cetacean populations (e.g. common bottlenose dolphins, *Tursiops truncatus*: Bearzi et al. 2004, 2009; Valdés Hansen 2009; short-beaked common dolphins, *Delphinus delphis*: Bearzi et al. 2004; killer whales, *Orcinus orca*: Oien 1988). Despite progress through international agreements, harvesting remains a major threat for cetaceans (Schipper et al. 2008). Directed takes (e.g. as a source of food or live capture for display in aquariums) of various coastal cetacean species still occur in several countries of the world and, in certain case, pose a major threat to the survival of coastal cetacean populations (Weir & Pierce 2013).

Nowadays, a major source of mortality for coastal cetaceans worldwide is accidental mortality through fishery by-catch (i.e. non-target species taken in gillnet, purse seine, or pelagic trawl fishery: Read 2008; Read et al. 2006; Bearzi et al. 2009), incidental captures (i.e. aquaculture: Díaz López & Shirai 2007; Díaz López 2012), and vessel strikes (Donaldson et al. 2010). Fisheries by-catch lead coastal cetacean species (e.g. vaquita, *Phocoena sinus*: Rojas-Bracho et al. 2006) and local populations to the edge of extinction (e.g. Hector's dolphin, *Cephalorhynchus hectori*: Slooten et al. 2006; Indo-Pacific humpback dolphin, *Sousa plumbea*: Dungan et al. 2016). With marine traffic (e.g. shipping, fisheries, tourism) increasing worldwide, coastal cetaceans are also particularly vulnerable to vessel strikes, which can cause severe injuries and mortality (van Waerebeek et al. 2007; Donaldson et al. 2010) (**Figure 1.5**).

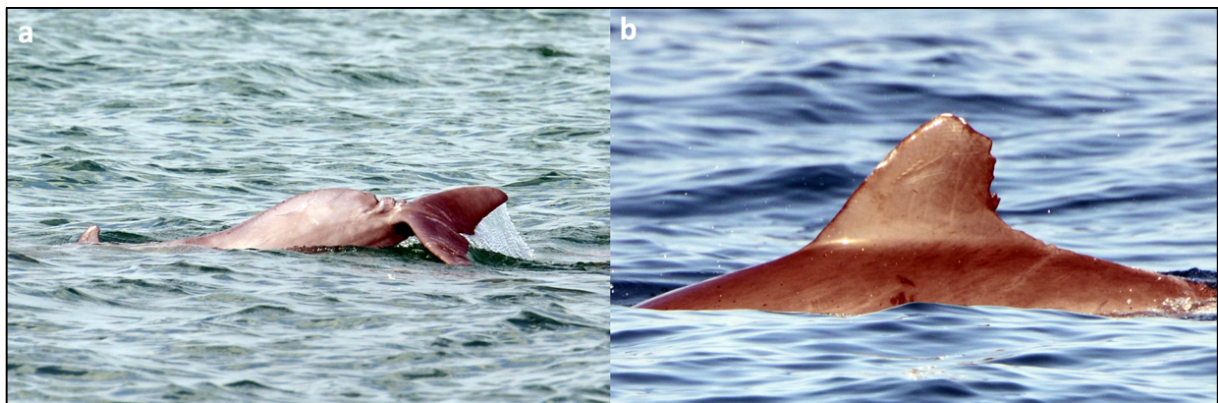


Figure 1.5. Photographs of (a) an Indo-Pacific humpback dolphin with propeller cuts on the peduncle, and (b) an Indo-Pacific bottlenose dolphin with a propeller cut on the dorsal fin (Persian Gulf) (source: Bruno Díaz López, BDRI).

Pollution (i.e. release of potentially harmful chemical, biological, or physical agent to the environment by human activities; Weilgart 2007) is considered to be a significant threat to

coastal cetaceans (Schipper et al. 2008). Chemical contaminants (e.g. from agricultural runoff, sewage, oil spills, anti-fouling paint) can lead to the impairment of reproduction, disruption of endocrine systems, lesions and cancer, and suppression of immune function in cetaceans (Harwood 2001; Islam & Tanaka 2004; Aguilar & Borrell 2005). The transfer of bacterial, fungal, and viral pathogens, released via sewage or agricultural runoff, to cetaceans can occur via prey or wounds (Van Bresse et al. 2009). Runoff may also cause eutrophication leading to environmental hypoxia, thus decreasing local fish abundance which may potentially induce behavioural changes in cetaceans (Bearzi et al. 2009). Marine debris is also a significant cause of mortality in cetaceans through ingestion or entanglement (Lusher et al. 2018) (**Figure 1.6**). Noise pollution (i.e. shipping, military sonar, seismic exploration, drilling, coastal constructions, pile driving; Nowacek et al. 2007) has been theorised as a potential cause of cetacean mass strandings (Cox et al. 2006), increase in stress level, tissue damage, and temporary hearing loss (Nowacek et al. 2007; Weilgart 2007; Tyack 2008).



Figure 1.6. Photographs of bottlenose dolphins carrying plastic on their rostrum (Galicia, Spain) (source: Bruno Díaz López, BDRI).

Anthropogenic activities may induce changes in cetacean habitat use, abundance, and behaviour. Cetaceans live in patchy environments, to an increasing extent, because of the fragmentation of natural habitats thus inducing changes in habitat use (Watson-Capps & Mann 2005). Changes in cetacean habitat use can occur through habitat alteration (e.g. Indo-Pacific bottlenose dolphin, *Tursiops aduncus*: Watson-Capps & Mann 2005), noise pollution (e.g. killer whale: Morton & Symonds 2002) (**Figure 1.7**), marine traffic (e.g. harbour porpoise, *Phocoena phocoena*: Díaz López & Methion 2018a), and fisheries (e.g. common bottlenose dolphin: Bearzi et al. 2009; short-beaked common dolphin: Díaz López et al. 2019). On the long term, changes

in habitat use can lead to variation in abundance in particular regions (e.g. Sprogis et al. 2016b; Díaz López 2019). Ultimately, habitat loss has been linked to decline in survival and reproduction in coastal cetaceans (Wild et al. 2019).

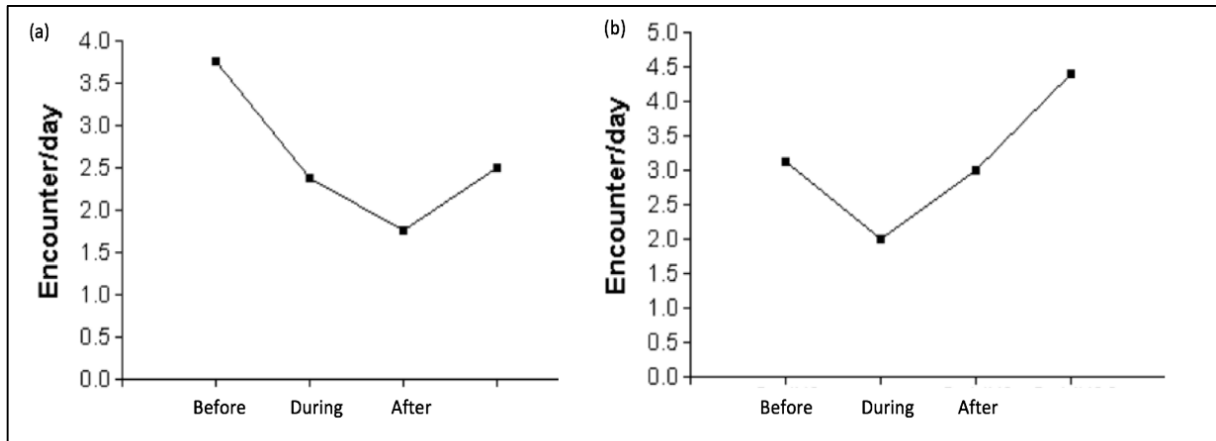


Figure 1.7. Sighting rates for (a) Minke whale, *Balaenoptera acutorostrata*, and (b) harbour porpoise before, during, and after military sonar exercises (Scotland) (source: Parsons et al. 2000).

Tourism and whale-watching activities affect coastal cetacean behaviour by reducing foraging and resting behaviours, and increasing travelling behaviour (Constantine et al. 2004; Stockin et al. 2008; Arcangeli & Crosti 2009). In the long term, tourism activities induced area avoidance and decline in relative abundance (Lusseau 2005; Bejder et al. 2006). The feeding of wild coastal cetaceans can alter their behaviour substantially by creating dependency on humans, modifying foraging strategies and social relationships, and encouraging animals to approach vessels and people (Samuels & Bejder 2004; Finn 2005; Cunningham-Smith et al. 2006; Díaz López 2019).

Although human activity and infrastructure can be a source of disturbance to cetaceans, they can also be a source of reliable food resources that are relatively easy to access (Díaz López 2012). Anthropogenic resources (i.e. fisheries and aquaculture) alter both resource distribution and abundance within a landscape (Dempster et al. 2009). As a result, some cetaceans interact with fisheries and aquaculture, and either depredate on the target-species (e.g. killer whales and sperm whales *Physeter macrocephalus* with long-lines fisheries: Hucke-Gaete et al. 2004; Tixier et al. 2015, 2017; common bottlenose dolphins with trawler fisheries: Chilvers &

Corkeron 2001; and with finfish aquaculture: Díaz López 2019) or predate on wild fish concentrated around the source of food (e.g. Díaz López 2006a). Such interactions have been associated with changes in diet, abundance, demography, life history traits, space use, and social behaviour (**Figure 1.8**) (e.g. Chilvers & Corkeron 2001; Díaz López & Shirai 2008; Ansmann et al. 2012; Díaz López 2012, 2019; Tixier et al. 2015, 2017). Conversely, cetaceans being attracted to high food availability in anthropogenic areas face many threats such as direct persecution (Bearzi et al. 2009), habitat loss and modification (Watson-Capps & Mann 2005), accidental mortality (Díaz López 2012), and pollution (Kannan et al. 1996).

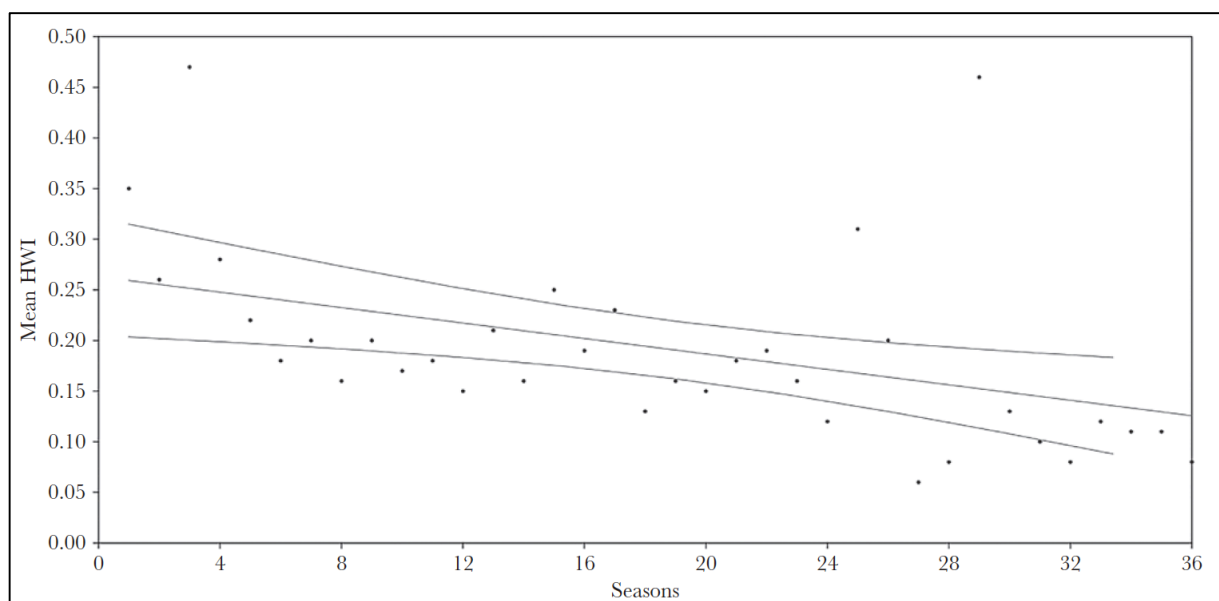


Figure 1.8. Temporal trend of social patterns in bottlenose dolphin, associated to a temporal switch to the food sources provided by finfish aquaculture (Italy). HWI: Half Weight Index (associations between individuals). Seasons: seasons of the year, from January 2005 to December 2013 (source: Díaz López 2019).

As anthropogenic activities (e.g. marine traffic, pollution, habitat modification) along the coasts are likely to develop over the years, due to a growing human population (FAO 2018), there is a need to further our understanding on cetacean ecology and behaviour for their conservation and management. Yet, studying the biological effects of human-induced changes in the marine ecosystem on cetaceans is complex and depends on how species respond to local changes in the environment (Brook et al. 2008; Brierley & Kingsford 2009; Tuomainen & Candolin 2011). The intensity of the responses of cetaceans to human activities may vary over a species' range because the effects of human activities are spatially heterogeneous. This may result in some species having a higher vulnerability in specific areas of their range (MacLeod 2009).

1.2 Studying cetacean ecology and behaviour

Cetacean ecology describes the relationships between cetaceans and their environment (biological and physical), including their interactions with prey, predators, competitors, and anthropogenic activities (Ballance 2018). Studying population ecology is essential for the effective conservation and management of a species (Blumstein & Fernández-Juricic 2010). Population ecology is the study of the processes that affect the abundance and distribution of a species' populations (Hutchinson 1978). A population may be defined as a subset of individuals of the same species occupying a particular geographical area at a particular time (Krebs 1994). The way individuals within a population interact with their environment (both biological and physical) determine population abundance and distribution patterns, as well as social organisation (Krebs 1994).

Cetaceans live in heterogeneous environments where resources (e.g. food, mates, suitable habitats for finding protection against predators, resting, and nursing) are scarce and patchy. Therefore, individuals take advantage of the resources by exhibiting some degree of habitat selection to enhance their fitness (survival and reproduction) (Heithaus 2001a; Frid & Dill 2002). Cetaceans have a slow growth rate, reach sexual maturity late, and usually give birth to one offspring at a time (every 1 to 6 years depending on the species and the individual) (Chivers 2018). Consequently, cetaceans are particularly vulnerable, in terms of abundance and distribution, to changes or perturbations occurring within their environment.

As reviewed in an earlier section, cetacean populations inhabiting coastal habitats are increasingly threatened by a multitude of anthropogenic activities. In order to identify and monitor the potential influence of anthropogenic activities on cetacean populations, it is essential to obtain baseline data about their ecology and behaviour (Whitehead et al. 2000). First, knowledge of population parameters is crucial to assess the status of a population (i.e. estimation of abundance) and to further identify population changes and trends (Boyd et al. 2010). Second, understanding the habitat use of cetacean populations is necessary to identify key areas and for the development of further conservation measures (e.g. Ingram & Rogan 2002). Additionally, assessing the behavioural pattern of cetacean populations within their habitat is essential for the protection, management and conservation of critical areas (e.g.

Bailey & Thompson 2006). Likewise, studying the social organisation of a population is important to gain insights into the nature, quality, and temporal patterning of individual relationships as well as on the evolutionary processes shaping the social system (e.g. Wells et al. 1987). Finally, determining the influence of ecological and anthropogenic factors on population abundance, habitat use, behaviour, and social organisation can further our understanding of cetacean ecology for the development of conservation and management strategies (e.g. Chilvers & Corkeron 2001; Lusseau & Higham 2004; Bejder et al. 2006; Díaz López 2019).

1.2.1 Abundance estimates

As reviewed earlier, many species of cetaceans have been, and continue to be, the target of exploitation in the form of direct takes, accidental mortality, or otherwise threatened by anthropogenic activities that cause disturbance or loss of habitat. The International Union for Conservation of Nature (IUCN) Global Mammal Assessment assessed the status of all cetacean species under revised criteria that are heavily reliant on information on abundance (Hammond 2010) (**Table 1.1**). For example, management procedures for determining the impact of fishery by-catch on populations rely on estimates of abundance (Dans et al. 2003; Slooten 2007). Population estimates provided trends in population size, allowing us to understand the long-term effects of changes in the environment and identify potential threats (e.g. Bejder et al. 2006; Díaz López 2019). Estimating demographic parameters of a cetacean population is crucial in order to take appropriate conservation and management actions. This is achieved through assessing their conservation status and identifying the potential effects of anthropogenic or natural pressures (Smith et al. 2013).

Table 1.1. Conservation status of cetaceans (adapted from IUCN red list, www.iucnredlist.org, accessed 1 July 2019).

Category	Number of species	Examples
Critically Endangered	3	Baiji dolphin (<i>Lipotes vexillifer</i>), Vaquita (<i>Phocoena sinus</i>)
Endangered	10	Hector's dolphin (<i>Cephalorhynchus hectori</i>), North Atlantic Right whale (<i>Eubalaena glacialis</i>)
Vulnerable	7	Australian snubfin dolphin (<i>Orcaella heinsohni</i>), Finless porpoise (<i>Neophocoena phocaenoides</i>)
Near Threatened	5	Antarctic minke whale (<i>Balaenoptera bonaerensis</i>), Chilean dolphin (<i>Cephalorhynchus eutropia</i>)
Least Concern	36	Common bottlenose dolphin (<i>Tursiops truncatus</i>), Short-beaked common dolphin (<i>Delphinus delphis</i>)
Data Deficient	27	Indo-Pacific bottlenose dolphin (<i>Tursiops aduncus</i>), Long-beaked common dolphin (<i>Delphinus capensis</i>)

The dynamics of most populations are influenced by both density-dependent and density-independent factors, and the relative effects of these factors vary among cetacean populations (Fowler 1987). Density-independent factors also known as limiting factors, tend to affect population sizes through abiotic instances, regardless of population density. Conversely, density-dependent factors are sometimes referred to as regulating factors because of their potential for maintaining population density (Berryman 2004). Given cetacean's inconspicuous nature and the changing environment they inhabit, determining the factors driving cetacean abundance is challenging (Hammond 2010). The effects of density-dependent factors intensify as the population increases in size. For example, some diseases spread faster in cetacean populations where individuals live in close proximity with one another than in those whose individuals live farther apart (e.g. morbillivirus: Morris et al. 2015). Similarly, competition for food and other resources rises with density and affects an increasing proportion of the population (Fowler 1987; Chivers & DeMaster 1994). Density-independent factors, such as environmental and anthropogenic factors, exert their influences on population size regardless of the population density. In cetaceans, population size is mainly driven by the availability of prey (Ballance 2018). Yet, as prey availability is not an easy variable to obtain, other environmental variables are often used as indicators of prey availability (Pirodda et al. 2011). Several physiographic (e.g. depth, bottom slope, bottom aspect), oceanographic (e.g.

sea surface temperature), and biological variables (e.g. chlorophyll-a concentration) have been employed to describe cetacean habitat preference indirectly (e.g. Tynan et al. 2005; Pirotta et al. 2011; Cox et al. 2017). Variation in cetacean abundance has been linked to environmental factors which regulate their prey (e.g. water temperature: Wild et al. 2019; El Niño-Southern Oscillation: Sprogis et al. 2018) (**Figure 1.9**). Changes in cetacean population size have also been link to human activities (e.g. decline in abundance linked with dolphin-watching activities: Bejder et al. 2006; increase in abundance linked with finfish aquaculture: Díaz López 2019).

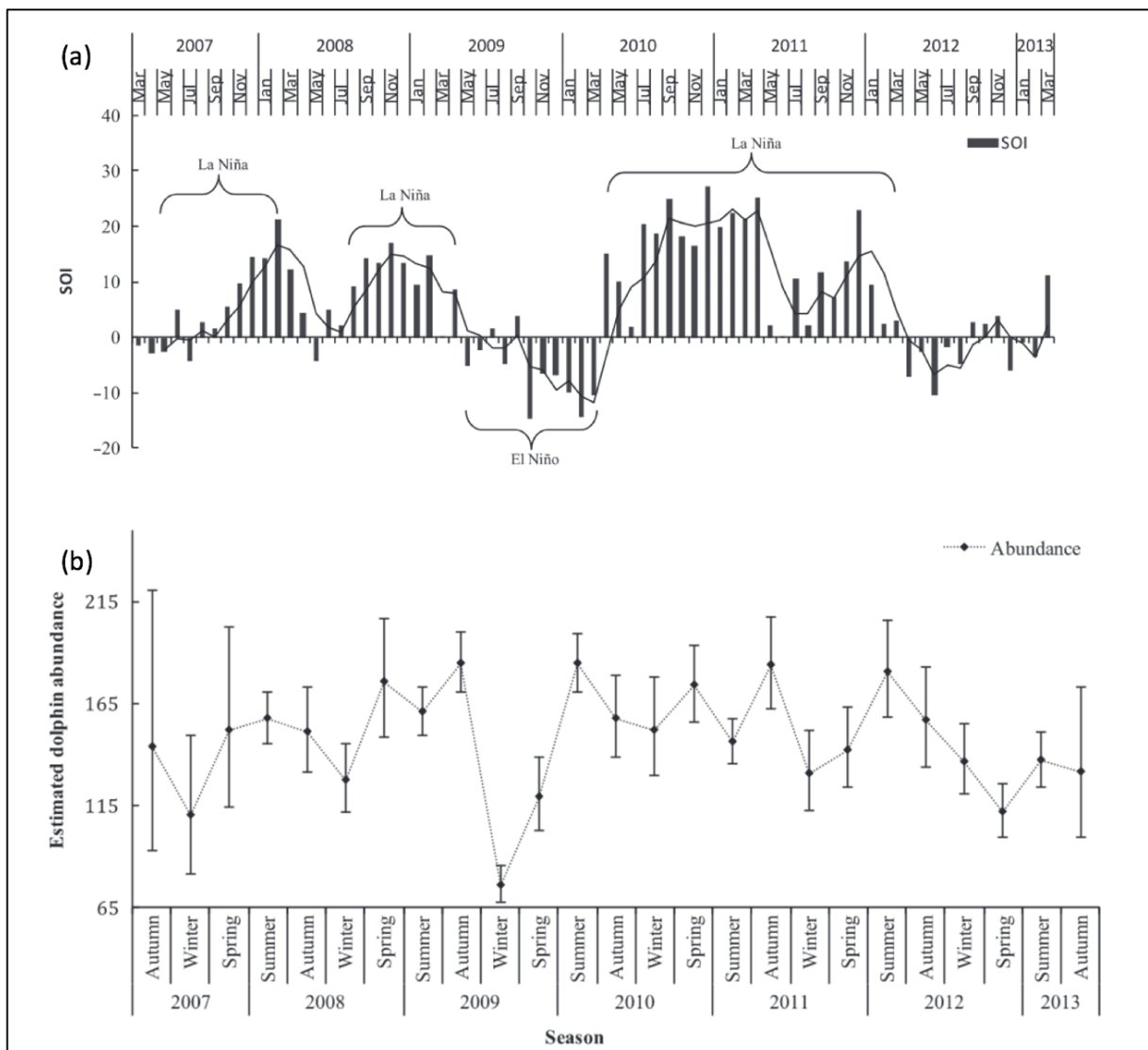


Figure 1.9. Time-series data for (a) monthly Southern Oscillation Index values and (b) seasonal abundance estimates for bottlenose dolphins (Western Australia) (source: Sprogis et al. 2018).

There are different methods to estimate the abundance of cetaceans including extrapolating from counts of individuals (e.g. distance sampling: Hammond et al. 2013), and mark–recapture analyses using capture histories of individuals marked with photographs (e.g. Speakman et al. 2010). The latter is the most widely used technique for estimating the population size and survival rates of coastal cetacean populations (e.g. Currey et al. 2008; Silva et al. 2009; Speakman et al. 2010). Photo-identification is a non-invasive (no physical capture, handling, or application of a mark) mark-recapture technique which consists of taking photographs ('capture') of the natural markings of individual cetaceans (Würsig & Jefferson 1990). This technique is extensively used in coastal cetacean studies and much of what is known about their biology comes through photo-identification studies (Hammond 2010). Several cetacean species can be identified through natural marks present on their dorsal fin (e.g. bottlenose dolphins: Wilson et al. 1999, pilot whales *Globicephala melas*: Auger-Méthé & Whitehead 2007), humpback whales *Megaptera novaeangliae* and sperm whales can be identified through the marks present on their flukes, and blue whales *Balaenoptera musculus* can be identified through the coloration pattern present on their body (e.g. Matthews et al. 2001; Calambokidis & Barlow 2004). To estimate abundance using mark–recapture methods, the basic data required are the capture histories of individually identified animals. A capture history simply describes whether or not an animal was captured in a series of sampling occasions, discrete periods of data collection (Hammond et al. 2013). The estimate of abundance obtained is therefore the number of individuals using a study area during a study period.

A variety of mark-recapture models is available to estimate abundance of animal populations (Amstrup et al. 2010). Models are usually selected depending on the nature or characteristics of a given population, that is, if it is considered closed or open (Nichols 1992). A closed population remains constant in composition and size with no recruitment (births or immigration) or loss of individuals (death or emigration) during the course of a given study. In contrast, an open population allows for births, deaths, emigration, and immigration. For open models, births cannot be differentiated from immigration, while deaths cannot be differentiated from emigration. Consequently, the term 'apparent survival' is used to describe variations in survival. Pollock's (1982) capture–recapture robust design has been increasingly used to obtain accurate estimates of abundance and other demographic variables of bottlenose dolphin populations (e.g. Silva et al. 2009; Speakman et al. 2010; Nicholson et al.

2012; Bassos-Hull et al. 2013; Smith et al. 2013; Fruet et al. 2015; Santostasi et al. 2016; Sprogis et al. 2016b). This design, unlike standard open models, takes into account the degree of residency, including temporary emigration, thus more accurately reflecting reality in the results (Kendall et al. 1997; Nicholson et al. 2012; Smith et al. 2013). Pollock's (1982) robust design combines open population models (open sampling event; termed 'primary periods') and closed population models (multiple closed events within the open sampling event; termed 'secondary periods'; Kendall et al. 1997). Although the population is assumed to be open between primary periods (i.e. allowing for births, deaths and permanent or temporary emigration and immigration), each secondary period assumes an effectively closed unit (i.e. births, deaths, immigration and emigration do not occur) (Kendall et al. 1997).

1.2.2 Distribution and habitat use

Given the heterogeneity of the environment cetaceans live in, individuals often exhibit some degree of habitat selection in order to take the greatest advantage of the resources (Bräger et al. 2003; Parra 2006). Behaviours such as foraging, mating, and resting are thus usually performed in particular habitats so that habitat preferences and the resulting space-use may differ with time and between individuals (e.g. Heithaus & Dill 2002; Tyne et al. 2015; Sprogis et al. 2016a). Hence, within the overall range of a species, there are areas that are occupied more than others (e.g. Karczmarski et al. 2000). Therefore, to understand a species' ecology and to assess the overlap with human activities, it is essential to determine cetacean habitat use and what environmental characteristics influence their habitat choice (Matthiopoulos et al. 2010) (e.g. **Figure 1.10**). Ultimately, identifying critical habitats cetaceans occupy is fundamental for their effective conservation management (Hoyt 2002).

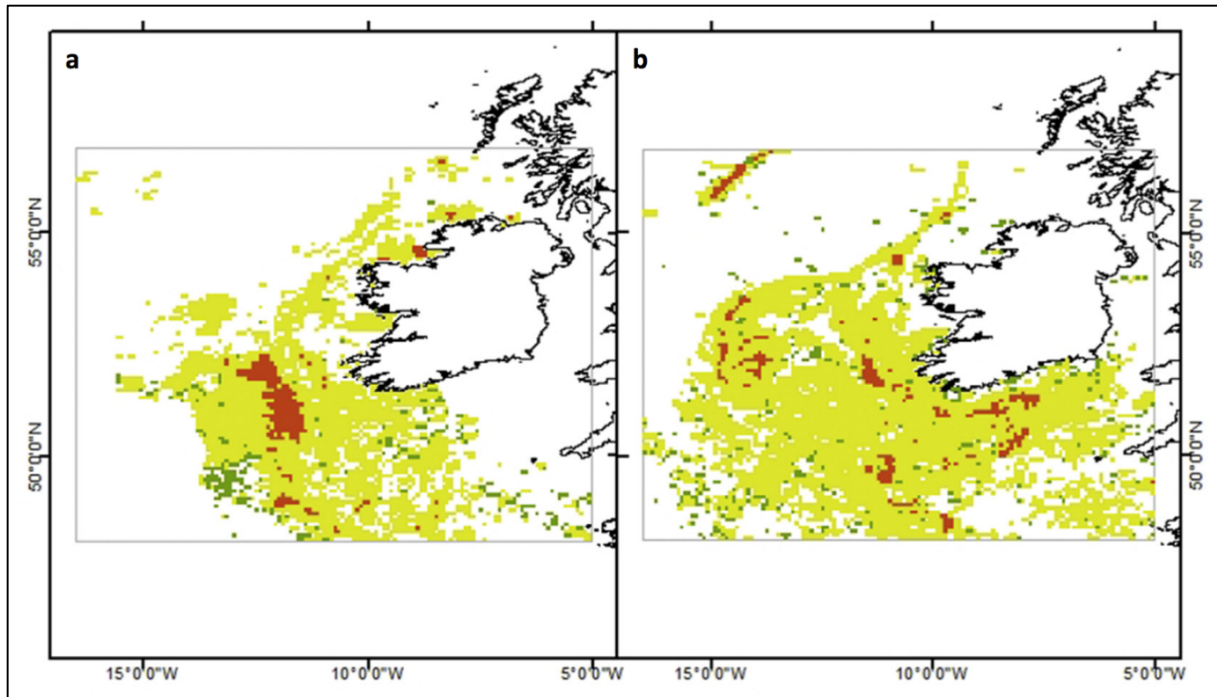


Figure 1.10. Exposure of (a) white-sided dolphins, *Lagenorhynchus acutus*, to pelagic trawls and (b) bottlenose dolphins to gillnets in Irish and UK waters. Green indicates lower exposure and red indicates higher exposure (source: Breen et al. 2016).

Cetacean habitat use is driven by a number of biotic and abiotic factors (Ballance 2018). Food availability is suggested to be the main driver of cetacean distribution and movement patterns (Hindell et al. 2009). Environmental factors affect the distribution and abundance of cetacean prey, the latter indirectly determining cetacean habitat use (Pirodda et al. 2011; Díaz López & Methion 2019). Other potentially important drivers that influence cetacean habitat use include behavioural state (e.g. resting areas for dolphins: Tyne et al. 2015), presence of calves (e.g. nursing: Hartman et al. 2014), predation risk (Heithaus & Dill 2002), competition (Heithaus 2001b), and reproductive needs (e.g. breeding areas for baleen whales: Smith et al. 2012). Human activities are also known to affect cetacean habitat use (e.g. Watson-Capps & Mann 2015; Díaz López & Methion 2018a, 2019; Díaz López et al. 2019).

Studying the spatial distribution of cetaceans is particularly challenging (Matthiopoulos et al. 2010). Cetacean spatial distribution models often rely on presence/absence data (e.g. Laran & Gannier 2008; De Stephanis et al. 2008). With survey effort data, absences are generated from surveyed areas and can be used along with presence data in presence-absence models such as generalized linear and additive models (GLMs, GAMs) or Classification and Regression Trees

(CARTs). However, while species presences can be confirmed, species absences cannot be confirmed with certainty. Therefore, an adequate sampling effort, both in space and time, must be performed in order to obtain accurate presence/absence data (Thorne et al. 2012).

Environmental and anthropogenic variables are often linked to presence/absence data of cetaceans to address space-use questions. As information on both distribution and abundance of cetacean prey is often hard to measure directly, environmental variables are often used as proxies to explain cetacean habitat use, even if they are not always directly and causally related with cetacean presence (e.g. Viddi et al. 2010; Pirotta et al. 2011; Díaz López & Methion 2018a, 2019). Several oceanographic (e.g. sea surface temperature), biological (e.g. chlorophyll-a surface: Tynan et al. 2005), and topographic (e.g. depth, slope, aspect: Pirotta et al. 2011) variables have been used to indirectly describe cetacean habitat use. Anthropogenic factors are also increasingly used to explain cetacean distribution (e.g. Díaz López & Methion 2018a, 2019; Díaz López et al. 2019). In this context, models that use environmental and anthropogenic factors to assess the distribution of a cetacean species have gained increasing importance in the different steps of spatial and conservation planning (e.g. Pirotta et al. 2011; Díaz López et al. 2019).

1.2.3 Behavioural pattern

Integrating behavioural studies into conservation strategies is an important step for the protection of wildlife and contributes to reducing the consequences of human disturbances (Sutherland 1998; Buchholz 2007). The identification and protection of critical habitats, such as foraging, resting, or breeding grounds, are particularly difficult tasks but essential to the conservation of cetaceans (Williams et al. 2006). The time cetaceans allocate for various activities (i.e. feeding, resting, socialising) has significant implications for their survival and reproduction (Constantine et al. 2004). Therefore, determining cetacean behavioural activity in particular areas, as well as defining the variables that influence their behaviour, can help with the protection, management, and conservation of these species (Matthiopoulos et al. 2010) (Figure 1.11).

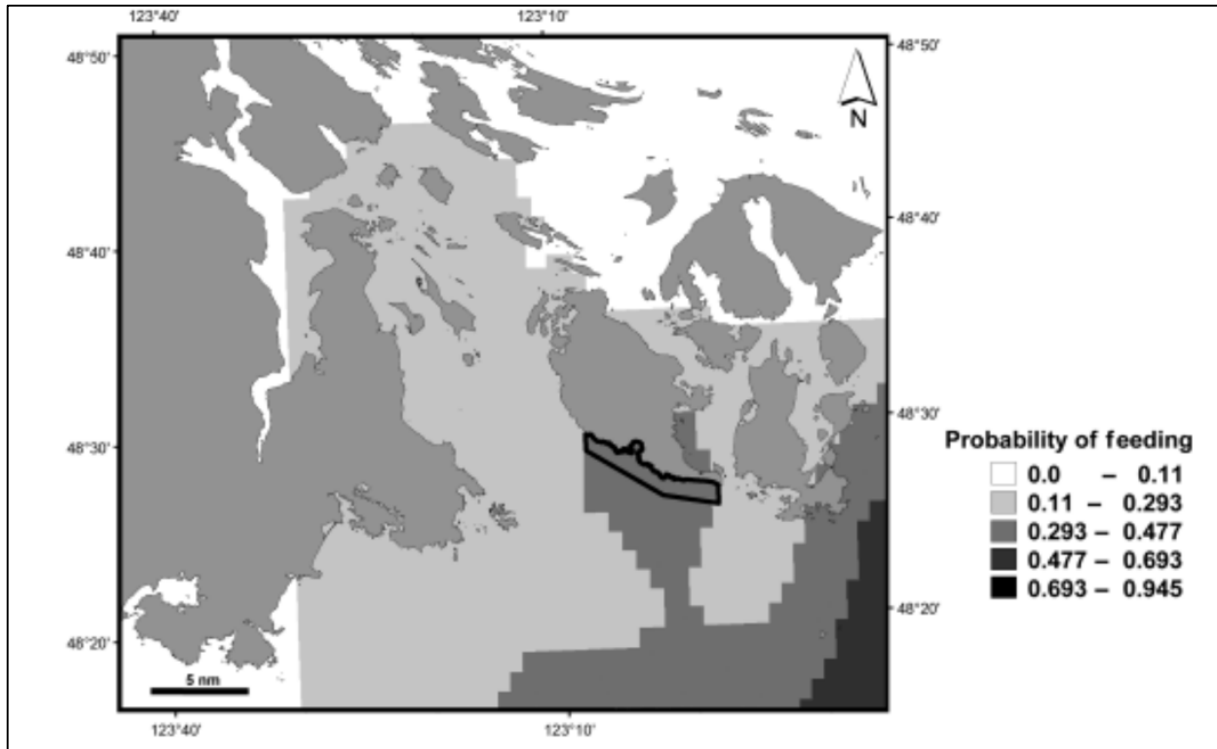


Figure 1.11. Proposed marine protected area for killer whale for a priority feeding area in Washington state, USA, and British Columbia, Canada (source: Ashe et al. 2010).

In cetaceans, variation in behavioural activity has been linked to physiological needs (Baird et al. 2005), availability of prey (Heithaus & Dill 2002), environmental factors (e.g. sea surface temperature: Mann & Watson-Capps 2005; bathymetry: Tyne et al. 2015; tidal state: Mendes et al. 2002; time of day: Bräger 1993; season: Chilvers et al. 2003), and predation risk (e.g. Mann & Watson-Capps 2005). Several studies have also found links between cetacean behavioural activity and anthropogenic activities (e.g. Constantine et al. 2004; Lusseau 2005; Bejder et al. 2006; Williams et al. 2006; Díaz López 2019). Likewise, some studies point out that anthropogenic food resources affect the foraging behaviour of cetaceans (e.g. trawler fisheries: Chilvers & Corkeron 2001; finfish aquaculture: Díaz López 2006b, 2012, 2019).

Studying the behaviour of cetaceans is particularly challenging because they are difficult to observe (they spend a lot of time under water) and they often surface rapidly making their behaviour easy to miss (Heithaus & Dill 2009). Standard methods of following cetaceans from small boats and observing them when they surface have been used effectively to determine the behaviour of coastal cetaceans (Mann 1999; Cecchetti et al. 2018; Miketa et al. 2018). In recent years, technological advances have supplemented behavioural data collection for

cetaceans (e.g. Falcone et al. 2017; Pearson et al. 2017). Yet, these methods are expensive, and not always feasible for studying large numbers of individuals or for small cetaceans (< 5 metres). Observer-based methodologies are therefore still necessary and important (Díaz López et al. 2008b; Karniski et al. 2015).

For a behavioural study, two sampling decisions must be taken; the first is concerned with which subject(s) to observe and for how long (individual-follow vs. group-follow); the second is concerned with how to record the behaviour (reviewed in Mann 1999). In a group-follow, the identities of all group members and their behavioural states are recorded, when possible (Mann 1999). In an individual-follow, the behaviour of the focal individual, as well as interactions and associations between the focal animal and any others are recorded (Mann 1999). The behaviour can be recorded as events (i.e. brief behaviours, measured in frequency) or states (i.e. long behaviours of measurable duration) (Altmann 1974). Sampling method for cetaceans, which refers to the procedures used to sample the behaviour of individuals or groups, include 'continuous sampling' (all behaviours), 'focal-animal' (the behaviour of the focal animal), 'predominant activity' (the state of the majority of the group members), 'point' (the state of an individual or individuals at a particular time), and 'scan' (the state of an individual or individuals when observed) (reviewed in Mann 1999). For small cetaceans, most studies have used group-follows and predominant activity sampling to determine cetacean behaviour and linked them with environmental and anthropogenic variables (e.g. Bearzi 1999; Neumann 2001; Degradi et al. 2012; Lundquist et al. 2012; Cecchetti et al. 2018).

1.2.4 Social behaviour

Social structure has been defined as the content, quality, and patterning of relationships between individuals within a group (Hinde 1976) (**Figure 1.12**). In most cetacean populations, not all individuals interact with each other (e.g. Wiszniewski et al. 2009; Dungan et al. 2012). Individuals exhibit differences in the number of social interactions, their degree of centrality in the population network, and their tendency to interconnect different communities that form substructures within networks (e.g. Lusseau & Newman 2004; Lusseau 2007; Dungan et al. 2012). The structure of animal societies may influence population fitness (Formica et al. 2012), reproductive success (Cameron et al. 2009), genetic structure (Altmann et al. 1996), and

transmission of learned behaviour (Whitehead 2010) and pathogens (Keeling & Eames 2005). Given such broad implications, studying population social organisation is essential for understanding the biology of cetaceans and for their conservation (Anthony & Blumstein 2000).

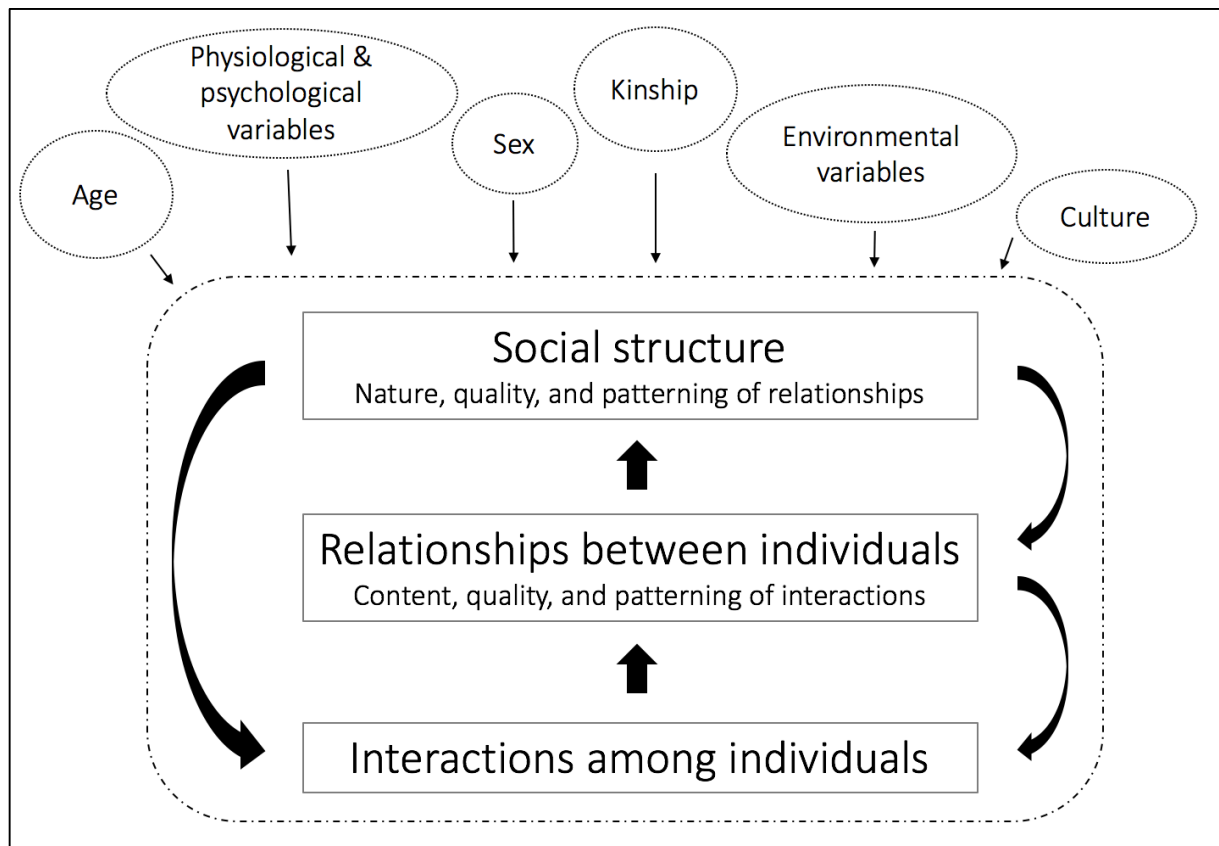


Figure 1.12. Hinde's (1976) framework. Circles represent independent factors that may operate at different levels of the framework (adapted from Whitehead 2008).

Multiple variables may play a role in shaping cetacean societies including predation risk (Heithaus & Dill 2002), mating opportunities (Möller et al. 2001), access to resources (Gowans et al. 2007), sex (Diaz-Aguirre et al. 2018), and kinship (Wiszniewski et al. 2010). Human activities also affect cetacean social organisation (e.g. Chilvers & Corkeron 2001; Díaz López & Shirai 2008; Ansmann et al. 2012; Díaz López 2019).

Social relationship measures for cetaceans usually take the form of interaction rates or association indices (Hinde's framework; Hinde 1976). As interactions between individuals are difficult to assess in cetaceans, association patterns are frequently used in social analyses (Whitehead 2008). Individual cetaceans are mostly identified photographically (i.e. via photo-

identification) and their associations with other individuals are recorded either directly or using group memberships (Whitehead & Van Parijs 2010). Association indices are then calculated between pairs of individuals (i.e. dyads) and used as relationship measures to analyse the social organisation (Cairns & Schwager 1987; Whitehead 1995). For cetacean studies, associations are usually defined using spatio-temporal groups, and group membership is defined using spatial proximity and behavioural state measurements (Whitehead 2008). A group is generally defined as individuals engaged in the same behaviour and ranging within a certain distance of each other (e.g. Bearzi 1999; Díaz López 2006b). Individuals are therefore considered associated if they are members of the same group (Whitehead 2008).

Social network theory provides a conceptual framework for describing social organisation, allowing characterisation of social structure that integrates all levels from individual interactions to population processes (Krause et al. 2009). Social network analyses are increasingly used to accurately describe cetacean societies and to understand the influence of environmental, biological, or anthropogenic factors on social organisation (Farine & Whitehead 2015).

1.3 Marine aquaculture and cetaceans

1.3.1 Marine aquaculture: an industry in worldwide expansion

More than one third of the human population lives within 100 km from the coastline and relies on marine coastal habitats and resources (FAO 2018). Marine coastal ecosystems are important for fisheries and aquaculture, which provide people in many countries with a key source of protein, as well as livelihood opportunities. In 2015, fish accounted for about 17% of animal protein consumed by the global human population (FAO 2018). However, this demand for seafood product lead to a decline of wild stocks. The percentage of stocks fished at biologically unsustainable levels increased from 10% in 1974, to 33.1% in 2015 (FAO 2018). With capture fishery production relatively static since the late 1980s, aquaculture has been responsible for the continuing impressive growth in the supply of fish for human consumption (**Figure 1.13**). According to the FAO (2014), world aquaculture continues to grow faster than other major food production sectors, and production attained an all-time high of 110.2 million tonnes in 2016 (USD 243.5 billion). The contribution of aquaculture to the global production of capture fisheries and aquaculture combined has risen continuously, reaching 46.8% in 2016, up from 25.7% in 2000 (FAO 2018).

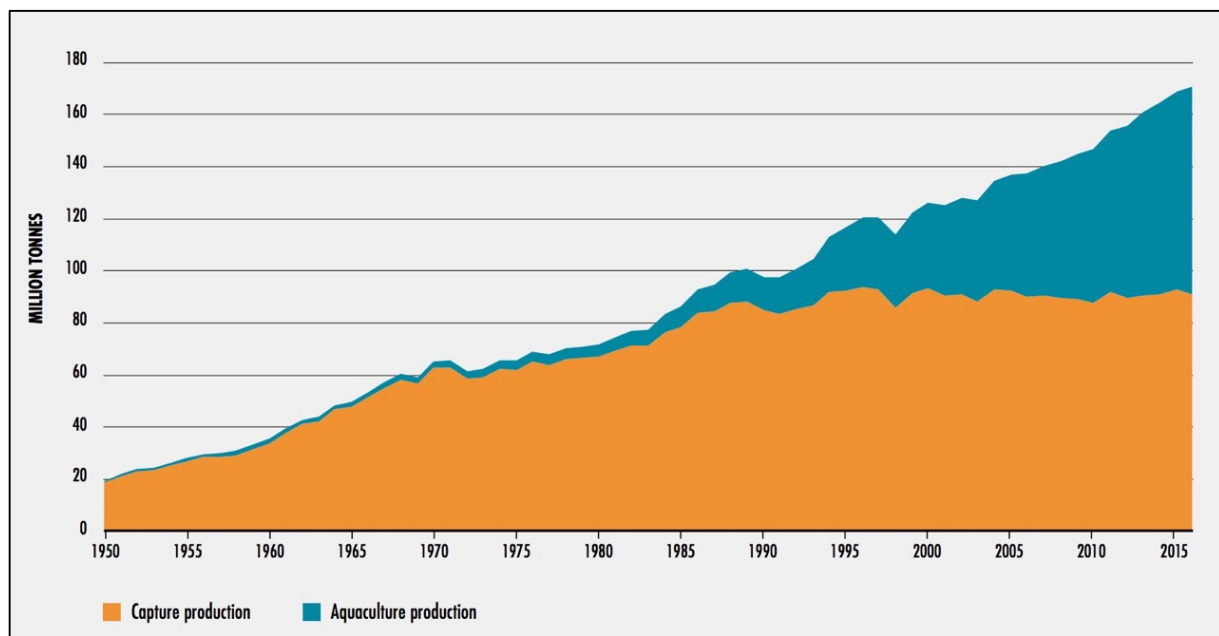


Figure 1.13. World capture fisheries and aquaculture production (source: FAO 2018).

Marine aquaculture, that is, the farming of plant and animal species from the sea, is one of the fastest-growing food production sectors in the world, and continues to expand globally (FAO 2014). An increasing demand for seafood products, declining wild stocks (mostly due to overfishing), together with globalization of trade and economic incentives, have resulted in this rapid growth in finfish and shellfish farming (Naylor et al. 2000; Bostock et al. 2010). Official statistics indicate that 59.6 million people were engaged in the primary sector of capture fisheries and aquaculture in 2016 (19.3 million in aquaculture and 40.3 million in capture fisheries). FAO recorded 28.7 million tonnes (USD 67.4 billion) of seafood production from marine aquaculture in 2016.

Finfish farming is the concentrated cultivation of captive finfish (mostly salmon, sea bass, and sea bream) in net pens, pods, cages, or other devices, and accounts for 23% of the total marine aquaculture production (FAO 2018) (**Figure 1.14**). Finfish culture is an intensive industry that involves an addition of nutrients to the marine environment (Díaz López 2011).

Shellfish farming, which is the culture of invertebrates such as molluscs, is the main sector of the marine aquaculture industry accounting for 59% of the total production, and, like other forms of aquaculture, is expanding (FAO 2018) (**Figure 1.14**). Bivalve molluscs are typically filter-feeders, feeding exclusively on the plankton and detritus present in the water (Pillay 2008). In contrast with finfish aquaculture, shellfish are not provided with external food. Worldwide, the major cultivated molluscan species groups (based on their production) are clams, oysters, mussels, and scallops (FAO 2016), whereas the main farmed species differing by country (FAO 2018). Bivalves are farmed using a variety of methods based on the species and the prevailing hydrographic, social, and economic conditions (i.e. presence of predators, turbidity, food supply). There are two main types of culture methods, bivalves can be grown using either on-bottom (grown directly on the seafloor) or off-bottom cultures (e.g. long-lines, rafts, floating bags, trays, cages, and poles) (Pillay 2008).

Category	Africa	Americas	Asia	Europe	Oceania	World
Inland aquaculture						
Finfish	1 954	1 072	43 983	502	5	47 516
Crustacea	0	68	2 965	0	0	3 033
Molluscs			286			286
Other aquatic animals		1	531			531
Subtotal	1 954	1 140	47 765	502	5	51 367
Marine and coastal aquaculture						
Finfish	17	906	3 739	1 830	82	6 575
Crustacea	5	727	4 091	0	6	4 829
Molluscs	6	574	15 550	613	112	16 853
Other aquatic animals	0		402	0	5	407
Subtotal	28	2 207	23 781	2 443	205	28 664
All aquaculture						
Finfish	1 972	1 978	47 722	2 332	87	54 091
Crustacea	5	795	7 055	0	7	7 862
Molluscs	6	574	15 835	613	112	17 139
Other aquatic animals	0	1	933	0	5	939
Total	1 982	3 348	71 546	2 945	210	80 031

Figure 1.14. Aquaculture production of main groups of food fish species (source: FAO 2018).

1.3.2 Impacts of marine aquaculture in the environment

The development of the aquaculture industry has been accompanied by a range of environmental impacts (reviewed by Pillay 2008). Marine aquaculture usually occurs in coastal or estuarine waters, and therefore adds pressure on environments already influenced by a wide range of anthropogenic activities. The intensity and type of environmental impacts of marine aquaculture depend on the species farmed, the intensity of production, and the farm location.

Addition of nutrient and accumulation of waste

One of the greatest concerns raised about the effects of marine aquaculture on the environment is related to alteration of nutrient exchange and enhanced bio-deposition (reviewed in McKindsey et al. 2011) (Figure 1.15). Both finfish and shellfish production can cause a build-up of organic material, as a result of either particulate fall-out from the farms and/or from the altered hydrodynamics around the farm (Norkko et al. 2001; Sutherland et al. 2007). In finfish aquaculture, organic material comes from waste feed (i.e. uneaten food, fish excretory, and organic matter from net-cleaning that enter water column and/or settle to the

seabed) (Silvert 1992). Active filter-feeding by bivalves results in the excretion of undigested material (feces or pseudo-feces), which increases bio-deposition in areas where bivalves occur in high densities, such as farms (Norkko et al. 2001). Shellfish culture can also lead to changes in the sedimentary environment at the culture site due to sediment trapping (Ysebaert et al. 2009). The organisms associated with farm structure (e.g. tunicates) may also contribute to the deposition of organic matter (Lacoste & Gaertner-Mazouni 2015). The accumulation of organic matter (i.e. organic loading) beneath the farms, especially in areas of poor current flow, can produce major changes in the sediment chemistry (Porrello et al. 2005). Increased bio-deposition may result in increased organic content load, reducing the sediment oxygen levels, which therefore induces the subsequent production and release of methane and toxic hydrogen sulphide (Wu et al. 1994; Islam 2005). Changes in benthic sediment biogeochemical properties (i.e. benthic respiration and nutrient fluxes at the sediment-water interface) in turn have effects on the substrate ecosystem, resulting in major changes to the benthic communities (i.e. abundance, diversity, structure, and trophic composition of infaunal and macro-epifaunal communities) (McKindsey et al. 2011). In areas surrounding farms, sediment grain size is smaller and particulate organic carbon, nitrogen, and phosphorous concentrations are higher than in nearby locations free of farms (Ysebaert et al. 2009). The effects of aquaculture on the benthic environment are usually found within a short distance from the farm boundary (Crawford et al. 2003; Ysebaert et al. 2009). Farmed species and other associated fauna release dissolved nitrogen (e.g. ammonium) into the water column, which can cause localised enrichment. This will alter the composition and density of phytoplankton species, increasing the risk of toxic algal blooms, which in turn may affect the farmed species (Bouwman et al. 2011). Increased organic content load is also a contributing factor of eutrophication (Bouwman et al. 2011).

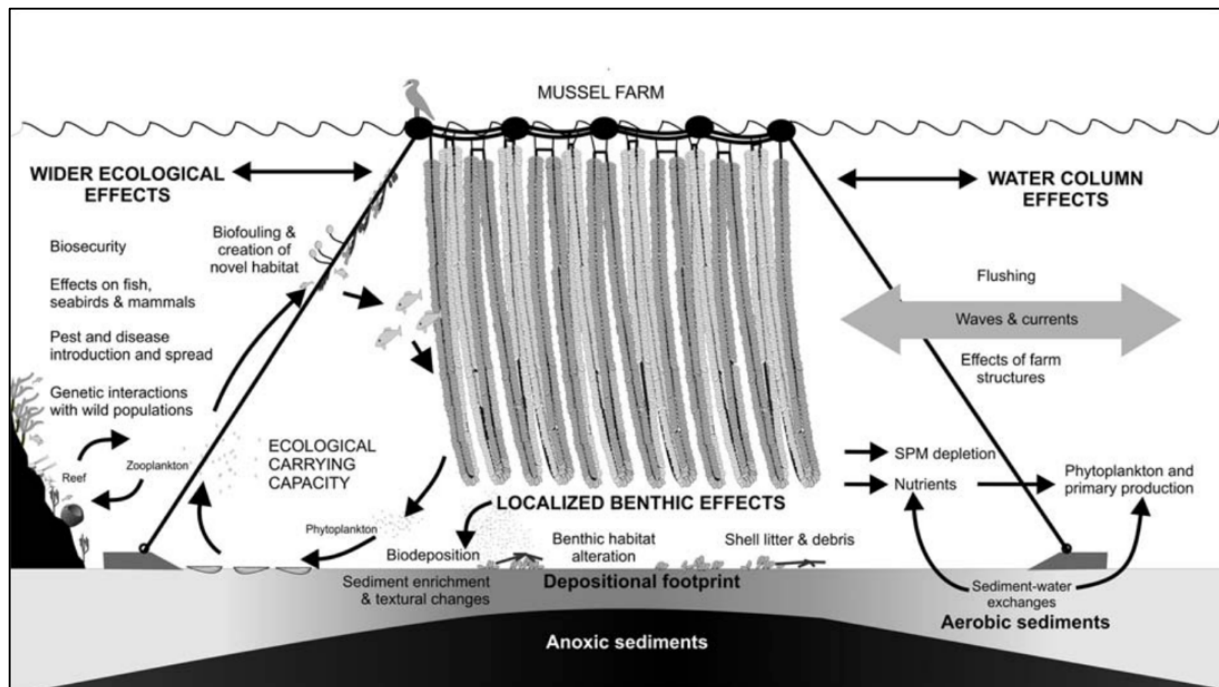


Figure 1.15. Ecological effects of farming shellfish (source: Keeley et al. 2009).

Farm structure and operation

A number of impacts may occur as a result of the physical farm infrastructure and operations (as reviewed in McKindsey et al. 2011). Habitat modification and disturbance such as increased turbidity, shading, and sedimentation, may alter the structure of benthic communities. Possible variations in behavioural responses of fauna may also result from disturbances in and around the farm, for example from increased boating activity. Habitat concerns resulting from the physical structure associated with aquaculture include the alteration of hydrodynamics and current velocities, as well as reduced flow rates. Reduced currents may increase sedimentation, with the potential for re-suspension during flood tides.

Extraction power

Marine bivalves are sometimes described as extractive species; they can benefit the environment by removing nutrients from the water column, thus lowering the nutrient load in the water (Ysebaert et al. 2009). This ecosystem service may result in increasing the amount of underwater light, extending the euphotic zone and potentially enabling the recovery of submerged aquatic vegetation and macro-algae (McKindsey et al. 2011). Submerged aquatic vegetation provides further ecosystem services, such as a refuge and nursery for juvenile fish, and increased sediment stability (Yamamuro et al. 2006). Shellfish farming may provide further

benefits through reduced eutrophication, which decreases the cycling time of suspended organic matter by removing the opportunity for bacterial re-mineralization, and therefore the onset of hypoxia and anoxia (Ferreira et al. 2007; Burkholder & Shumway 2011).

Escaping and introduction of non-native species

The escaping of farmed species may be an area of concern, for both finfish and shellfish farming. Farmed species may breed with other distinct populations of the same species, possibly resulting in a genetic shift in the local population, and a loss of genetic diversity (Naylor et al. 2000). Similarly, hybridisation may occur between endemic species and farmed species where the species are genetically compatible (e.g. Elo et al. 1997). Concerns with escaping species also include predation on native species, competition for resources, and transmission of disease (Naylor et al. 2001).

Transfer of pathogens and pharmaceuticals

The concentration of farmed species in a particular place can lead to the spread of pathogens. Increased food resources near farm cages attract large concentrations of escaped and wild fishes, which may in turn, act as vectors for the transfer of parasites and diseases to wild populations (Murray & Peeler 2005). Moreover, the use of antibiotics in finfish aquaculture is a concern because residuals not absorbed by the fish can potentially enter the environment as uneaten feed and faeces. In recent years, antibiotic residues in the aquatic environment have received much attention due to their large-scale use and long-term adverse effects (e.g. Fortt et al. 2007). Examples of reported adverse effects for antibiotics include reduced feeding rates, impacts on survival, and changes in immune response (reviewed in Gaw et al. 2014).

Reduction of wild stock

The sourcing of stock from the wild for aquaculture has the potential to impact wild populations. Where seed-stock is sourced from the wild for shellfish farming, there is potential for collection to have an impact on native stocks (Kaiser et al. 1998). For finfish aquaculture, fry is usually hatched in freshwater facilities using brood stock maintained by the aquaculture industry (Lee 2003). However, the farming of carnivorous fish species requires large inputs of feed from external sources mostly derived from wild-fish-stock (Aubin et al. 2009), which contribute to wild fish depletion (Naylor et al. 2000)

Chemical usage

Chemicals are used in marine aquaculture for a wide range of applications. Not only are they used in fish health, but also to control nuisance organisms on equipment such as nets, and to disinfect and improve water quality (e.g. Burrige et al. 2010). Anti-foulants are an important part of the maintenance of nets and cages in marine farms (e.g. Kalantzi et al. 2016). Chromium, copper and arsenic-based anti-foulants are frequently used, with resultant damage to both wild and farmed organisms (Ratcliff et al. 2016; Tornero & Hanke 2016).

Farms as Fish Aggregating Devices (FADs)

Marine aquaculture introduces considerably hard physical structure into the environment (both at the bottom and on the water column) (Moroney & Walker 1999; Carman et al. 2010; McKindsey et al. 2011). Marine farms often create favourable structures and habitats for invertebrates and fishes by providing refuges from predation and adverse environmental conditions (Brooks 2000; Gutierrez et al. 2003; McKindsey et al. 2011). The physical farm infrastructure (i.e. buoys, ropes, anchors, cages, or nets) provides substrate for sessile organisms from a wide range of taxa, including macro-algae, bryozoans, molluscs, tunicates, and cnidarians (Willemssen 2005). Plankton accumulates around aquaculture farms which aggregate wild fish that feed on this resource (Díaz López et al. 2008a; Fernández-Jover et al. 2016) (**Figure 1.16**). Likewise, the associated fouling and related communities, including amphipods, small fish, and gastropods, also provide additional trophic resources to aggregated fish which may then be transferred to higher trophic levels (Lacoste & Gaertner-Mazouni 2015). In shellfish aquaculture, fouling organisms can also develop on shellfish, which provide a hard structure (Mazouni et al. 2001). Shellfish fall-off (as well as shells) and associated organisms from suspended culture have the potential to create benthic structure that would not normally occur on soft sediment bottoms, similar to that of hard-bottom reefs (McKindsey et al. 2011). Shellfish fall-off enhances the amount of food available to benthic predators and scavengers increasing their abundance (e.g. crustaceans, polychaetes, molluscs, echinoderms) (McKindsey et al. 2011; Callier et al. 2017). The farm structures and associated organisms therefore act as FADs by attracting invertebrates and fish (Callier et al. 2017). In turn, many top predator species are attracted by the presence of fish around the farm (e.g. Díaz López 2017).

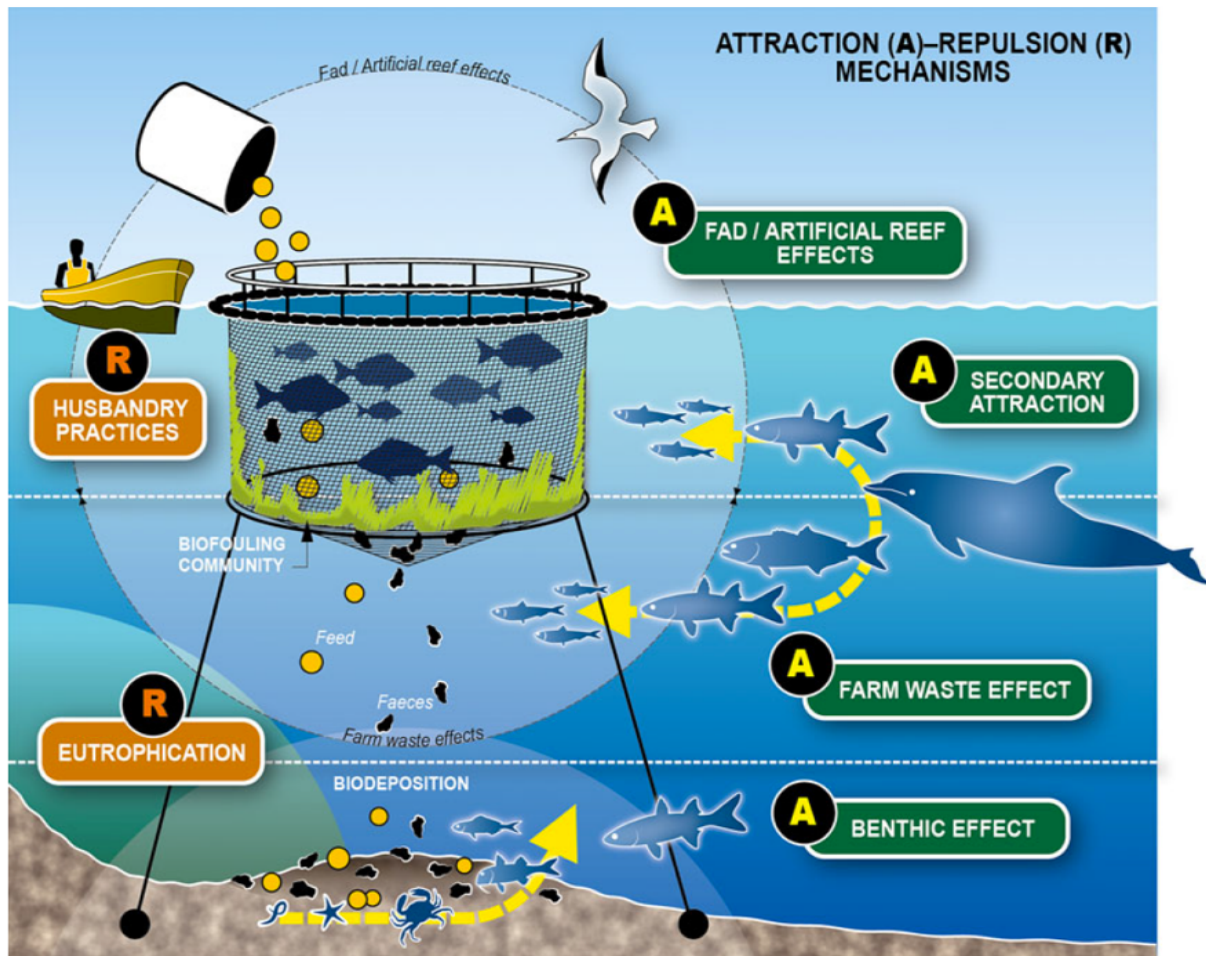


Figure 1.16. Attraction (A) and repulsion (R) mechanisms of mobile wild species by fish farming cages (source: Callier et al. 2017).

1.3.3 Interaction between marine aquaculture and cetaceans

Many cetacean species have a coastal distribution and thus overlap with marine aquaculture. Cetaceans may avoid or be attracted by the marine aquaculture farms, depending on the culture method, the environmental conditions, and the ecology of a given species. This interaction may, in turn, influence the ecology of cetacean species (i.e. abundance, habitat use, foraging behaviour, social organisation) and the aquaculture product (e.g. damage to gear, depredation of farmed fish).

Impact of cetaceans on the marine aquaculture industry

Owing to the development of the marine aquaculture industry, the amount of coastal areas utilised is leading to increased conflicts between aquaculture and cetaceans. The result of these interactions can cause damage to the aquaculture industry (Würsig & Gailey 2002; Díaz López 2012). In finfish aquaculture, cetaceans are blamed for (i) depredating on farmed finfish, (ii) scaring the farmed fish, (iii) increasing farmed fish susceptibility to disease or decrease growth owing to stress, and (iv) destroying gear which can cause farmed fish to escape through torn pens (reviewed in Würsig & Gailey 2002). As a result, a variety of methods to attempt to dissuade cetacean depredation are used, such as anti-predator nets and acoustic harassment or deterrent devices (AHD and ADD) (e.g. Díaz López & Mariño 2011). Yet, these methods result in low effectiveness and produce a high impact on both target and non-target species (Díaz López & Shirai 2007; Díaz López & Mariño 2011).

Influence of marine aquaculture on cetacean ecology and behaviour

The presence of marine aquaculture farms can be detrimental to cetaceans. The physical structure added to the water column in both finfish and shellfish farming may pose an entanglement risk (Díaz López & Shirai 2007). Cetaceans may become entangled in thin ropes and those that are not under tension (e.g. common bottlenose dolphin: Díaz López 2012) (**Figure 1.17a, c**). Baleen whales have been trapped in cages of finfish farms (e.g. humpback whale; Minke whale reviewed in Kemper et al. 2003). The use of anti-predator nets poses also a potential risk of entanglements of both target and non-target species (Würsig & Gailey 2002; Díaz López & Shirai 2007) (**Figure 1.17 d**). Several species of dolphins get regularly entangled in loose anti-predator netting around finfish farms (e.g. common bottlenose dolphin: Díaz López & Shirai 2007; Peale's dolphin, *Lagenorhynchus australis*; Indo-Pacific bottlenose dolphin and short-beaked common dolphin: reviewed in Kemper et al. 2003).

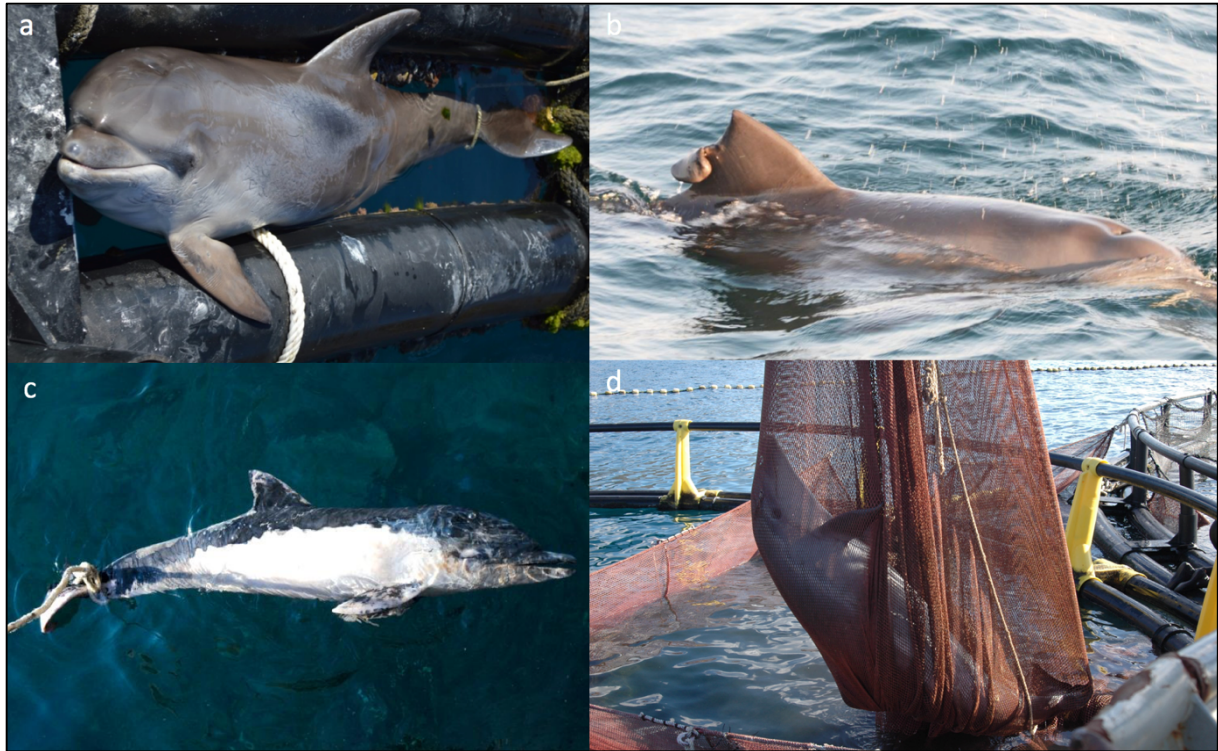


Figure 1.17. Bottlenose dolphins incidentally catch in lines from a finfish cage (a, c), in anti-predator net from a finfish farm (d), and exhibiting a dorsal fin cut probably due to a boat strike (Sardinia, Italy) (source: Bruno Díaz López, BDRI).

The aquaculture industry is responsible for an increase of boat traffic, which in turn alter cetacean diving patterns, respiration rates, and swimming speeds (Constantine et al. 2004). These reactions may cause cetaceans to leave important foraging and breeding areas, which might result in reduced biological fitness from increased energy consumption (Ribeiro et al. 2005). Moreover, the development of boat traffic increases the risk of boat strikes (Donaldson et al. 2010) (**Figure 1.17 b**).

Likewise, the use of acoustic deterrent and harassment devices may not have the intended effect. Several studies suggest that the use of AHD to prevent the depredation from particular target species displaced the regular movement of non-target cetacean species and made former habitat unavailable to them (e.g. killer whales: Morton & Symonds 2002). An additional study reported that AHD does not effectively deter cetacean species, particularly when other motivating factors, such as food, were present (Díaz López & Mariño 2011).

Several studies suggest that the three-dimensional scale of shellfish farming reduces the coastal areas used by cetaceans for potentially important biological and social activities. Multiple species of dolphins, in various locations around the world, appear to avoid areas occupied by shellfish farming, indicating a potentially large impact of this industry on small cetaceans (e.g. Indo-Pacific bottlenose dolphins in Australia: Watson-Capps & Mann 2005; Dusky dolphins, *Lagenorhynchus obscurus*, in New-Zealand: Markowitz et al. 2004; Pearson 2009; Pearson et al. 2012; Chilean dolphins, *Cephalorhynchus eutropia*, in Chile: Ribeiro et al. 2007) (**Figure 1.18**). Würsig & Gailey (2002) suggested that this avoidance may be due to the farm structure inhibiting the dolphin's ability to aggregate fish prey. Likewise, harbour porpoises avoid finfish farms when high disturbance activities occur (food delivery, cage cleaning) (Haarr et al. 2009) and killer whales were displaced from their habitat because of the use of AHD around salmon farms (Morton & Symonds 2002).

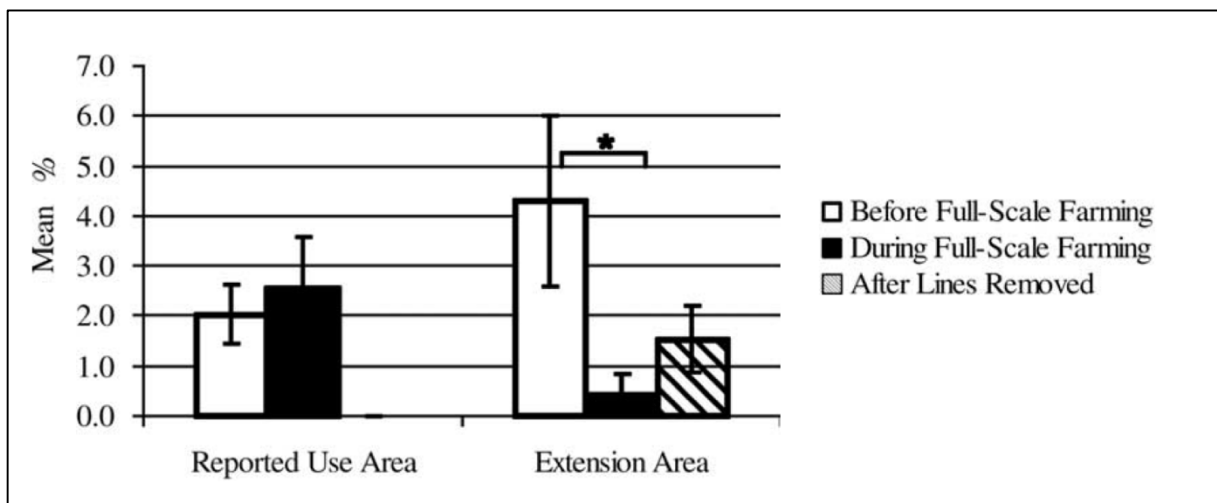


Figure 1.18. Percentage of bottlenose dolphin observations before and during the implementation of oyster farms, and after their removal in Shark Bay (Australia) (source: Watson-Capps & Mann 2005).

Conversely, some cetacean species may be attracted to marine aquaculture farms because of the increased food availability in these areas (Díaz López 2019). As reviewed earlier, the accumulation of nutrients around the marine farms can lead to a concentration of wild fish, which are then available to dolphins (Díaz López 2006a). A series of studies carried out in Sardinia (Italy) revealed that common bottlenose dolphins are attracted to finfish cages because of the presence of both wild and farmed fish (Díaz López 2006a; 2009). Indeed,

bottlenose dolphin occurrence increased in coastal areas after the implementation of a marine finfish farm (Díaz López et al. 2005) and in close proximity to the farms (Bonizzoni et al. 2014). On the contrary, the spatial distribution and habitat use of Chilean dolphin were not influenced by the presence of finfish cages (Ribeiro et al. 2007).

The attraction to marine aquaculture farms induces changes in the abundance, behaviour, and sociality of cetaceans. A longitudinal study revealed a significant upward trend in density of bottlenose dolphins due to the presence of a marine finfish farm (Díaz López 2017; 2019). In several areas, most of the time, dolphins present around marine farms were engaged in foraging activities (e.g. bottlenose dolphin and finfish farms: Díaz López 2012; Chilean dolphin and shellfish farms: Ribeiro et al. 2007). However, marine aquaculture areas are not associated for other important activities such as socialising or resting (Ribeiro et al. 2007; Díaz López 2012). Studies carried out with bottlenose dolphins around finfish farms highlighted that only some individual dolphins exhibit high site fidelity to marine finfish farm areas (Díaz López 2012; Díaz López et al. 2013). These bottlenose dolphins develop specialised feeding strategies for both preying on wild fish present around finfish farm and depredating on farmed fish from the nets (Díaz López 2006a; 2009). Besides, the social interaction between individuals is affected by the presence of aquaculture activities. Different studies found that aquaculture farms affect the level of association between individual dolphins (Díaz López & Shirai 2008; Pace et al. 2011). Therefore, studying the link between marine aquaculture and cetacean behaviour can provide important baseline data, from which effective management and conservation strategies can be designed.

1.4 Objectives and outlines of the thesis

1.4.1 Background context

Given the global expansion of marine aquaculture (i.e. finfish and shellfish farming), interactions between cetaceans and aquaculture are likely to intensify. Therefore, studying the potential influence of aquaculture on cetaceans is essential for the conservation of cetaceans and for an effective management of the aquaculture industry. As reviewed earlier, most of the literature has focused on cetaceans and finfish farming (Díaz López et al. 2005; Díaz López 2006a, 2006b, 2009, 2012, 2017, 2019; Díaz López & Shirai 2007, 2008; Díaz López et al. 2008a; Haarr et al. 2009; Pace et al. 2011; Bonizzoni et al. 2014) and there is a paucity of information on cetaceans and shellfish farming (but see Markovitz et al. 2004; Watson-Capps & Mann 2005; Ribeiro et al. 2007; and Pearson et al. 2012). This is particularly true for common bottlenose dolphins (hereafter referred to as bottlenose dolphin) and shellfish aquaculture, for which no specific study has been carried out.

Having a near shore distribution, bottlenose dolphins (**Figure 1.19**) are particularly likely to interact with human activities (Würsig & Gailey 2002; Bearzi et al. 2009; Díaz López 2019). Bottlenose dolphins show a high behavioural and ecological plasticity that allows them to capitalize on human activities such as gillnet and trawl fisheries, and finfish aquaculture (Chilvers & Corkeron 2001; Díaz López 2006b, 2012; Fertl & Leatherwood 1997). This marine top predator can therefore be used as a suitable model species to gain information about the potential influence of shellfish farming on coastal cetaceans.



Figure 1.19. Bottlenose dolphins between shellfish farms in Galicia, North-West Spain (source: Bruno Díaz López, BDRI).

Bottlenose dolphins are highly vulnerable to a variety of anthropogenic stressors, such as habitat loss and modification (Díaz López 2019), pollution (Tanabe 2002), and incidental takes (Díaz López & Shirai 2007). Atlantic bottlenose dolphins are listed under several conservation agreements and directives: Appendix II of the Convention on the conservation of Migratory Species of wild animals (CMS, also known as the Bonn convention; www.cms.int accessed 15 April 2019); Appendix II (Strictly Protected Fauna Species) of the Convention on the Conservation of European Wildlife and Natural Habitats (Bern convention; www.coe.int accessed 15 April 2019); Agreement on Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas (ASCOBANS; www.ascobans.org accessed 15 April 2019); Agreement on the Conservation of Cetaceans in the Black Sea, Mediterranean Sea and Contiguous Atlantic Area (ACCOBAMS; www.accobams.org accessed 15 April 2019); Annexes II and IV of the European Union's Habitats Directive (Council Directive 92/43/EEC; www.ec.europa.eu accessed 15 April 2019) as a species whose conservation requires the designation of Special Areas of Conservation and in need of strict protection. Studying the ecology of this marine top predator is therefore essential to identify the potential effects of anthropogenic and natural pressures in order to take appropriate conservation and management actions.

Galicia (North-West Spain) has been characterized by ancestral and close interactions between humans and bottlenose dolphins, from peaceful coexistence (humans taking advantage of

dolphins to locate fish schools) to deliberate culling. In 1782, an extensive work about fish and fishing activities throughout Europe (Duhamel du Monceau 1782) mentioned that bottlenose dolphins were most abundant in Galicia. The *Encyclopédie Méthodique* further relates that there were regular observations of bottlenose dolphins in the southern Galician rías (“Rías Baixas”) at the time of writing, yet the number of observations were higher two centuries before (Diderot & D’Alembert 1782-1832). In fact, bottlenose dolphins have been persecuted for centuries in Galicia (Valdes Hansen 2009). The local human population was deliberately killing bottlenose dolphins for several reasons. From the 12th to the 19th century, bottlenose dolphins were used as a source of food and were commonly sold for their meat in Galician public markets (López 2003). Additionally, the spread of hatred towards dolphins among the fishermen can be attributed to the expansion of inshore fishing activities especially since the 16th century, the use of increasingly larger fishing gear, as well as the progressive abandonment of traditional fishing methods since the late 19th and early 20th centuries (Valdes Hansen 2009). Reduced fishery catches were often blamed on bottlenose dolphins, which led to extreme measures. These dolphins were considered detrimental to fishing activities (for scaring schools of sardines and destroying fishing gear) and were killed in retaliation (Valdes Hansen 2009). Up to the middle of the 20th century, local populations were both occasionally killing dolphins (harpooning or firing at dolphins that approached the shoreline or the bow of the boats) and systematically organising extermination campaigns (Valdes Hansen 2004). At the beginning of the 19th century, local population of the Rías Baixas started what was called the “corridas de arroaces” (Valdes Hansen 2004), a hunting technique which consisted of enclosing dolphins with nets (that were spread from one side to the other of a bay) and killing the trapped animals using harpoons (**Figure 1.20**), sticks, stones, and firearms (Valdes Hansen 2004). Likewise, at the end of the 19th century and in the 20th century, local fishermen and patrol boats from the Navy devoted themselves intensively to the culling of bottlenose dolphin, especially in the rías de Arousa and Muros, where dolphins were considered most harmful to fishing activities (“La ilustración gallega y asturiana” 1879, cited in Valdes Hansen 2009). Today, bottlenose dolphins are protected but have to deal with a wider variety of human activities, including the shellfish aquaculture industry, which is one of the major socio-economic benefits to local Galician communities.

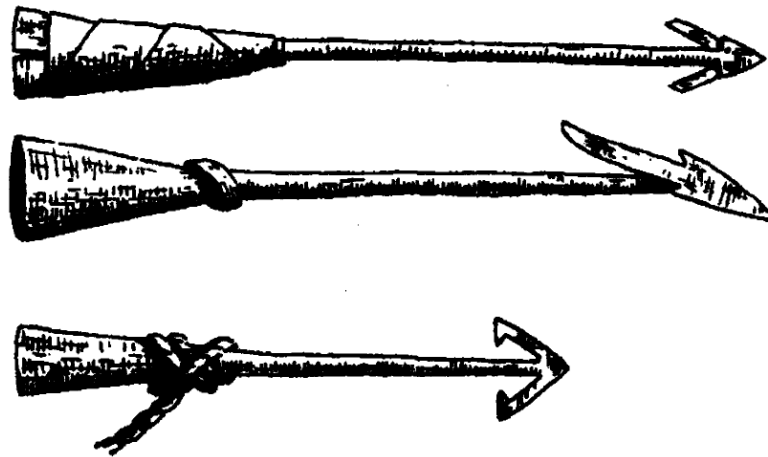


Figure 1.20. Illustration of harpoons used for killing bottlenose dolphins in Galicia (source: Valdes Hansen 2004).

Shellfish farming has occurred in Galician waters since the late 1940s (Miguez et al. 2009) and has developed over the years, making this area the European leader in this sector (FAO 2014). With 13% of the world's mussel production cultured in Galicia every year (FAO 2014), this area is the third most important producer in the world after China and Thailand (Rodriguez et al. 2011). Although bottlenose dolphins are the most common coastal cetaceans in Galician waters (López et al. 2004), few insights into their ecology and behaviour have been gained for this species in these waters. Most studies about bottlenose dolphins in Galician waters were done with data from stranded individuals, and observational data from either land-based or opportunistic platforms (fishing vessels) (López et al. 2002, 2004; Pierce et al. 2010; Fernández et al. 2011a, b, 2013; Spyrakos et al. 2011; Méndez-Fernández et al. 2012, 2013, 2014a, 2014b; Louis et al. 2014; Nykänen et al. 2019). Pierce et al. (2010) therefore mentioned the need for dedicated boat-based surveys to enable the identification of critical areas (such as feeding areas) for bottlenose dolphins and for future studies focusing on bottlenose dolphin interaction with human activities.

The Galician rías, being one of the world's most important areas for shellfish farming and a place where bottlenose dolphins are regularly present (López et al. 2004), exhibit adequate conditions to study the potential influence of shellfish farming on bottlenose dolphin ecology and behaviour. This dissertation therefore investigates the ecology and behaviour of bottlenose dolphins living in an area characterized by intense shellfish aquaculture activities. The work is

mainly based on data collected from 2014 to 2018 by the Bottlenose Dolphin Research Institute (hereafter BDRI). The BDRI is carrying out long-term studies about the ecology of cetaceans in different part of the world (Galician coast, North-West Spain, since 2014: Díaz López et al. 2019; Persian Gulf, United Arab Emirates, since 2014: Díaz López et al. 2018a; Sardinia Island, Italy, 2004-2013: Díaz López 2019) and focuses on understanding the interactions between anthropogenic activities and cetaceans.

1.4.2 Objectives

The general aim of this thesis is to fill a gap of knowledge about the ecology and behaviour of a marine top predator, the bottlenose dolphin, living under the pressure of shellfish farming. This thesis will give baseline information about the abundance and behaviour of bottlenose dolphins in an area subject to significant anthropogenic pressures. By describing and understanding the habitat use, behaviour, and social organisation of bottlenose dolphins in relation to shellfish farming, this work aims at studying the potential influence that this industry may have on this marine top predator. The proposed outcomes of this work are threefold: (i) to provide baseline data, which can be used to inform management agencies on the status of bottlenose dolphins within an area highly affected by human activities, (ii) to further the understanding of the influence of shellfish farming on cetaceans, and (iii) to suggest appropriate management and conservation measures for bottlenose dolphins, as well as regulations for the shellfish farming industry.

The scientific objectives of this thesis are to:

- Estimate the abundance, apparent survival, and temporary emigration rates of bottlenose dolphins in the most important shellfish farming area of Europe by using a systematic, photo-identification sampling design, and robust mark-recapture models. These results will provide important baseline information in an area subject to significant anthropogenic pressures. It will allow for future comparisons with other bottlenose dolphin populations living under the pressure of human activities, such as fisheries and aquaculture (Chapter 3; Methion & Díaz López 2018).

- Investigate the influence of multiple environmental parameters (water temperature, water salinity, chlorophyll-a, and dissolved oxygen) on the fluctuations of bottlenose dolphin group size in a coastal area subject to intense anthropogenic activities. The hypothesis that environmental conditions influence bottlenose dolphin grouping patterns will be tested. These results will provide significant information about the potential vulnerability of this species to environmental changes in coastal ecosystems (Chapter 4; Methion, Díaz López, & Corrège, submitted).

- Investigate the spatio-temporal distribution of bottlenose dolphins and identify the environmental and anthropogenic factors driving bottlenose dolphin habitat use. The hypothesis that shellfish farming, which increase the abundance of fish species relative to adjacent areas, could attract bottlenose dolphins, therefore driving their habitat use, will be tested (Chapter 5; Díaz López & Methion 2017).

- Assess whether the shellfish farming industry influences bottlenose dolphin behaviour. Specifically, the behaviour of bottlenose dolphins inside and outside the shellfish farm areas will be described. Then, environmental and anthropogenic (i.e. shellfish farms) drivers of bottlenose dolphin foraging behaviour will be examined. The hypothesis that shellfish farms, increasing the abundance of fish species within shellfish farm areas relative to adjacent areas, could be an important foraging ground for bottlenose dolphins, will be tested (Chapter 6; Methion & Díaz López 2019a).

- Determine whether individual bottlenose dolphins vary in the frequency with which they use shellfish farms as foraging grounds and evaluate whether this variation is linked to their social organisation. The hypothesis that the concentration of food resources associated with shellfish aquaculture could induce individual foraging variation, with some individuals foraging more regularly within shellfish farms than others, will be tested. Subsequently, another hypothesis stating that this foraging variation could influence bottlenose dolphin social organisation, with weaker associations between individuals showing foraging preferences for higher food availability areas (i.e. shellfish farms), will also be tested. Through this framework, the aim is to further the understanding of individual foraging variation that drives social organisation in a marine top predator (Chapter 7; Methion & Díaz López 2019b).

1.4.3 Thesis structure

This thesis builds on five scientific articles included as distinctive chapters as they independently provide answers to the different objectives of the thesis (**Figure 1.21**). Chapters 3, 5, 6, and 7 correspond to scientific studies that have been published in peer-reviewed journals, and Chapter 4 has been submitted for publication. As there are several authors, “we” is used in these chapters. In Chapter 2 (General methods), the study area, the model species, and the data collection methods are described. Finally, in Chapter 8 (General discussion), the key findings are summarized, and suggestions for appropriate management and conservation measures for bottlenose dolphins, and regulations for the shellfish farming industry are proposed.

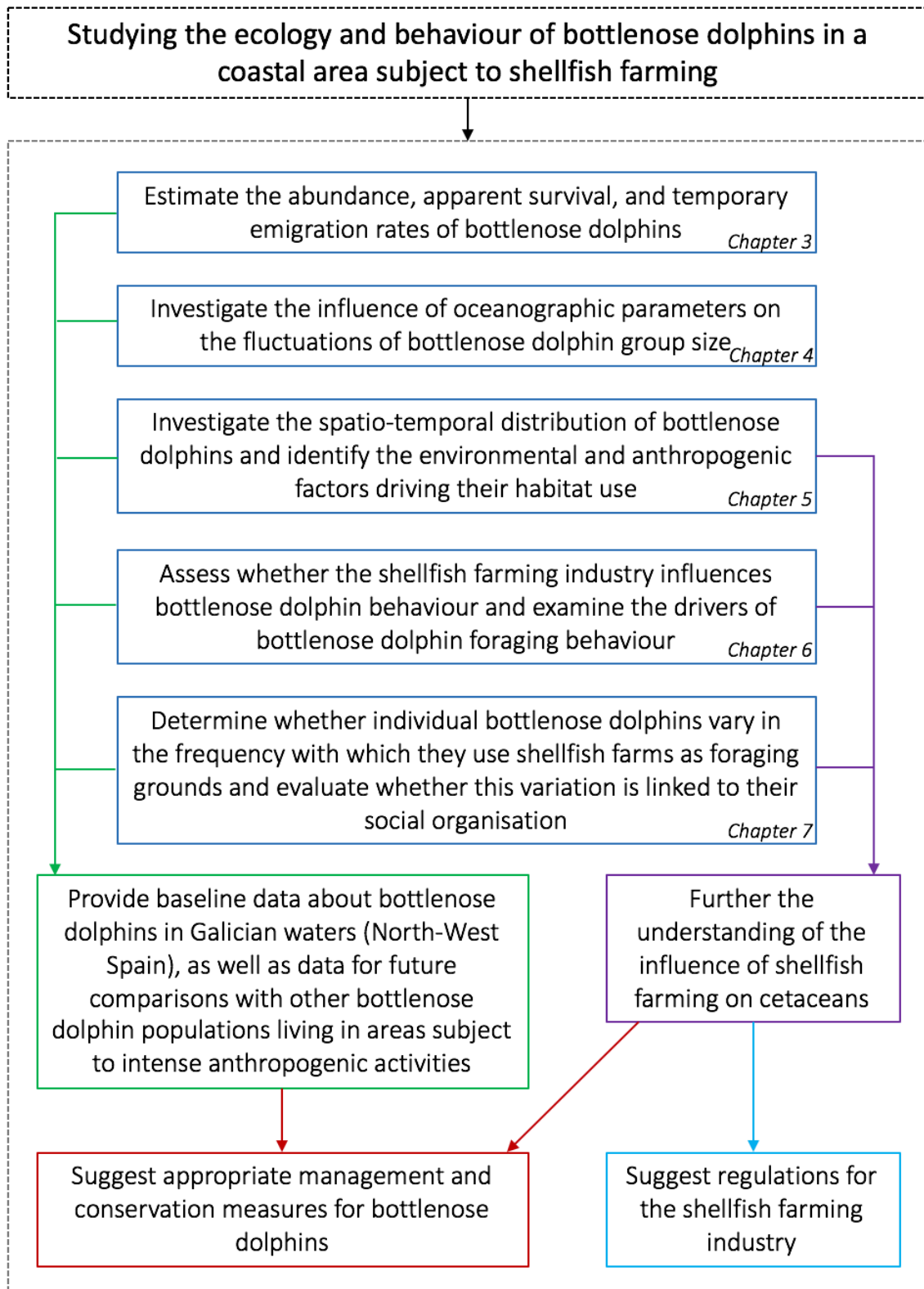


Figure 1.21. Flowchart of the PhD strategy.

Chapter 2. General methods

In this chapter, the study area (the Ría de Arousa, Galicia, North-West Spain) is first described and then the ecology of the model species, the bottlenose dolphin, is reviewed. In the last part of this chapter, the data collection methods are described.

2.1 Study area: the Ría de Arousa (Galicia, Spain)

2.1.1 Environmental characteristics of the study area

The study was performed along the North-Western coast of the Iberian Peninsula (North-West Spain), specifically in the largest of the Galician rías (which are ancient drowned tectonic valleys that were taken over by the sea), the Ría de Arousa (Evans & Prego 2003; Prego et al. 1999). This ría is located between the Ría de Muros-Noia (North) and the Ría de Pontevedra (South) (Figure 2.1).

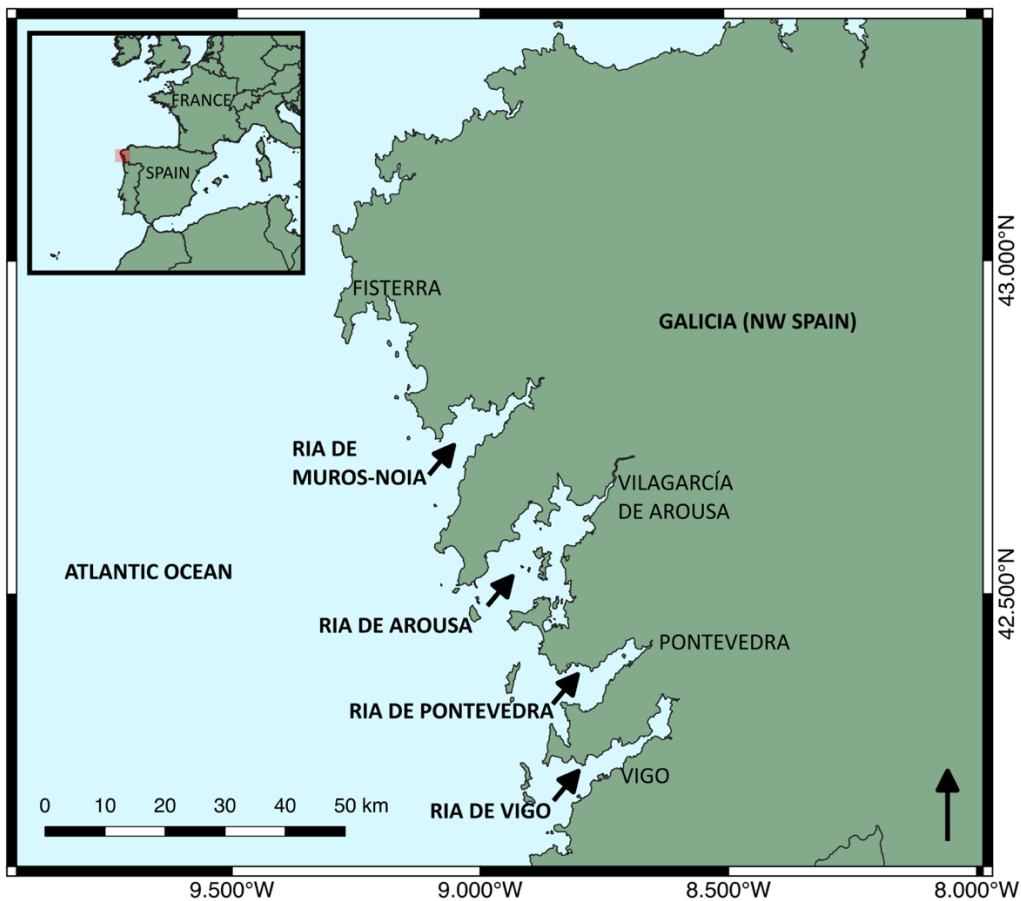


Figure 2.1. Map of the Southern Galician coast (North-West Spain).

Galicia lies at the northern edge of one of the four major upwelling areas in the world: the eastern boundary system off North-West Africa and South-West Europe (North Atlantic Upwelling System) (Bode et al. 2003). In this region, northerly winds that favour upwelling predominate from April to October (Álvarez et al. 2011). During upwelling events, the cold and

nutrient-rich Eastern North Atlantic Central Water (ENACW) moves onshore and upward and surface waters move offshore (Fraga 1981; Alvarez et al. 2005) (**Figure 2.2**). The upwelling events result in nutrient enrichment in coastal waters sustaining a high primary productivity and making this area one of the most productive oceanic regions in the world (Figueiras et al. 2002). The rest of the year, southerly winds that favour downwelling prevail, and warm and salty surface waters of subtropical origin pile on the shelf (Alvarez et al. 2005; Torres & Barton 2007).

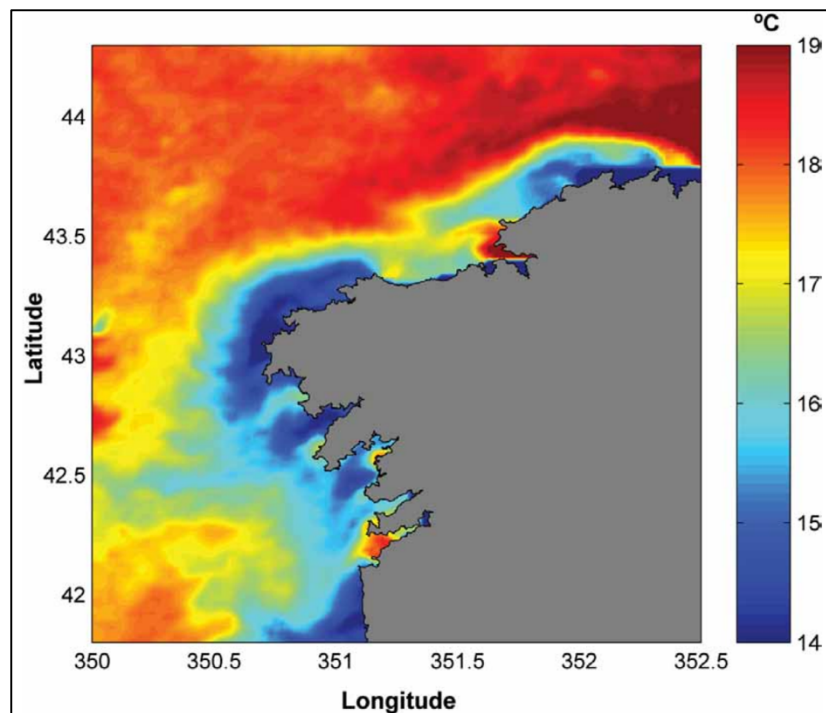


Figure 2.2. Satellite image of sea surface temperature during an upwelling event along the Galician coast (source: Alvarez et al. 2005).

The Rıa de Arousa covers an area of 240 km² and has a length 25 km (Prego et al. 1999; Figueiras et al. 2002) (**Figure 2.3**). The rıa is oriented in a northeast-southwest direction. The topography of the Rıa de Arousa is complex; there are four large islands (Salvora, Arousa, Cortegada, and La Toja), a number of smaller islands and rocks, and several secondary embayments within the rıa (Otto 1975). The average depth of the rıa is 19 m and the maximum depth is 70 m (Lapointe et al. 1981). The rıa is connected to the open sea by two entrances due to the existence of an island (Salvora) situated at the outermost part (Alvarez et al. 2005). The southern mouth width is 4.6 km and 55 m deep, and the northern mouth is 3.7 km, and 5 m deep (Alvarez et al. 2005).

The total volume of the ría is estimated to be about 4.43 km³ (Alvarez et al. 2005). Water circulation in the ría is driven by the tide, wind regime over the continental shelf, wind regime over the ría, freshwater discharge, air temperature, and upwelling events (Otto 1975; DeCastro et al. 2000; Alvarez et al. 2005). The entire system is exposed to a semidiurnal, mesotidal tide regime, varying from 1.1 m during neap tides to 3.5 m during spring tides, respectively (Alvarez et al. 2005). The main freshwater input is located in the innermost part of the ría and comes from two rivers: the Ulla River (river flow = 79.3 m³s⁻¹) and the Umia River (river flow = 16.3 m³s⁻¹) (Alvarez et al. 2005). These rivers show a high seasonal variability in river flow, with the highest value in winter and the lowest in summer, following the rainfall pattern (Alvarez et al. 2005). The ría is divided into zones that show an external oceanic area (exposed to oceanic processes, deeper) and an internal estuarine area with important tidal influence (exposed to fluvial processes, shallower and secluded areas) (Evans & Prego 2003). The ría behaves as a partially mixed estuary with a positive residual circulation where the partial stratification is maintained by the river discharge in winter, and by solar heating and coastal upwelling in summer (Alvarez et al. 2005). The rest of the year, there is a dominance of downwelling conditions (Figueiras et al. 2002), during which warmer, nutrient-depleted surface waters move inshore and downward reducing the strength of exchange flow (Alvarez et al. 2005). Residence time of water in the Ría de Arousa is 5 to 10 days (Alvarez-Salgado et al. 1996).

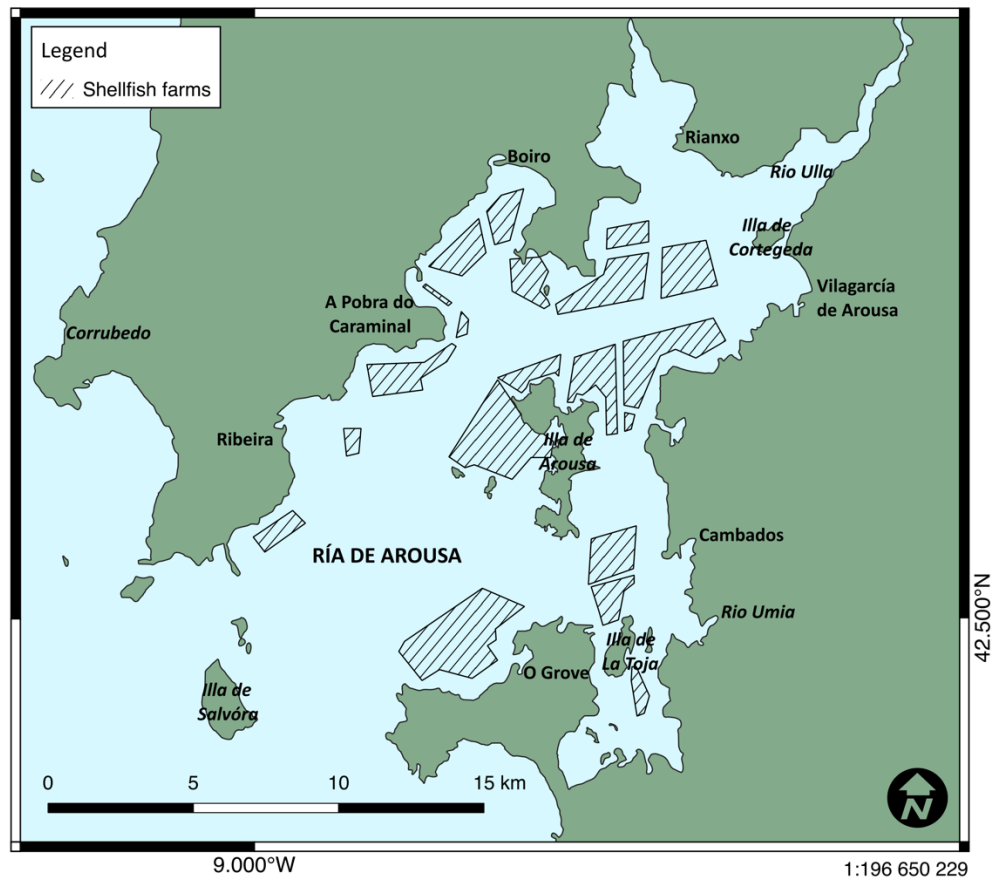


Figure 2.3. Map of the study area, the Ría de Arousa (North-West Spain).

2.1.2 Human activities: importance of shellfish aquaculture

There are 13 main municipalities along the coast of the Ría de Arousa, containing around 180 000 inhabitants (Instituto Español de Estadística 2018, www.ine.es, accessed on 15 April 2019). Owing to the high primary production along this coast, Galicia is an important area for fisheries and shellfish aquaculture, and more specifically for the production of mussels and oysters (Prego et al. 1999). Shellfish production gives employment to 9 000 people directly and to 20 000 indirectly and is, therefore, an activity of great socio-economic importance for the region (Labarta 1999, 2000). Galicia is also the most important fishing region of Spain and one of the most important in the world (López et al. 2003; López et al. 2004). In the Ría de Arousa, there are 12 commercial fishing harbours, which are used by more than 3 000 commercial fishing boats (Instituto Galego de Estatística, www.ige.eu, accessed on 13 May 2019). These boats operate both in inshore and offshore waters, using traps, trawls, gill-nets, and longlines,

and target fish, molluscs, and crustaceans (López et al. 2003). One study estimated that nearly 85% of the biomass of the Ría de Arousa is removed by humans (Outeiro et al. 2018).

Shellfish farming has occurred in Galicia since the late 1940s (Miguez et al. 2009) and has developed over the years, making this area the European leader in this sector (FAO 2014) and the third most important mussel producer in the world after China and Thailand (Fuentes et al. 2000; Rodriguez et al. 2011). Galicia produces an average of 270 000 metric tonnes of Mediterranean mussels (*Mytilus galloprovincialis*) per year (Instituto Galego de Estatística, www.ige.eu, accessed on 13 May 2019), which represent 13% of the world’s mussel production (50% of Europe and 98% of Spain productions) (FAO 2014). In 2017, Galicia produced also around 300 metric tonnes of European flat oysters (*Ostrea edulis*) and 380 metric tonnes of Pacific oysters (*Crassostrea gigas*) (Gobierno de España, Ministerio de agricultura, pesca y alimentación, www.mapa.gob.es, accessed on 13 May 2019). The Ría de Arousa, which is a highly productive coastal ecosystem (Tenore et al. 1995), presents the largest abundance of filter feeders comparing to other estuarine systems, but the ecological carrying capacity of cultured shellfish has been exceeded (Outeiro et al. 2018) (Figure 2.4).

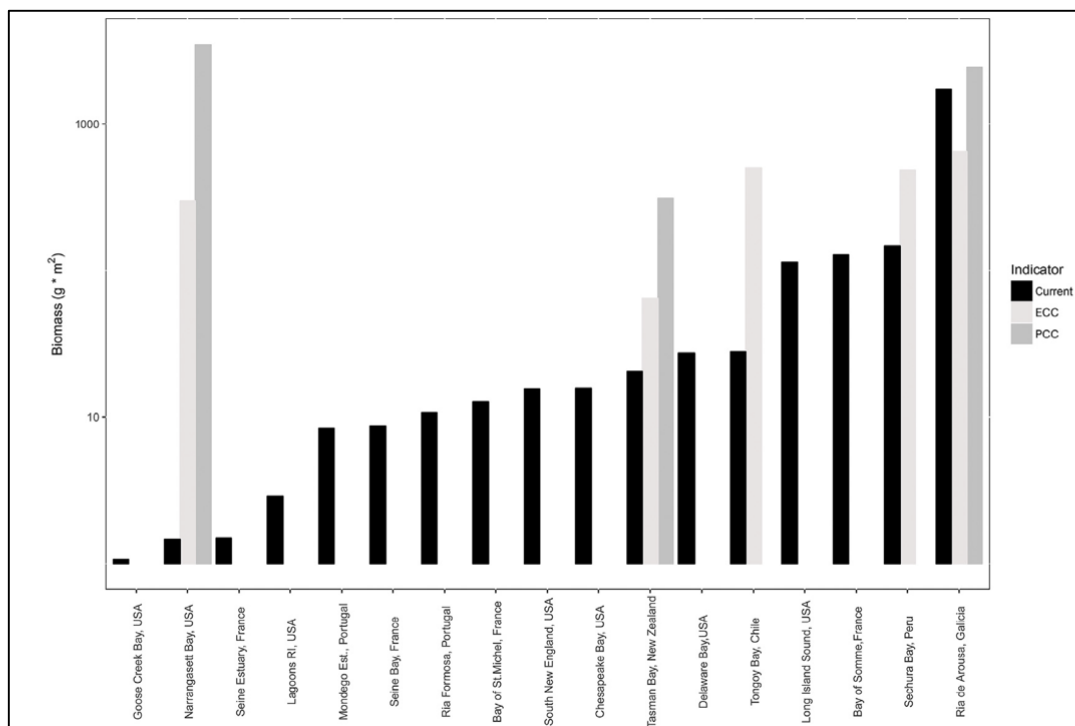


Figure 2.4. Filter feeders’ biomasses and carrying capacity of shellfish aquaculture in coastal ecosystems around the world. ECC: ecological carrying capacity; PCC: production carrying capacity (source: Outeiro et al. 2018).

In Galicia, the shellfish are grown on rectangular floating platforms (named 'batea'), in contrast to other systems of production, such as long-lines or poles (Perez Camacho et al. 1991). The rafts keep afloat with a system of floating devices and keep in place by chains bound to a block of concrete resting on the sea floor. The rafts are configured in a rectangle shape, generally made of wood, and the bivalves are grown on ropes tied to the platforms (**Figure 2.5**) (**Figure 2.6**). Mussels are extracted from natural local populations (from the rocks) and then attached to the ropes. It is forbidden to pick natural mussels from January to June, and the minimum size should be 50 mm (<http://observatorio-acuicultura.es>, accessed on 1 July 2019). Each individual raft has a maximum of 500 ropes (with a length of about 12 m long) and covers an area of up to 500 m² used for shellfish cultivation (Fuentes et al. 2000; Figueiras et al. 2002). The first raft was placed in 1946 in this ría. The number of rafts in Galicia then increased over the years: 400 rafts in 1956, 2537 rafts (including 1 782 in the Ría de Arousa) in 1967, and around 3 300 rafts in 1976. Concession sites became limited in 1976 (<http://observatorio-acuicultura.es>, accessed on 1 July 2019). Today, there are about 3 337 shellfish cultivation rafts in the Galician rías, of which about 70% are situated in the Ría de Arousa (Figueiras et al. 2002).

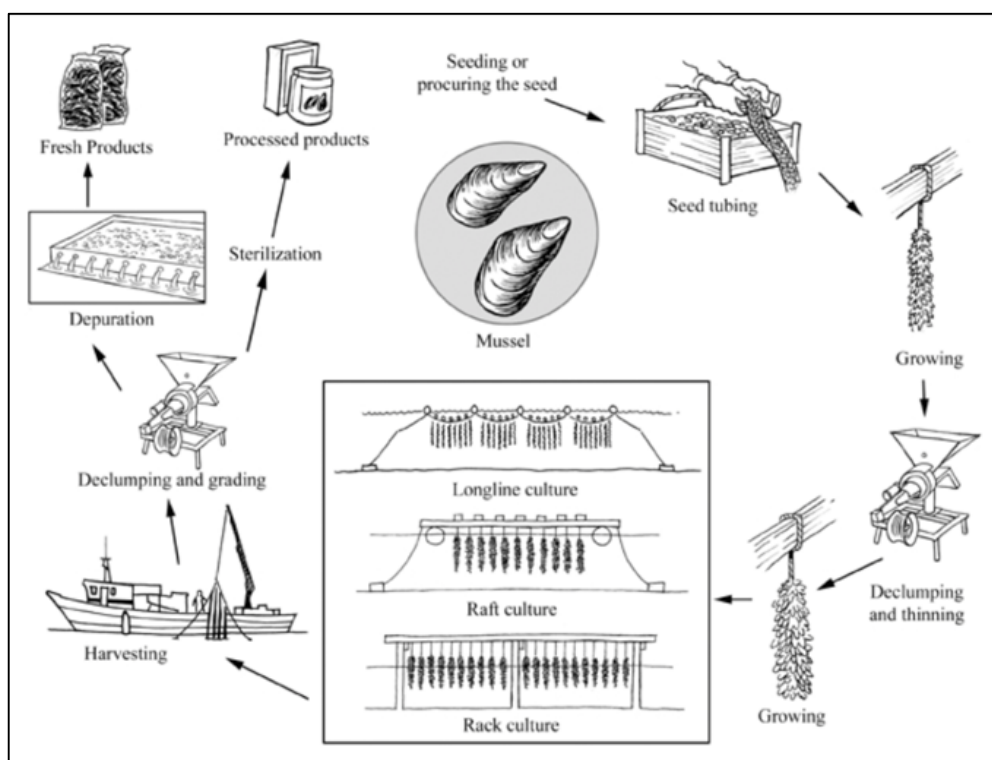


Figure 2.5. Flowchart diagram of mussel aquaculture production on floating rafts (source: FAO 2014).

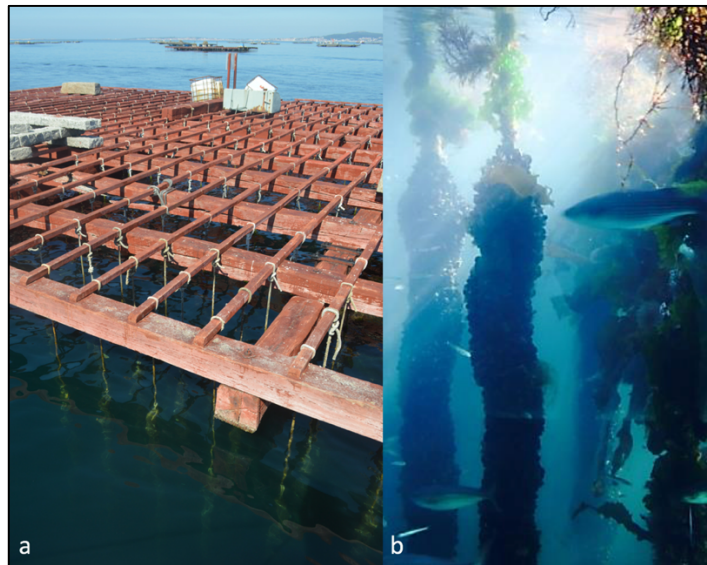


Figure 2.6. Photographs of (a) a floating platform for shellfish cultivation and (b) underwater view of a shellfish platform with ropes where mussels are growing in the Ría de Arousa (source: Séverine Methion).

In the Ría de Arousa, there are around 2 300 shellfish rafts (around 2 100 for mussel production and 200 for oyster production) covering approximately 17% (41 km²) of the total surface of the ría (Figueiras et al. 2002) (**Figure 2.7**). Shellfish culture began in Ría de Arousa in 1946 with rafts of 125 m², each raft having around 500 hanging ropes, 5 m long (Figueiras et al. 2002).



Figure 2.7. Aerial view of shellfish cultivation in the Ría de Arousa (source: Bruno Díaz López).

Shellfish culture causes changes in the structure of the pelagic and benthic food webs in the Ría de Arousa (Tenore et al. 1976). Particularly, the three-dimensional structure of the shellfish rafts, acting as “fish aggregating devices” (Rountree 1989), together with the cascading effect from the presence of an associated high epifaunal and macroalgal biomass (Mckindsey et al. 2011), induce an increase in pelagic and demersal fish species abundance and biomass in the immediate vicinity and inside of shellfish aquaculture zones (Chesney & Iglesias 1979).

In Galicia, shellfish farming and aquaculture is managed by national and regional authorities. The raft technology used for shellfish farming is subject to certain regulatory limits in terms of size and density of production (www.xunta.gal accessed 1 July 2019). The government of Galicia does not grant authorization for the implementation of new rafts, and shellfish farming is dominated by small-scale (one or two rafts) family-owned farms (Rodríguez Rodríguez 2009).

2.2 The common bottlenose dolphin (*Tursiops truncatus*)

2.2.1 Systematic and general appearance

The common bottlenose dolphin (*Tursiops truncatus*, Montagu 1821, hereafter bottlenose dolphin) belongs to the mammalian order of Cetacea, sub-order Odontoceti, and family Delphinidae (Jefferson et al. 2015). Bottlenose dolphins are recognizable by their robust body, a sharp demarcation between the melon and a short rostrum, a high and falcate dorsal fin, and countershading which results in a dark skin colouration, ranging from a dark grey on the upper side to a pale cream on the underside of the body (Wells & Scott 2009) (**Figure 2.8**). Colouration varies individually, but also geographically, with some individuals all grey and other having a whiter belly or darker cape (Jefferson et al. 2015). The length of adults can range from 2.5 m to about 4.1 m, and varies with the geographic location (bottlenose dolphins are usually larger in colder water temperatures) (Wells & Scott 2009). The body weight varies from 150-650 kg (Jefferson et al. 2015). Bottlenose dolphins exhibit sexual dimorphism in body length and mass, which vary with geographical location (males are typically larger than females) (Tolley et al. 1995). Variation in size, colouration, and cranial characteristics are also attributed to differences between bottlenose dolphin ecotypes ('coastal' vs. 'pelagic') (Wells & Scott 2009).



Figure 2.8. A common bottlenose dolphin, *Tursiops truncatus* (source: NOAA fisheries, www.fisheries.noaa.gov, accessed 1 July 2019).

2.2.2 Life history

Female bottlenose dolphins may live more than 50 years and males more than 40 years (Wells & Scott 2009). Females become sexually mature at five to thirteen years of age and males at nine to fourteen (Wells & Scott 2009). The gestation period is 12 months and a female give birth to a single offspring that remains with its mother for several years (from two to eleven years) (Connor et al. 2000). Calves typically nurse up to age to three to six (Wells & Scott 2009). Interbirth interval with surviving calves varies from two to six years (Connor et al. 2000).

2.2.3 Distribution

Bottlenose dolphins are found in temperate and tropical marine waters around the world (**Figure 2.9**), and inhabit a wide range of habitats due to their behavioural plasticity (Connor et al. 2000). They adapt to a variety of marine and estuarine habitats, and frequently enter harbours, bays, lagoons, and rivers (Connor et al. 2000). Bottlenose dolphins can have a coastal distribution ('coastal' ecotype; also sometimes referred to as 'inshore'), but are also found in pelagic waters, near oceanic islands, and over the continental shelf, especially along the shelf break ('pelagic' ecotype; also sometimes referred to as 'offshore') (Leatherwood & Reeves 2012). Limits to the species' range appear to be temperature related, either directly or indirectly, through the distribution of their prey (Leatherwood & Reeves 2012). The coastal ecotype often exhibits high site fidelity for coastal areas with high prey availability and protection from predators (e.g. Di Giacomo & Ott 2017; Vermeulen et al. 2017). In contrast, pelagic bottlenose dolphins generally undertake large seasonal movements (e.g. Wells et al. 1999).

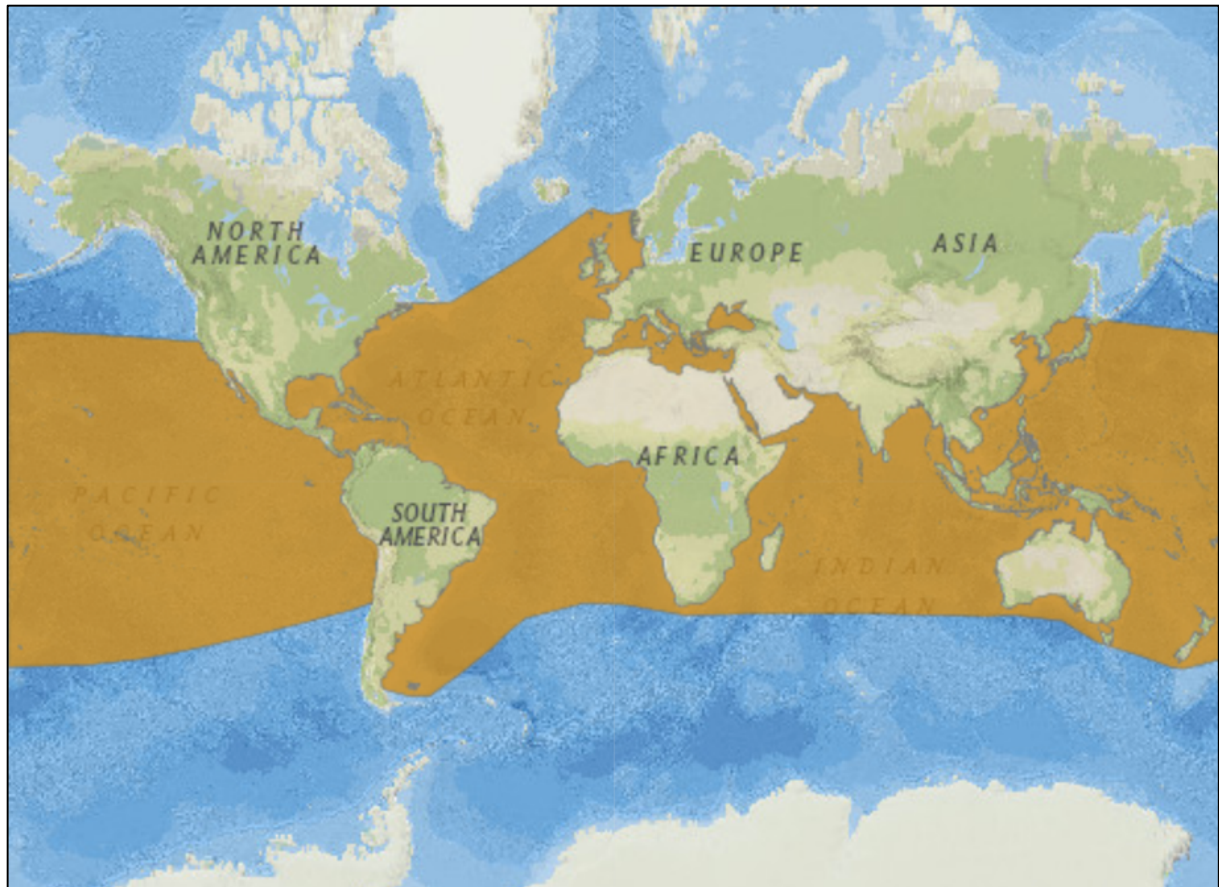


Figure 2.9. Geographic range of the common bottlenose dolphin (source: Wells et al. 2019).

2.2.4 Diet and foraging behaviour

Bottlenose dolphins feed on locally abundant prey species, mainly demersal and pelagic fish (e.g. Scombridae, Congridae, Merluccidae, Gadidae, Clupeidae, and Salmonidae; around 98% of the diet), and cephalopods (sepiida, squids, and octopus; around 2% of the diet) (Blanco et al. 2001; Santos et al. 2001, 2007).

The bottlenose dolphin is an opportunistic species that is capable of developing, over its range, a multitude of adaptive strategies. These include specialised feeding techniques, which involve a high degree of diet flexibility, social organisation, and behavioural adaptation (Connor et al. 2000; Díaz López & Shirai 2008; Díaz López 2012, 2019). Foraging behaviour is driven by multiple physiological, morphological, environmental, and cultural factors, and differs in different parts of its range and among individuals of the same population (Díaz López 2009; Torres & Read 2009). Bottlenose dolphins may appear to be generalists with regards to prey,

but there is evidence of intra-specific variation in foraging behaviour and dietary preferences, with individuals within a population exhibiting some degree of specialisation (e.g. Gazda et al. 2005). Foraging specialisation may reflect increased experience, improved diving and prey catching abilities, and can also be related to increased stomach capacity (Fernández et al. 2011a).

Bottlenose dolphins exhibit a high behavioural and ecological plasticity that allows them to live in coastal areas with human activities (Díaz López 2006b, 2019; Bearzi et al. 2009). They were well known to both ancient Romans and Greeks for their interaction with fishermen. Pliny the Elder (32-79 AD), and a number of other ancient writers for other localities along the Mediterranean Sea, described the interaction between bottlenose dolphins and fishermen, in which both humans and dolphins were catching fish together (Pliny the Elder “Natural History” vol. IX, verses 9 Perseus Digital Library 2017, www.perseus.tufts.edu, accessed 24 April 2019; Montgomery 1966). Today, bottlenose dolphins continue to take advantage of human activities to facilitate prey capture in a variety of ways.

In different parts of the world, bottlenose dolphins interact with gillnet and trawl fisheries, and finfish aquaculture (Fertl & Leatherwood 1997; Chilvers & Corkeron 2001; Noke & Odell 2002; Díaz López, 2006b; 2012) (**Figure 2.10**). In Mauritania and Brazil, bottlenose dolphins regularly drive schools of mullet (*Mugil* spp.) toward fishermen wading with nets in shallow water (Simões-Lopes et al. 1998). Likewise, bottlenose dolphins regularly forage around commercial trawling gear, crab traps, or recreational fishing gear (Wells & Scott 1999). They collect discarded fish from behind trawlers and small purse seines (Chilvers & Corkeron 2001; Bearzi 2009), or eat netted fish from various types of fishing gears (e.g. gillnet fisheries: Reeves et al. 2001; Read et al. 2003; Díaz López 2006a). Fisheries provide a reliable food source for dolphins through the agglomeration of prey (Díaz López 2006b). Even through the sounds of fishing boat engines, food patches created by fishing boats are detectable by dolphins over kilometres (Chilvers & Corkeron 2001). Bottlenose dolphins have also been documented regularly interacting with finfish aquaculture (e.g. Díaz López et al. 2005; Díaz López 2006a, 2006b, 2009, 2012, 2017, 2019; Díaz López & Shirai 2007, 2008; Díaz López et al. 2008a; Pace et al. 2011; Bonizzoni et al. 2014). Studies suggest that bottlenose dolphins feed more efficiently in areas with a high concentration of prey around finfish cages, allowing them to shorten their dive time.

Consequently, this gives them more flexibility with speed and swimming mode as a result of higher oxygen availability (Díaz López 2009). In this way, dolphins reduce the proportion of time spent searching for food and increase the quantity of food consumed (Díaz López 2012).



Figure 2.10. Bottlenose dolphins interacting with a fishing boat in Galicia (source: Bruno Díaz López, BDRI).

2.2.5 Predators

Bottlenose dolphins have few predators. The most important predators of bottlenose dolphins are sharks (e.g. silky shark, *Carcharchinus falciformis*; bull shark, *Carcharhinus leucas*; tiger shark, *Galeocerdo cuvier*; great white shark, *Carcharodon carcharias*; and dusky shark, *Carcharhinus obscurus*), although they may occasionally be preyed upon by killer whales (Wells & Scott 2009). In the North-East Atlantic, bottlenose dolphins are thought to live relatively free from shark predation, unlike bottlenose dolphins in warmer waters (Wells & Scott 2009).

2.2.6 Social ecology

Bottlenose dolphins are complex social animals often found in groups of varying size (Wells & Scott 2009). Average group size for coastal bottlenose dolphins ranges from 4-20 individuals, although agglomerations of several hundred have been reported (Connor et al. 2000). Groups form and split on a daily basis, over the course of few hours ('fission-fusion society') (Connor et al. 2000). Fission-fusion grouping pattern reflects a requirement to spread out to reduce

feeding competition during periods of low resource availability and enhance cooperative effects through group cohesion when the ecological costs of aggregating are low (Chapman 1990; van Schaik 1999). The group composition of bottlenose dolphins is very dynamic (Connor et al. 2000; Wells & Scott 2009). Bottlenose dolphins exhibit long-term and stable social bonds (Connor et al. 2000). Social organisation in bottlenose dolphin species varies between locations and depends on access to resources (Gowans et al. 2007), predation risk (Heithaus & Dill 2002), mating access (Möller et al. 2001), foraging specialisation (Díaz López & Shirai 2008) (Figure 2.11), sex (Diaz-Aguirre et al. 2018), and kinship (Wiszniewski et al. 2010).

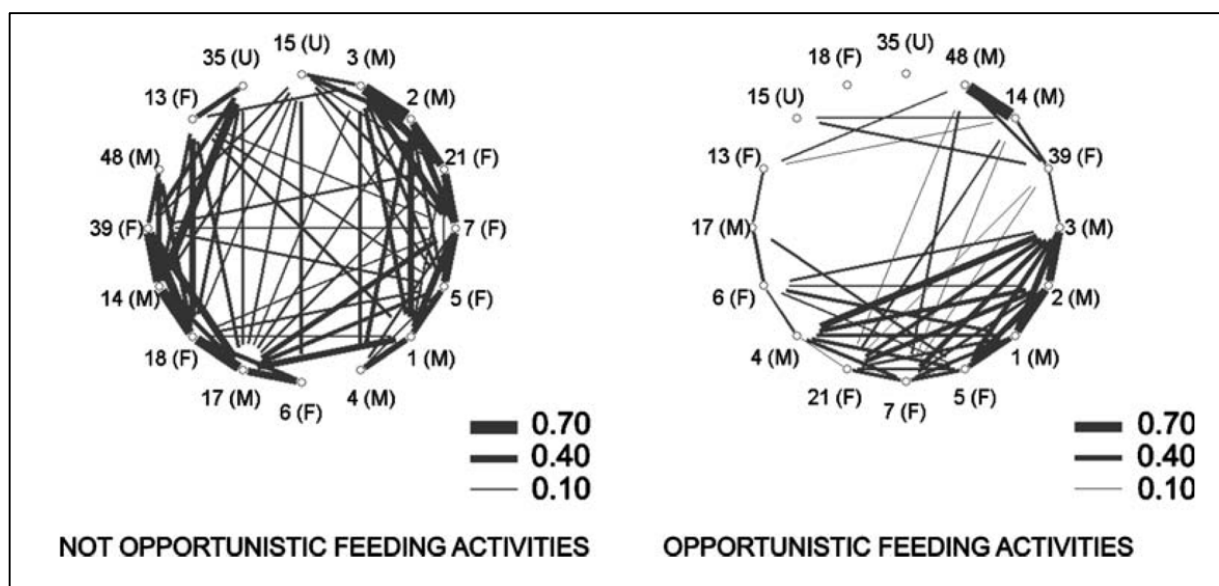


Figure 2.11. Associations between bottlenose dolphins during different feeding activities in Sardinia (Italy) (source: Díaz López & Shirai 2008).

2.2.7 Threats

Having a near-shore distribution, coastal bottlenose dolphins are exposed to numerous threats such as marine traffic (Constantine et al. 2004), fisheries (Read 2008), aquaculture (Díaz López 2012), pollution (Tanabe 2002), the effects of global warming (Simmonds & Isaac 2007), and habitat modification (Lotze et al. 2006).

Considerable incidental mortality of bottlenose dolphin is known to occur throughout the species' range, through entanglement (including in bottom-set gillnets, drift nets, purse seines, trawls, longlines, and antipredator nets), hooking, and ingestion of debris (i.e. fishing gear, plastic) (Wells et al. 1998; Díaz López & Shirai 2007; Wells et al. 2008). Bottlenose dolphins interacting with human activities (e.g. fisheries, aquaculture, or conditioned to receive food) are more likely to be injured, leading to decreased survival (Bedjer et al. 2006; Donaldson et al. 2010).

Bottlenose dolphins suffer mortality and serious injury from collisions with boats (Wells et al. 2008). The literature suggests that with long-term exposure, bottlenose dolphin relative abundance declined with increased marine traffic (e.g. dolphin-watching tours: Bedjer et al. 2006), and that their diving patterns (Nowacek et al. 2001) and communication may change in the presence of vessels (Buckstaff 2004).

Habitat alteration is known to affect bottlenose dolphin ecology. For example, the implementation of aquaculture farms, land reclamation, dredging, and demolition associated with marine construction and other forms of habitat modification (including anthropogenic noise) have been demonstrated to temporarily displace bottlenose dolphins from their habitat (Buckstaff et al. 2013; Pirodda et al. 2013).

Environmental contaminants can result in a decline in bottlenose dolphin survival (Lane et al. 2015), immune function (Lahvis et al. 1995), and reproductive success (Kellar et al. 2017). First-born calves receive 80% of their mother's body contaminant residues (polychlorinated biphenyls (PCB) and dieldrin), perhaps leading to increased neonatal mortality (Schwacke et al. 2002). Jepson et al. (2016) reported that bottlenose dolphins in Europe had mean PCB concentrations that greatly exceeded all known marine mammal PCB toxicity thresholds (**Figure 2.12**).

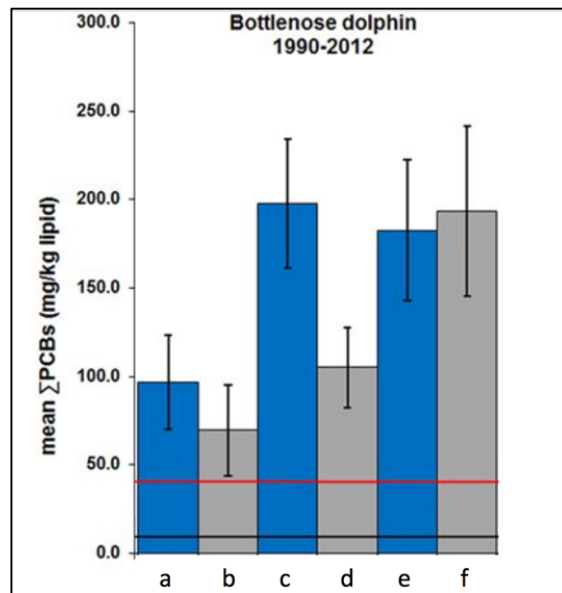


Figure 2.12. Mean PCBs concentrations in bottlenose dolphins in European waters.

The blue bars are males and the grey bars are females. a-b: UK & Ireland; c-d: Iberian Atlantic; e-f: western Mediterranean. The lower line is the equivalent Σ PCBs concentrations threshold (9.0mg/kg lipid) for onset of physiological effects in experimental marine mammal studies. The upper line is the equivalent Σ PCBs concentrations threshold (41.0mg/kg lipid) for the highest PCB toxicity threshold published for marine mammals based on marked reproductive impairment in ringed seals in the Baltic Sea. Error bars=1 Standard Error of the Mean (adapted from Jepson et al. 2016).

Direct takes of bottlenose dolphin occurred, and still occur, in many parts of the world (e.g. Peru, Sri Lanka, Faroe Islands, and Japan) for human consumption, bait, public display, research, and military application (Wells & Scott 2018). Bottlenose dolphins are also killed by fishermen to prevent damage to their fishing gear, or stealing of the catch or bait (Leatherwood & Reeves 2012).

2.2.8 Conservation

Although there are many threats operating on local populations, bottlenose dolphin is widespread and there are an estimated 600 000 individuals worldwide. Therefore, the bottlenose dolphin is classified by the IUCN as “Least Concern” (Wells et al. 2019). Yet, specific populations living under high human pressure might be considered threatened. For example, the bottlenose dolphins from the Mediterranean Sea have been classified as “Vulnerable” by the IUCN because of decades of intentional killing and ongoing threats including incidental

mortality in fishing gear, reduced availability of prey caused by overfishing, and environmental degradation (Bearzi et al. 2009).

Atlantic bottlenose dolphin populations are listed under several conservation agreements and directives as reviewed in Chapter 1. Both the coastal and pelagic ecotypes are present in the North-East Atlantic (Louis et al. 2014). As coastal environments are under increasing anthropogenic pressures, coastal bottlenose dolphins require conservation policies to preserve their habitats.

2.2.9 Bottlenose dolphins in Galician waters

Bottlenose dolphin is the most frequently cetacean species sighted in Galician coastal waters, particularly in the Galician rías (Fernández-Cordeiro et al. 1997; López et al. 2004; Pierce et al. 2010) (Figure 2.13).

Species	Presence	Number	SPUE (n/h)
All species	0.187	2.693	4.317
<i>Tursiops truncatus</i>	0.107	1.273	2.113
<i>Delphinus delphis</i>	0.037	1.292	2.009
<i>Phocoena phocoena</i>	0.016	0.046	0.067
<i>Globicephala melas</i>	0.002	0.019	0.026
<i>Grampus griseus</i>	0.004	0.013	0.025
Unidentified cetaceans	0.045	0.010	0.069

Figure 2.13. Overall sightings rates of cetaceans along the Galician coast from 2003 to 2007.

Presence: proportion of observation periods during which cetaceans were seen. SPUE: Sighting Per Unit of Effort (source: Pierce et al. 2010).

This species is also sighted in offshore Galician waters (López et al. 2004; Díaz López & Methion 2018), which might be individuals from the pelagic ecotype (Spyrakos et al. 2011). Indeed, two studies demonstrated the existence of ecological and genetic differences between bottlenose dolphins stranded in southern Galician rías (suggested as the coastal ecotype) and those stranded elsewhere (Fernández et al. 2011a, b). Likewise, another study suggested that the variability in isotope ($\delta^{13}\text{C}$) values found in stranded bottlenose dolphins could reveal the presence of both coastal and pelagic bottlenose dolphins in Galicia (Méndez-Fernández et al. 2012, 2013).

In coastal Galician waters, bottlenose dolphins appear to be associated with productive areas (areas with higher chlorophyll-a concentration) and a wide continental shelf (Pierce et al. 2010). A study carried out in 1998–1999 from opportunistic platforms (i.e. fishing vessels) suggested that there were between 600 and 1 000 bottlenose dolphins in Galician waters (including both pelagic and coastal bottlenose dolphins) (López et al. 2004). Yet, these estimates were derived from data on relative abundance, and the authors mentioned the need of robust estimates.

Bottlenose dolphins in Galician waters have a varied diet that includes 23 families of fish (98% of the diet) and 12 species of cephalopods (2% of the diet). Their main prey (numerically and in terms of biomass) seems to be blue whiting (*Micromesistius poutassou*), European hake (*Merluccius merluccius*), grey mullet (*Mugil cephalus*), Atlantic horse mackerel (*Trachurus trachurus*), and conger eel (*Conger conger*) (data obtained from stranded individuals of unknown origin) (Santos et al. 2007; Fernández et al. 2011a) (**Figure 2.14**).

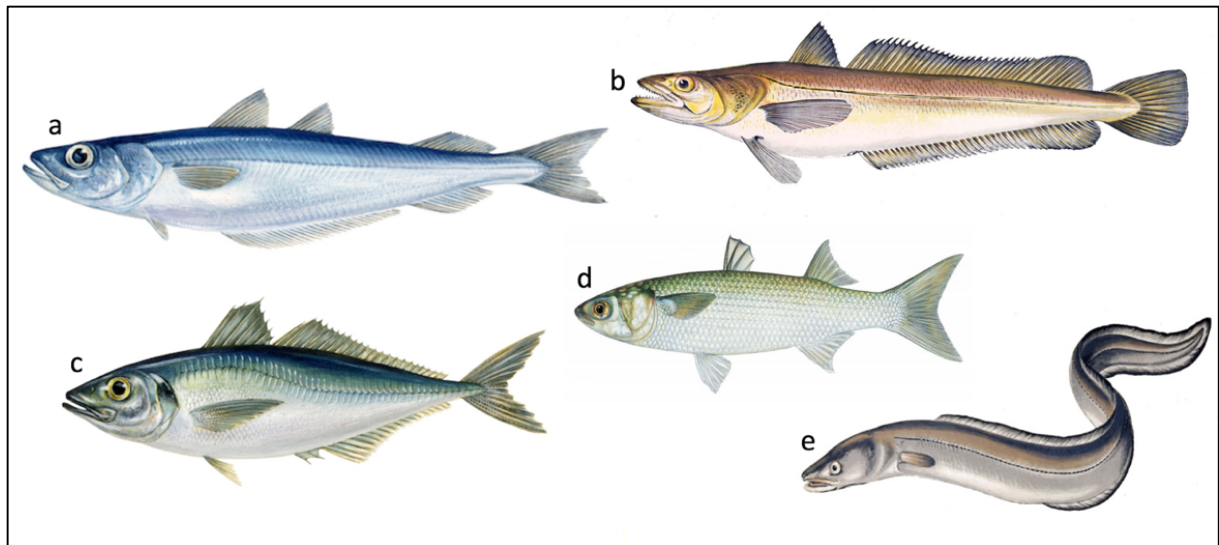


Figure 2.14. Most common prey species of bottlenose dolphins in Galician waters.

(a) Blue whiting, (b) European hake, (c) Atlantic horse mackerel, (d) grey mullet, and (e) conger eel (sizes of the fish are not proportional) (adapted from Gervais & Boulart 1877).

Studies suggested that there are low levels of genetic diversity in Galician bottlenose dolphins, meaning that, despite the lack of physical barriers, gene flow with adjacent sites might be restricted (Fernández 2011b; Nykänen et al. 2019). Bottlenose dolphins are vulnerable to a number of human impacts that affect coastal areas throughout the Atlantic coastline such as marine traffic, by-catch (López et al. 2003), overfishing (Freire & García-Allut 2000), and oil spills (Vieites et al. 2004). In Galicia, bottlenose dolphins are strongly associated with depredation and gear damage, particularly for set gillnets (Goetz et al. 2014). Studies suggested that between 53 and 136 bottlenose dolphins are by-caught every year in Galician waters (in set gillnets and trawl fisheries) (López et al. 2003; Goetz et al. 2014) and around 14% stranded bottlenose dolphins recorded in Galicia show evidence of by-catch mortality (López et al. 2002, 2003). High level of PCBs, mercury, and cadmium were also found in stranded individuals, which exceeded the toxic threshold of $17 \mu\text{g g}^{-1}$ lipid weight (PCBs Aroclor equivalent) for health effects on marine mammals (Méndez-Fernández et al. 2014a, b).

In Spanish waters, the bottlenose dolphin is listed in the 'Listado de Especies Silvestres en Régimen de Protección Especial' (Real Decreto 139/2011; www.boe.es, accessed on 15 May 2019) and classified as 'Vulnerable'. A royal decree (Real Decreto 1727/2007; www.boe.es, accessed on 15 May 2019) controls all marine activities, especially the behaviour of recreational boats, restricting the approach of boats with engines to any cetacean species.

2.3 Data collection and analysis

The data used in the following chapters were obtained in different ways. Presence-absence, behavioural, and mark-recapture data of bottlenose dolphins, along with environmental variables (2.3.1.1) were collected on-board the Bottlenose Dolphin Research Institute (BDRI)'s research vessel. Additional data were obtained from mark-recapture analysis (2.3.2), external repositories (2.3.3), and GIS (2.3.4), and were then linked to the data collected on-board.

Data were subsequently analysed through the use of different methods and software, depending on the objective of each study presented in this thesis. The collected and obtained data were reviewed and entered in a database in the software Microsoft Access (www.microsoft.com). All GIS analyses were performed with the software QGIS (QGIS Development Team 2016) (www.qgis.org) (Chapters 2, 3, 4, 5, 6, 7, and 8) (2.3.4). Statistical analyses were carried out with the software R (R Development Team 2011) (Chapters 3, 4, 5, 6, and 7). The software DARWIN was used for the matching of the individual bottlenose dolphins (Hale 2008) (Chapters 3 and 7). Abundance estimates, survival, and temporary emigration rates were calculated with the software MARK (White & Burnham 1999) (Chapter 3). Analyses of social structure were performed with the software SocProg (Whitehead 2008) and Netdraw (Borgatti et al. 2002) (Chapter 7).

In the following section, the techniques used to obtain the data are described. Details on statistical analysis are described in each corresponding chapter of the thesis.

2.3.1 Data collection from boat-based surveys

The main focus of the field trips was to obtain accurate presence-absence, behavioural, and mark-recapture data of bottlenose dolphins, by recording their behaviour for an extended period of time (> 20 min; focal group-follow: Mann 1999) and identifying the highest number of individuals present in each group in order to minimize the heterogeneity in capture probability (Pollock 1982).

Environmental variables (2.3.1.1) were also collected during each survey to be used as explanatory variables of bottlenose dolphin presence-absence, grouping dynamics, behaviour, and sociality.

Systematic boat-based surveys were conducted with the BDRI research vessel monthly, from March 2014 to November 2018 in the Ría de Arousa (Galicia, Spain). The research vessel is a 12 m long fly-bridge motor boat with two inboard engines (**Figure 2.15**).



Figure 2.15. Research vessel used for the data collection (source: Séverine Methion, BDRI).

The surveyed area and the daily tracks were designed to cover all parts of the study area equally, every month, although the geographic distribution of effort could vary according to weather conditions and time constraints.

As the visual detection of highly mobile marine species, such as the bottlenose dolphin, may be difficult because they spend short periods of time at the surface, distinction between true absences (i.e. when bottlenose dolphins are not present in the sampled location) and false absences (i.e. when bottlenose dolphins are present but could not be detected) can be challenging (Praca & Gannier 2008; Elith & Leathwick 2009). In order to maximise the detection of bottlenose dolphins, boat surveys were therefore carried out during daylight hours, at a constant speed of 6 kn, when the sea conditions were no greater than 3 on the Douglas sea force scale (approximately equivalent to the Beaufort wind force scale), and visibility was not reduced by rain or fog.

During the surveys, at least three experienced observers were stationed on the flying bridge (4 m above sea level), scanning 360 degrees of the sea surface in search of bottlenose dolphins (with the naked eye or 10 x 50 binoculars) (**Figure 2.16**). The minimum number of observers and vessel speed remained consistent during the study period, making data suitable for comparative analysis.



Figure 2.16. Observers onboard the research vessel, scanning the sea surface in search of bottlenose dolphins (source: Séverine Methion, BDRI).

2.3.1.1 Instantaneous point sampling

On each survey, a suite of variables (**Table 2.1**) was recorded as an instantaneous point sample every 20 minutes (hereafter '20-min sample'; Díaz López 2017). These 20-min samples were used to summarize field conditions and distribution of the survey effort, irrespective of bottlenose dolphin presence (Díaz López 2017). The spatial resolution of these 20-min samples was 2 nm (given a speed of 6 kn).

These variables were selected because they were considered to have potential ecological significance (based on a priori investigation of the literature; Pierce et al. 2010; Blasi & Boitani 2012; Carlucci et al. 2016; Pitchford et al. 2016).

Table 2.1. List of variables collected every 20 minutes during each boat survey.

<i>Variable (unit)</i>	<i>Procedure</i>
<i>Date</i>	GPS-Plotter Map Sounder
<i>Time (UTC)</i>	GPS-Plotter Map Sounder
<i>GPS position (UTM)</i>	GPS-Plotter Map Sounder (UTM longitude and UTM latitude, WGS 84 UTM Zone 29N)
<i>Vessel speed (kn)</i>	GPS-Plotter Map Sounder
<i>Depth (m)</i>	Echo-sounder 83-200 kHz
<i>SST (°C)</i>	GPS-Plotter Map Sounder
<i>SSS (PSU)</i>	Portable refractometer
<i>Wind speed (m/s)</i>	Cup anemometer (4 m above the sea level, with research vessel stationary)
<i>Wind direction (degrees)</i>	Compass
<i>Searching effort (On/Off)</i>	On effort, searching for bottlenose dolphins, on the predetermined track; Off effort, not searching for bottlenose dolphin, out of the predetermined track
<i>Presence of bottlenose dolphins (Yes/No)</i>	Presence of bottlenose dolphins within a 1 nm radius of the research vessel position
<i>Type and number of boats</i>	Number of recreational, fishing, and shellfish farm boats, within a 1 nm radius of the research vessel position

Wind speed was used as a measure of the sea conditions to account for sampling bias and error (Díaz López 2017). Presence-absence of bottlenose dolphins was recorded using one-zero sampling (Altmann 1974).

2.3.1.2 Bottlenose dolphin sighting

A group of bottlenose dolphins was defined as one or more individuals observed within a 100-m radius, and if more than one, interacting with each other, and engaging in the same behavioural activity.

Upon sighting a group of bottlenose dolphins (a ‘sighting’), searching effort (on-effort time) ceased and the vessel slowly manoeuvred towards the group (off-effort time) in order to not alter their behaviour during the approach.

All sightings continued until the group composition changed, the group was lost, or until weather conditions became unfavourable (Douglas > 3, rain, or fog). At the end of a sighting, the search effort generally continued along the previously planned route.

On each bottlenose dolphin sighting, a suite of data (**Table 2.2**) was collected.

Table 2.2. List of variables recorded during a sighting of bottlenose dolphin.

<i>Variable (unit)</i>	Frequency of recording	Procedure
<i>Date</i>	Upon sighting	GPS-Plotter Map Sounder
<i>Time (UTC)</i>	Every 5 minutes	GPS-Plotter Map Sounder
<i>GPS position (UTM)</i>	Every 5 minutes	GPS-Plotter Map Sounder
<i>Depth (m)</i>	Every 5 minutes	Echo-sounder 83-200 kHz
<i>Presence of shellfish farms (Yes/No)</i>	Every 5 minutes	Presence or absence of bottlenose dolphins between shellfish rafts
<i>Group size</i>	Every 5 minutes	Details below
<i>Group behaviour</i>	Every 5 minutes	Details below
<i>Group composition (sex, age, identities)</i>	Every 5 minutes	Details below
<i>Photographs</i>	Continuous	Details below

Photographs taken for mark-recapture analysis

On each sighting, attempts were made to photograph both sides of the dorsal fin of every dolphin present in the group, regardless of the degree of marking, age class, or behaviour. Photographs were taken using digital single lens reflex (DSLR) cameras equipped with a 35- to 300-mm telephoto zoom lens.

Photographs were used for photo-identification (2.3.2) purposes, to assess the sex and the age of an individual, and to confirm the group size.

Group size

Group size was estimated based on the initial count of different individuals observed at one time in the area, before, during, and after the approach. Group size data was later verified with photographs taken during each encounter by increasing the number of individuals present if more individuals were photographed (Díaz López & Shirai 2008).

Behavioural sampling methods

Group-follow protocol was used to record the behaviour of bottlenose dolphins (Mann 1999). The behaviour of a group was recorded as behavioural states (i.e. long behaviours of measurable duration) (Altmann 1974). The behavioural state of a group was determined every five minutes based on the activity performed by at least 50% of the individuals present in the group, for at least 50% of the duration of the five-minute sample (predominant group activity sampling: Altmann 1974; Karniski et al. 2015).

As the determination of cetacean behaviour from surface observation can be challenging, several parameters were considered to assess the behavioural state in order to reduce potential bias: behavioural events (**Table 2.3**), dive duration, swimming speed and direction, inter-individual distance, and contact among individual dolphins (following Díaz López 2006a). To eliminate inter-observer variability, the behavioural state was determined by the same experienced observer during the full study period.

The behavioural states were classified into four categories: foraging, resting, socializing, and travelling (**Table 2.4**).

Table 2.3. Description of the behavioural event observed in bottlenose dolphins in the Ría de Arousa (North-West Spain).

Behavioural event	Description
<i>Regular dive</i>	Dolphin surfaces exposing only blowhole, part of back, and dorsal fin.
<i>Tail-stock dive</i>	Dolphin arches back and exposes peduncle, but not flukes, as submerges after breathing.
<i>Flukes-up dive</i>	Dolphin arches back and exposes flukes as dives.
<i>Fast surface</i>	Dolphin surfaces for a quick breath, causing a wake, and does either a regular or a tail-stock dive.
<i>Full leap</i>	Head-first ascension from the water with smooth, head-first re-entry; dolphin's entire body does not have to leave the water.
<i>Lateral leap</i>	Full leap with lateral re-entry in the water.
<i>Breach</i>	Head-first ascension with rough belly first re-entry causing splash on the surface.
<i>Lateral breach</i>	Head-first ascension with rough body side re-entry causing splash on the surface.
<i>Back breach</i>	Head first ascension with rough back first re-entry causing splash on the surface.
<i>Bow</i>	Airborne ascent followed by re-entry within one body length from point of exit.
<i>Somersault</i>	Acrobatic leap in which the tail roll over the head.
<i>Tail-slap</i>	Dolphin lifts flukes above water and deliberately slaps them on the water's surface; dolphin body is horizontally oriented.
<i>Inverted tail-slap</i>	Dolphin lifts flukes above water but doesn't slap the water surface (opposite direction than a tail slap).
<i>Head-slap</i>	Flat and noisy contact of head on water surface.
<i>Bow-riding</i>	Dolphin rides the pressure wake in the front of a boat.
<i>Wake-riding</i>	Dolphin rides the pressure wake at the back of a boat.
<i>Surf</i>	Dolphin uses energy from swell for forward motion.
<i>Catch prey</i>	Dolphin is observed with fish or invertebrate in its mouth.
<i>Kick fish</i>	Dolphin throws fish out of the water with the flukes or its mouth.
<i>Spy hop</i>	Head raised out of water far enough to expose the eyes for at least 3 seconds, dolphin stationary.
<i>Raspberry</i>	Sounds produced with the blowhole, dolphin floating on the surface.
<i>Body contact</i>	Two or more dolphins are in physical contact.
<i>Roll</i>	Dolphin turns along the longitudinal axis of its body at, or beneath the surface of the water.
<i>Biting</i>	Dolphin bites another dolphin.
<i>Charging</i>	Dolphin swims fast towards another individual and get in contact.
<i>Move</i>	Dolphin is at the surface, only moving like a shark.
<i>Floating</i>	Dolphin is stationary and only moving with the current.
<i>Tail-up</i>	Dolphin is orientated vertically and exposes peduncle and flukes above the water surface for > 3 seconds; dolphin stationary.
<i>Intromission</i>	Two or more dolphins engaged in sexual intercourse.
<i>Ventral swim</i>	Dolphin swims ventral side up / dorsal side down at, or near water surface.
<i>Belly-up</i>	Dolphin rolls body showing its belly at the surface for > than 3 seconds.

Table 2.4. Description of the behavioural states observed in bottlenose dolphins in the Ría de Arousa (North-West Spain).

<i>Behavioural state</i>	Description
<i>Foraging</i>	<p>Solitary or aggregation of bottlenose dolphins swimming in different directions in the same area. Dolphin(s) usually stay in the same area, involve carrousel and cross swimming. If large group, the group can be split into two or more subgroups spread over a large area (100 m); or the individuals can be completely spread between each other.</p> <p>Surface-feeding: includes fast surfacing (chase prey close to the surface), feeding rush towards the surface or towards obstacles (e.g. rocks, shellfish platforms), catching prey, fish kicking or tossing, ventral swimming.</p> <p>Deep diving: sequence of regular dives followed by steep dives (tail-stock or flukes-up dives), and then long dives (> 60 seconds) (Díaz López et al. 2008b).</p>
<i>Resting</i>	<p>Solitary or aggregation of bottlenose dolphins surfacing at a slow and constant speed (< 2 kn). Group is tight (< 1 body length, 3 m). Surfacing usually involves synchronous dive behaviour between two or more individuals and floating at the surface. Most of the ventilations are regular and the dives are short (< 60 seconds), with absence of steep dives. When this behavioural state finishes, there is a drastic change of behaviour (important changes of speed, direction, dive interval and behavioural events).</p>
<i>Socialising</i>	<p>Aggregation of bottlenose dolphins interacting at the surface and underwater with one other or, several other, dolphins. Can include synchronous dives, body contact, biting, rolling, charging, chasing, somersault, mating, genital inspections, tail slaps, leaps, bows, and breaches. Individuals change position in the group and swimming direction varies. The group can be split into small subgroups spread over a large area. The dive interval is short (< 60 seconds).</p>
<i>Travelling</i>	<p>Solitary or aggregation of bottlenose dolphins regularly surfacing (constant dive intervals) (< 60 seconds) at a constant speed (> 2 kn) and one goal direction. If there are several individuals in the group, the group is generally cohesive and the inter-individual distance is usually less than 3 bodies (approximatively 9 m).</p>

Group composition

Group composition (sex, age, and identification) was assessed by observing the animals in the field and was later verified with photographs taken during each encounter.

Age classification

Individual bottlenose dolphins were classified according to age at the time of the encounter (Scott et al. 1990). Bottlenose dolphins were classified as either new-born, immature, or adults based on behavioural cues and visual assessment of the size (both in the field and with photographs) (Table 2.5) (Figure 2.17).

Table 2.5. Age classification of bottlenose dolphins.

Age class	Definition
New-born	Dependent dolphin associated to mother, swimming in infant position (i.e. below the mother, lightly touching her abdomen). Uncoordinated surfacing behaviour. Born within the same calendar year. < 1.5 m, presence of foetal folds or lines.
Immature	Dependent dolphin, consistently swim beside & slightly behind mother (but not in infant position). Skin lighter colouration than adults, few rake marks and skin lesions. Two-thirds the length of an adult.
Adult	Between 2.5 and 3.5 m, darker skin coloration.



Figure 2.17. Photograph of (a) an adult with a new-born and (b) an adult with an immature bottlenose dolphin.

Sex classification

Sex was determined by direct observations and photographs of the genital region, as described by Díaz López (2012) (Table 2.6) (Figure 2.18).

Table 2.6. Sex classification of bottlenose dolphins.

<i>Sex class</i>	<i>Definition</i>
Male	Observation of an erection or by the gap > 2.5 cm between the genital and anal slits.
Female	(i) Observation of mammary slits and absence of gap between the genital and anal slits or (ii) Repeated observation with a new-born swimming in infant position.

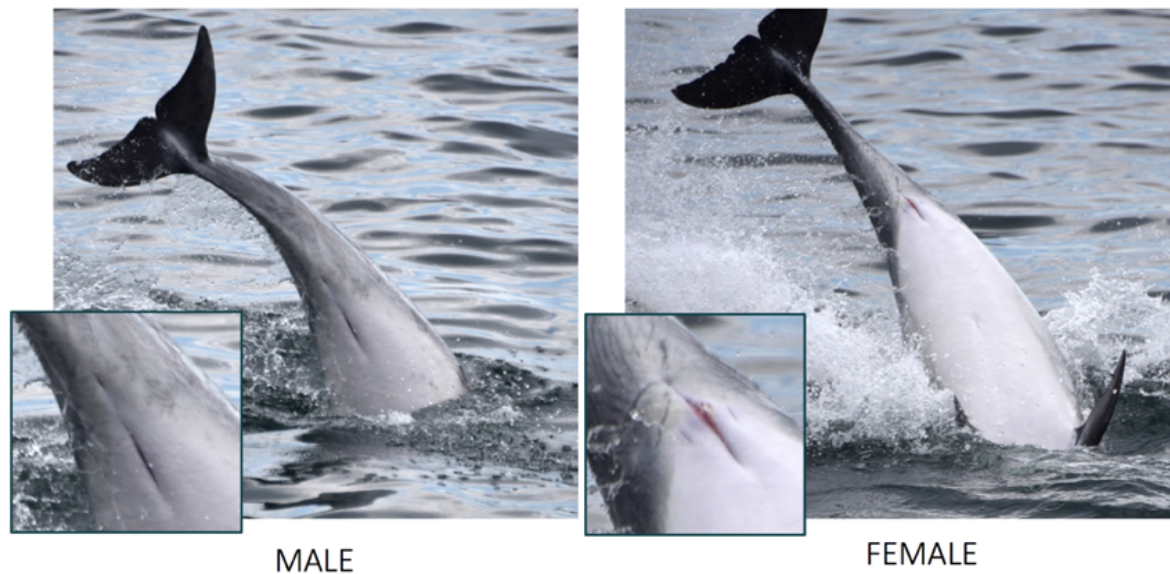


Figure 2.18. Ventral side of a male (left) and a female (right) bottlenose dolphin.

2.3.2 Mark-recapture analysis

Photo-identification was used as the capture-mark-recapture method (Würsig & Jefferson 1990). Bottlenose dolphins were identified based on natural markings (size, location and pattern of notches (i.e. an indentation or incision)) on the trailing edge of their dorsal fin from high-quality photographs (Würsig & Jefferson 1990) (**Figure 2.19**).

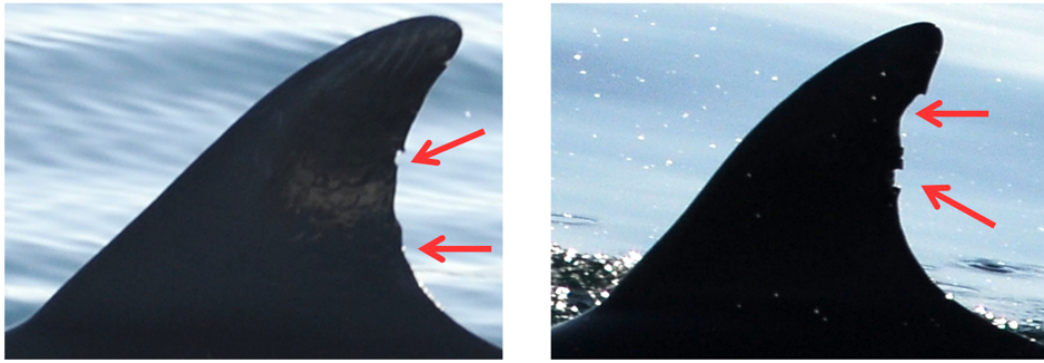


Figure 2.19. Photograph of the dorsal fin of two individual bottlenose dolphins. The arrows present the notches used for photo-identification analysis.

In this thesis, mark-recapture data was used for abundance estimation (Chapter 3) and analysis of social organisation (Chapter 7).

The first photograph collected of an individual bottlenose dolphin was considered as a visual 'mark', with each subsequent photograph considered as a visual 'recapture'. The record of marks and recaptures over time is referred to as capture histories, where each animal is considered as either absent '0' or present '1' during each sampling period (White & Burnham 1999).

In mark-recapture studies, marks are considered permanent and are recognisable. Mark-loss may occur when identifying features (such as dorsal fin notch(es) in dolphins) change over time. Likewise, this may occur when less-distinctive markings are used to identify individuals. In abundance estimations, violations to these assumptions may lead to false-positive errors, resulting in an underestimation of abundance, or false-negative errors, which overestimate the population size (Hupman 2016). To ensure this assumption, unique and evident notches were used to identify bottlenose dolphins, and digital photographs were double-checked by experienced researchers and posteriorly confirmed using matching software. Although marks are cumulative over time, which makes it difficult to match individuals if they acquire new marks or the marks change over time (Yoshizaki et al. 2009), the continuity and extension of the photographic identification work in this study allowed to register minor changes on the dorsal fins of individuals.

Photograph grading

All photographs containing a dorsal fin were graded for quality and degree of distinctiveness in order to minimise misidentification and heterogeneity in capture probabilities (Urian et al. 2015).

Photographs were given an absolute value score (1 = low; 4 = average; 10 = high) for: (a) the perpendicular angle of the dorsal fin to the camera; (b) sufficient focus of the image to allow all notches to be distinguished; (c) contrast and light intensity; and (d) the dorsal fin being suitably sized in the frame for all notches to be clearly visible (**Table 2.7**). The individual scores for each category were summed to obtain an overall quality score (OQS). OQs from 4 to 16 were considered poor quality; those from 19 to 25 were considered to be of average quality; and those ≥ 28 were considered excellent (**Table 2.8**). To ensure correct identification of individuals, only excellent quality photographs were used for individual identification.

Table 2.7. Photograph grading for the identification of individual bottlenose dolphin.

Photo grading (for each picture)			
	Low (1)	Average (4)	High (10)
Perpendicular			
Focus			
Contrast			
Size dorsal fin			

Table 2.8. Overall quality score for each photograph.

Overall quality scores (for each picture)		
Low	Average	Excellent
4-16	19-25	≥ 28

After identification, each adult individual was included in a distinctiveness category based on the amount of information contained on the dorsal fin. This ensured that more distinctly marked individuals would not have a higher probability of being identified.

A 'well marked individual' was considered to be a dolphin that is recognised not by a single large feature in the dorsal fin, but also by a matrix of evident notches (Würsig & Jefferson 1990). A 'marked individual' was considered to be a dolphin with a distinct dorsal fin with an average amount of information (i.e. a single large notch and several small notches). A 'poorly marked individual' was considered to be a dolphin with a dorsal fin that had a small amount of information (i.e. small notch(es) and secondary characteristics). Features such as body and dorsal fin scars, lesions, decolouration, and tooth rakings were used as secondary characteristics, thereby reducing the possibility of false positives (Wilson et al. 1999). Individuals with no notch on the dorsal fin ('unmarked individual') were not included in the catalogue (Table 2.9) (Figure 2.20).

Table 2.9. Distinctiveness category for individual bottlenose dolphins.

Distinctiveness category	Definition
Well marked	Dorsal fin with a matrix of evident notches.
Marked	Dorsal fin with a large notch and several small.
Poorly marked	Dorsal fin with small notch(es) and secondary characteristics.
Unmarked	Dorsal fin with no notch.

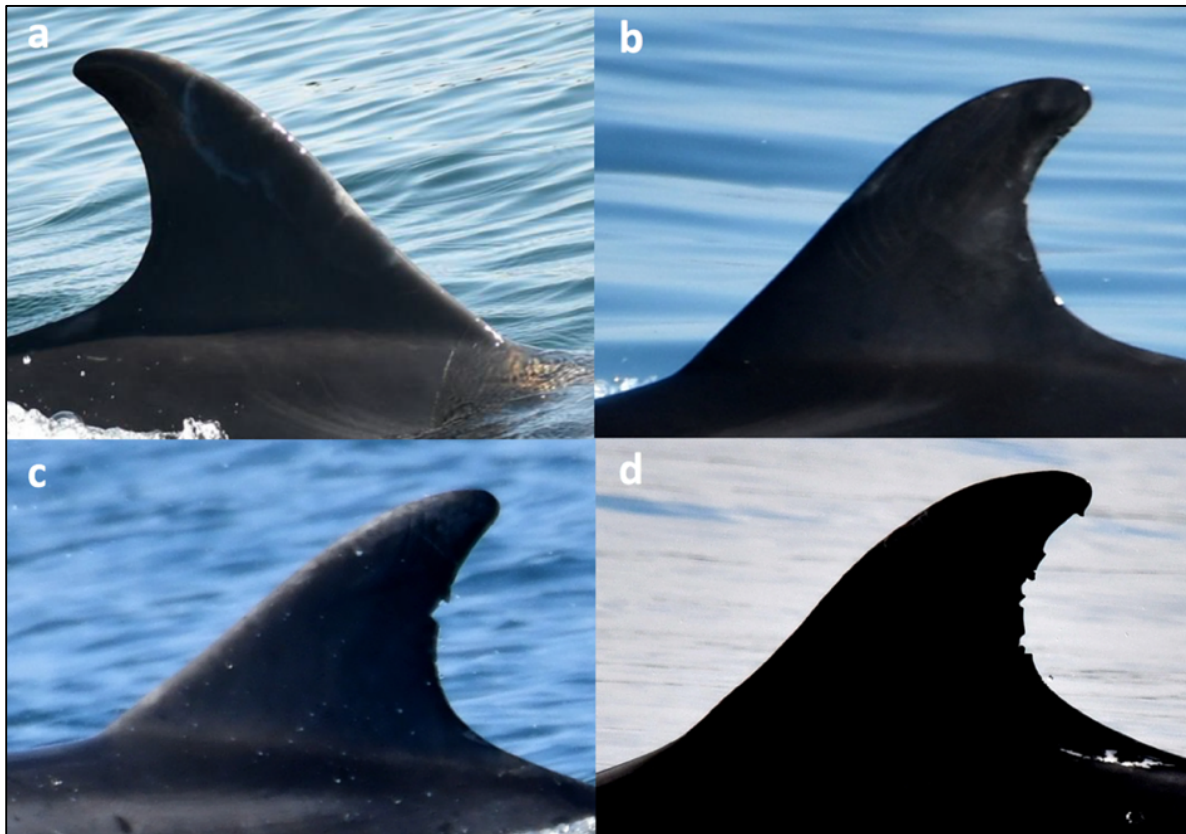


Figure 2.20. Photographs of (a) unmarked, (b) poorly marked, (c) marked, and (d) well marked bottlenose dolphins.

Every photograph of identified individuals was re-examined for false positives (different dolphins being assigned as the same individual) and false negatives (the same dolphin being assigned as multiple discrete individuals), and the final data were confirmed by two experienced observers.

Later, to avoid potential errors because of observer fatigue during the photographic identification analysis, the matching of the individuals was confirmed using the software Darwin 2.22 (Hale 2008) (**Figure 2.21**).

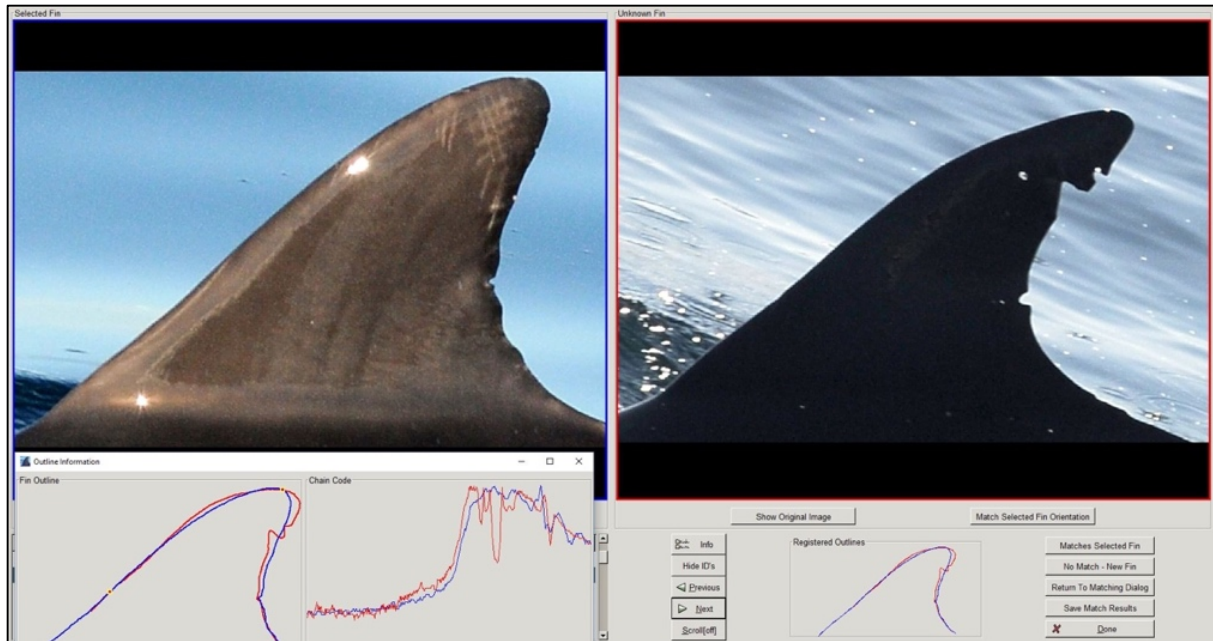


Figure 2.21. Screen capture of the dorsal fin of two individual bottlenose dolphins matched with the software Darwin.

Identified individual bottlenose dolphins were named with an alpha-numeric code. The best photographs of both sides of every adult bottlenose dolphin were kept in an identification catalogue. Photographs were regularly replaced in the catalogue as better-quality or more current images became available. The capture history (whether or not an identified bottlenose dolphin was present within a sampling period) of each individual was compiled after the photographic grading process.

2.3.3 Data obtained from external repositories

Supplementary variables were obtained from external repositories. These variables were used in some chapters of this thesis, based on the objectives of each study.

- **Tide level and tidal cycle (Chapters 5 and 6)**

Tide level (in metres) and **tidal cycle** (presence / absence of flood tide) were obtained from tide charts from the Galician weather service (www.meteogalicia.gal).

- **Temperature, salinity, dissolved oxygen, and fluorescence intensity (Chapter 4)**

Water temperature (in degree Celsius, °C), water salinity (in practical salinity unit, PSU), dissolved oxygen (in mL/L), and fluorescence intensity (in mg/m³) from 11 oceanographic stations distributed in the Ría de Arousa (**Figure 2.22**) were obtained from the Instituto Tecnoloxico para o Control do Medio Marino de Galicia (IntecMar; www.intecmar.gal). These variables were collected over the water column, every week, in each station, during the full study period.

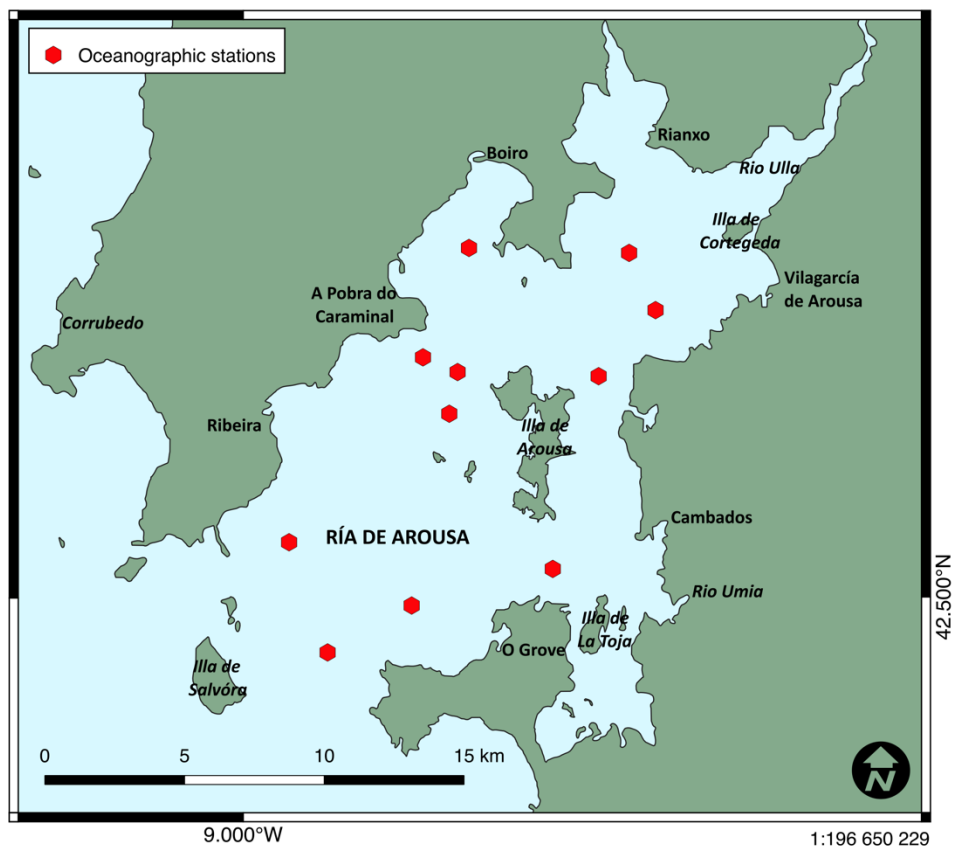


Figure 2.22. Map of the study area with the 11 oceanographic stations.

These variables were explored to detect errors of measurements with two packages of the software R (R Development Core Team 2011). The package ‘lubridate’ was used to work with dates and the package ‘dplyr’ was used for data manipulation (to filter and summarize the data).

For each of the variables, at each station, for each sampling day, the average values and standard deviation for the water column was calculated. A monthly average value, per variable, per station was also calculated.

2.3.4 Data obtained from GIS

QGIS (QGIS Development Team 2016), an open source Geographical Information System (GIS) software package, was used to display both effort and distribution of the sightings of bottlenose dolphins, and to obtain different variables (listed below). These variables were used in some chapters of this thesis, based on the objectives of each study.

- **Oceanographic variables (water temperature, water salinity, dissolved oxygen, and fluorescence intensity) (Chapter 4)**

To link the oceanographic data previously obtained from IntecMar to bottlenose dolphin presence-absence data and sightings, the oceanographic data were transformed to raster format (Hirzel et al. 2002).

QGIS was used to create the raster files, to extrapolate the monthly spatial variation across the study area, and for each one of the oceanographic variables. One raster was created for each of the oceanographic variables, for each month of the study period, from the 11 sampling stations. The maps were created by interpolating each variable (of each station, of each month) using the inverse distance weighted (IDW) interpolation.

IDW is a spatial interpolation method that assumes that values of nearby points are more similar than values of more distant points (Li & Heap 2008). Hence, it estimates values at unknown locations by giving a heavier weight to closer sampled points (Li & Heap 2008; Lu & Wong 2008). IDW is a spatial interpolation method that has been widely used to predict environmental variables (Li & Heap 2008). The 'point sampling' tool in QGIS was then used to extract the raster values (environmental variables) from multiple layers at each bottlenose dolphin encounter position in order to link the group size with the oceanographic variables.

- **Bottom slope gradient and bottom slope aspect (Chapters 4, 5, and 6)**

Bottom slope gradient (the maximum rate of change in depth in a given area of grid cell and expressed as per cent slope) and bottom slope aspect (the orientation of the slope with respect to true north) were computed from the bottom depth obtained from the General Bathymetric Chart of the Oceans (GEBCO08, <http://www.gebco.net>) dataset. This dataset was converted to

a raster format and then interpolated using QGIS software and terrain analysis tools. The 'point sampling' tool in QGIS plugin was then used to extract the raster values and polygon attributes from multiple layers at specify sampling points.

- **Distance to the coast and to the shellfish farm areas (Chapters 4, 5 and 6)**

A spatial analyst tool (nearest neighbour plugin NNJoin) in QGIS software allowed a distance calculation between different shape files (the minimum distances, in metres, to the coast and to the shellfish farm areas from each 20-min samples, each sightings, and each 5-min behavioural samples locations were calculated).

- **Sampling effort index (Chapter 5)**

To account for a different probability of encountering bottlenose dolphins depending on varying survey effort, a relative sampling effort index was included in analysis. This index was generated by calculating the number of 20-min sets (on-effort) within grid cells of 1 x 1 nm throughout the study area (**Figure 2.23**).

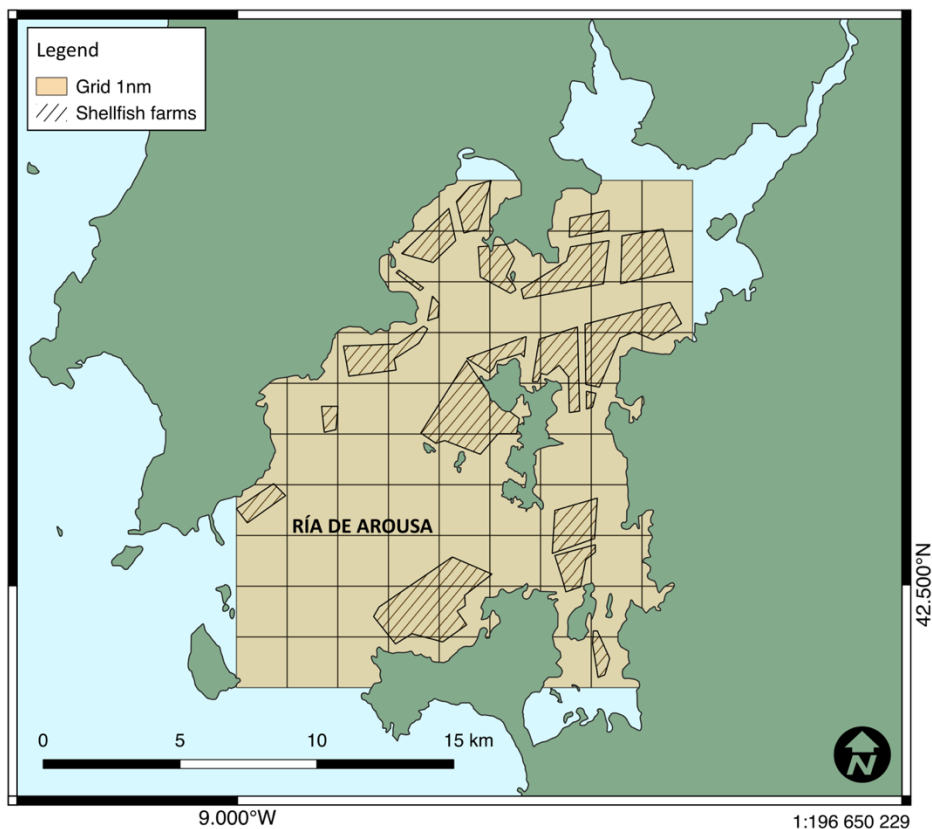


Figure 2.23. Map of the study area with a grid of 1 nm.

- **Space-use of individual bottlenose dolphins and spatial overlap between individuals (Chapter 7)**

Spatial distribution of the sightings of each individual was plotted using QGIS. Minimum convex polygon was used to compare space-use between individuals (Burgman & Fox 2003). The central tendency of an individual's space-use was represented by the centroid of the minimum convex polygon of all sightings of the individual.

Space-use overlap between each pair of individuals was determined by using the vector overlay features in QGIS (Figure 2.24).

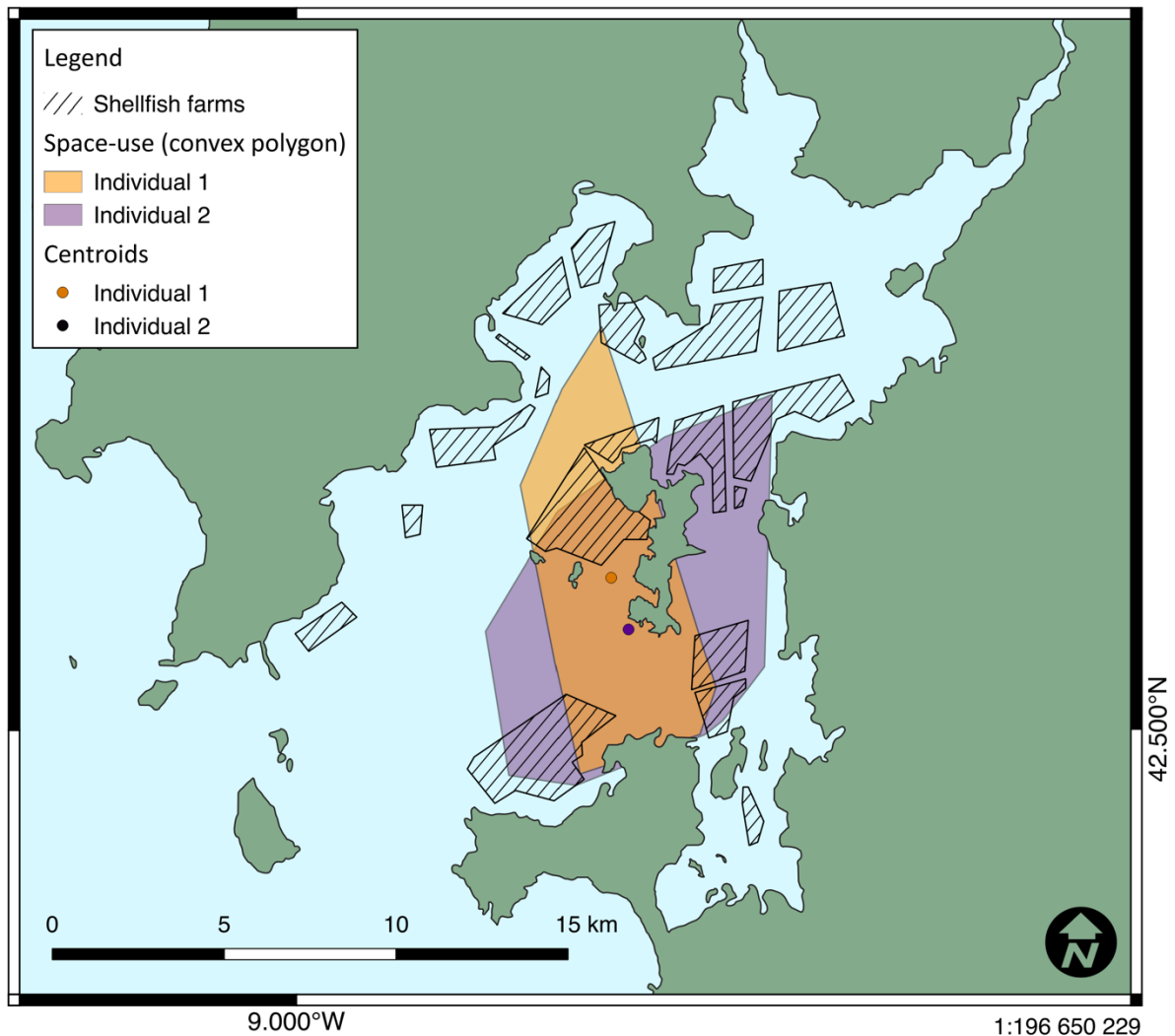


Figure 2.24. Minimum convex polygons and centroids for two individual bottlenose dolphins.

Chapter 3. Abundance and demographic parameters of bottlenose dolphins in a highly affected coastal ecosystem

Article published

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Personal contribution

I conceived and designed the study with BDL. I collected the data. I carried out the photo-identification analyses. I analysed the data with input from BDL. I interpreted the results and implication with BDL. I produced the figures. I wrote the paper with input from BDL.

3.1 Abstract

This study presents the first robust estimates of abundance and demographic parameters of common bottlenose dolphins (*Tursiops truncatus*) in a highly affected coastal ecosystem along the north-eastern Atlantic. Seasonal abundance, apparent survival, and temporary emigration rates were estimated using Pollock's robust design models. Photographic identification data were collected from 2014 to 2016 along the North-Western Iberian coast (Spain). Bottlenose dolphins were present year-round and with a high degree of occurrence in the study area, which is highly affected by human activity but is also a highly productive coastal ecosystem. Local abundance of bottlenose dolphins ranged from 56 in autumn 2014 to 144 in winter 2015. Apparent survival rate was high and constant, indicating no mortality and no permanent emigration. Temporal emigration rates varied seasonally and were lower from autumn to winter, suggesting that dolphins had a high probability of returning during the winter period. The observed changes in abundance and emigration rates most likely reflect seasonal fluctuations in abundance of prey species in this area. These results provide important baseline information in an area subject to significant anthropogenic pressures and for future comparisons with other populations of similar characteristics under the pressure of human activities, such as fisheries and aquaculture.

3.2 Introduction

Worldwide, coastal, and marine ecosystems are at risk as a result of human activities (Halpern et al. 2008b). Consequently, cetacean species that live near shore are highly vulnerable to a variety of anthropogenic pressures, such as fisheries (Read et al. 2006), aquaculture (Würsig & Gailey 2002; Díaz López 2012), pollution (Derraik 2002; Tanabe 2002), global warming (Simmonds & Isaac 2007), and habitat modification (Lotze et al. 2006). Estimating demographic parameters of a cetacean population is crucial for assessing their conservation status and to identify potential effects of anthropogenic or natural pressures in order to take appropriate conservation and management measurements (Smith et al. 2013).

Having a near shore distribution, the common bottlenose dolphin *Tursiops truncatus* (Montagu 1821), hereafter 'bottlenose dolphin', is among the most threatened cetacean species, and a more intense monitoring and management intervention is needed for this species (Bearzi et al. 2009). Atlantic bottlenose dolphin populations are listed in Appendix II of the Convention on the Conservation of Migratory Species of Wild Animals (CMS; see www.cms.int, accessed 15 October 2017), in Appendix II (Strictly Protected Fauna Species) of the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention; www.coe.int, accessed 15 October 2017) and under Annexes II and IV of the European Union's Habitats Directive (Council Directive 92/43/EEC; www.ec.europa.eu, accessed 15 October 2017) as a species whose conservation requires the designation of Special Areas of Conservation and in need of strict protection.

In order to obtain accurate and precise information about bottlenose dolphin populations, year-round survey efforts are essential, but these are expensive and logistically challenging (i.e. weather conditions, limited resources and personnel). In north-east Atlantic waters, although some studies have focused on local abundance (Silva et al. 2009; Berrow et al. 2012; Hammond et al. 2013), there is a lack of exhaustive robust assessments of population abundance, rates of apparent survival and temporary emigration of bottlenose dolphin populations. Bottlenose dolphins are present along the North-Western Iberian coast (López et al. 2003; Pierce et al. 2010; Louis et al. 2014; Díaz López & Methion 2017), a region where they are vulnerable to several human impacts that affect coastal areas throughout the Atlantic coastline, such as

marine traffic, bycatch (López et al. 2003), overfishing (Freire & García-Allut 2000), oil spills (Vieites et al. 2004), and the aquaculture industry (Díaz López & Methion 2017). A recent study demonstrated that bottlenose dolphins present a fine-scale pattern of habitat selection affected by anthropogenic activities in these waters (Díaz López & Methion 2017). However, the lack of exhaustive robust assessments of population abundance and demographic parameters hampers our ability to evaluate the effects of human activities on this species in the region.

Over the past few years, Pollock's (1982) capture–recapture robust study design has been increasingly used to obtain accurate estimates of abundance and other demographic variables of bottlenose dolphin populations (e.g. Silva et al. 2009; Speakman et al. 2010; Nicholson et al. 2012; Bassos-Hull et al. 2013; Smith et al. 2013; Fruet et al. 2015; Santostasi et al. 2016; Sprogis et al. 2016b). This design, unlike standard open models, takes into account the degree of residency, including temporary emigration, thus more accurately reflecting reality in the results (Kendall et al. 1997; Nicholson et al. 2012; Smith et al. 2013). Indeed, temporary or permanent emigration can potentially be confounded with mortality, and may result in imprecise, and in some circumstances biased, estimations (Kendall et al. 1997). By using Pollock's (1982) robust design model it is possible to control the effects of temporary emigration on the population, thus making the model less sensitive to the observed violations of 'equal catchability' when the recapture period is extended over time (Pollock 1982). Pollock's (1982) robust design combines open population models (open sampling event; termed 'primary periods') and closed population models (multiple closed events within the open sampling event; termed 'secondary periods'; Kendall et al. 1997). Although the population is assumed to be open between primary periods (i.e. allowing for births, deaths and permanent or temporary emigration and immigration), each secondary period assumes an effectively closed unit (i.e. births, deaths, immigration and emigration do not occur; Kendall et al. 1997).

In the present study, we used Pollock's (1982) robust design models on photographic identification data collected year-round to estimate seasonal abundance, apparent survival and temporary emigration rates of common bottlenose dolphins along the North-Western Iberian coast (Spain). These estimates are the first robust estimates for coastal bottlenose dolphins in

north-eastern Atlantic waters and provide important baseline information in an area subject to significant anthropogenic pressures.

3.3 Methods

3.3.1 Study area

The present study was performed along the North-Western coast of the Iberian Peninsula, specifically along the southern coast of Galicia (Spain), on which there are a series of ancient drowned tectonic valleys taken over by the sea (also referred to as 'rías'; Evans & Prego 2003). Owing to intense upwelling events that occur along this coast, resulting in very high primary production, the rías are important areas for fisheries and shellfish aquaculture, and more specifically for the production of mussels and oysters (Prego et al. 1999). Rías are often sites for human settlement, where many pollution problems exist, because they serve as harbours and waterways to urban and industrial centres (Prego & Cobelo-García 2003).

Boat-based surveys were conducted in the coastal waters of the largest of the Galician rías, the Ría de Arousa (Prego et al. 1999), and surrounding waters up to 20 km offshore, covering an area of 450 km² with a maximum depth of 150 m. The average depth of the Ría de Arousa is 19 m. The entire system is subjected to a semidiurnal and mesotidal tide regime, with a tidal range of 1.1 and 3.5 m during neap and spring tides respectively (Alvarez et al. 2005). During the study, the sea surface water temperature ranged between 9.8°C in winter and 22.8°C in summer.

3.3.2 Data collection

Boat-based surveys were conducted in the study area between March 2014 and June 2016 using a 12-m research vessel powered by two 180-hp inboard engines. Because of poor weather conditions during December in 2014 and 2015 we were unable to complete surveys during this month. In all, 25 months were spent in the field. The area was surveyed during daylight hours at a constant speed of 6 knots (~ 11.11 km h⁻¹) with at least three experienced observers stationed on the flying bridge (4 m above sea level) scanning 360 of the sea surface in search of common bottlenose dolphins (*T. truncatus*) with the naked eye or 10 x 50 binoculars. The minimum number of experienced observers and vessel speed remained consistent during the study period, making data suitable for comparative analysis. Boat-based observations were performed when the visibility was not reduced by rain or fog, and sea

conditions were <3 on the Douglas sea force scale (Díaz López 2006b). The survey area and track were designed to attempt to equally cover all parts of the study area, although the geographic distribution of effort could vary according to weather conditions (Díaz López & Methion 2017).

Upon encountering a group of bottlenose dolphins, searching effort ceased and the vessel slowly manoeuvred towards the group in order to minimise disturbance during approach. A group of dolphins was defined as either a solitary dolphin or any aggregation of bottlenose dolphins with close spatial cohesion, with interactions between individuals and participating in the same behavioural activities. The date, initial and final time, location (Universal Transverse Mercator, UTM, coordinates), and group size and composition were recorded for each encounter. Attempts were made to photograph both sides of the dorsal fin of every dolphin present in the group, regardless of the degree of marking, age class, or behaviour. Photographs were taken using digital single lens reflex (SLR) cameras equipped with a 35- to 300-mm telephoto zoom lens. Group size was assessed based on the initial count of different individuals observed at one time in the area. Field data were later verified with photographs taken during each encounter by increasing the number of individuals present if more individuals were photographed (Díaz López & Shirai 2008). Individual dolphins were classified according to age within each group at the time of the encounter (Scott et al. 1990). Age class definitions followed those of Díaz López & Methion (2017), whereby bottlenose dolphins were classified as either newborn, immature, or adult. Newborn dolphins were defined as dependent dolphins < 1.5 m with foetal folds or lines. Newborns were also defined on the basis of uncoordinated surfacing behaviour and swimming in the infant position (i.e. below the mother, lightly touching her abdomen). Immature dolphins were those with few rake marks and skin lesions and two-thirds or less the length of adults. Immature dolphins were often observed in close association with an adult, but never observed in the infant position. Adult dolphins were fully grown (length > 2.5 m) marked or unmarked animals with darker skin colouration. Sex was determined by direct observations and photographs of the genital region, as described by Díaz López (2012). The sex of male bottlenose dolphins was determined by the observation of an erection, by the gap (> 2.5 cm) between the genital and anal slits and a lack of mammary slits, or by the gap alone. Females were sexed by the observation of mammary slits or the consistent presence of a

newborn swimming in the infant position. After the end of an encounter, the search effort generally continued along the previously planned route.

Data collection in the present study complied with current laws of Spain, the country in which the study was performed.

3.3.3 Relative frequency of occurrence

In order to understand the temporal pattern in the presence of groups of bottlenose dolphins in the study area, a relative frequency of occurrence (hereafter referred to as the encounter ratio (ER); Díaz López 2006b) was computed as follows:

$$ER = \frac{Ne}{h}$$

where Ne is the total number of encounters and h is the total number of hours spent searching for dolphins.

Non-parametric tests (Mann–Whitney or Kruskal–Wallis) were used to investigate the equality of medians of quantitative samples. Statistical significance was tested at the $P < 0.05$ level. The data are presented as means \pm standard error (s.e.).

3.3.4 Analysis of photographs

All digital photographs were analysed independently by three experienced researchers. Only adult bottlenose dolphins were included in the photographic identification analysis; therefore, photographs containing calves (immature and newborn dolphins) were excluded. Adult bottlenose dolphins were identified from photographs based on the size, location and pattern of notches on the trailing edge of the dorsal fin (Würsig & Jefferson 1990). All photographs containing a dorsal fin were graded for quality and degree of distinctiveness in order to minimise misidentification and heterogeneity in capture probabilities (Urian et al. 2015). Following Díaz López et al. (2017), all photographs were given an absolute value score (1, low; 4, average; 10, high) for: (1) the perpendicular angle of the dorsal fin to the camera; (2) the

focus of the image being sufficient to allow all notches to be distinguished; (3) contrast and light intensity; and (4) the dorsal fin being suitably sized in the frame for all notches to be clearly visible. The individual scores for each category were summed to obtain an overall quality score (OQS). OQSs from 4 to 16 were considered poor quality; those from 19 to 25 were considered to be of average quality and those ≥ 28 were considered excellent. To ensure correct identification of individuals, only excellent quality photographs were used for individual identification. In addition, each adult individual was included in a distinctiveness category, based on the amount of information contained on the dorsal fin, to ensure that more distinctly marked individuals would not have a higher probability of being identified. A 'well-marked individual' was considered to be a dolphin that is recognised not by a single large feature on the dorsal fin, but also by a matrix of evident notches (Würsig & Jefferson 1990). A 'marked individual' was considered to be a dolphin with a distinct dorsal fin with an average amount of information (i.e. a single large notch and several small notches). Features such as body and dorsal fin scars, lesions, decolouration, and tooth rakings were used as secondary characteristics, thereby reducing the possibility of false positives (Wilson et al. 1999). A 'poorly marked individual' was considered to be a dolphin with a dorsal fin that had a small amount of information (i.e. a small notch and secondary characteristics). Because such characteristics are not necessarily permanent and not easily identifiable, adult individuals with no marks on the dorsal fin (unmarked) and poorly marked individuals were not included in further analyses. Every photograph of identified individuals was re-examined for false positives (different dolphins being assigned as the same individual) and false negatives (the same dolphin being assigned as multiple discrete individuals), and the final data were confirmed by two experienced observers. Later, to avoid potential errors because of observer fatigue during the photographic identification analysis, the matching of the individuals was confirmed using DARWIN (ver. 2.22, Eckerd College, Petersburg, FL, USA; Hale 2008). The best photographs of both sides of every adult bottlenose dolphin were kept in an identification catalogue. Photographs were regularly replaced in the catalogue as better-quality or more current images became available. The capture history (whether or not an identified bottlenose dolphin was present within a sampling period) for each individual was compiled after the photographic grading process.

3.3.5 Mark-recapture abundance models

In the present study we used Pollock's robust design model to estimate abundance and survival rates (Pollock 1982; Kendall et al. 1997) of the bottlenose dolphins studied. Primary periods were based on each season of the year: winter (January–March), spring (April–June), summer (July–September) and autumn (October–December). Secondary periods were based on the minimum number of photographic identification surveys necessary to monitor the entire study area and were completed within the shortest time possible (weather dependent; Smith et al. 2013). Nine primary periods (seasons of the year) and 22 secondary periods were included in the robust design models. There were two or three secondary periods within each primary period. The time taken to complete secondary periods was weather dependent and averaged 23 days \pm 2 s.e. (range 7–40 days) because of logistical reasons and weather conditions.

3.3.5.1 Model assumptions

Several assumptions need to be satisfied in order to obtain unbiased estimates with robust capture–recapture models, as detailed below.

1. Marks are unique, they cannot disappear and there are no misidentifications. To ensure this assumption, unique and evident nicks were used to identify 'well-marked' and 'marked' adult bottlenose dolphins, and digital photographs were double-checked by experienced researchers and posteriorly confirmed using matching software. Although marks are cumulative over time, which makes it difficult to match individuals if they acquire new marks or the marks change over time (Yoshizaki et al. 2009), the continuity and extension of our photographic identification work allowed us to register minor changes on the dorsal fins of individuals. The time between two primary sampling periods did not exceed 89 days, allowing for the identification of new marks in the dorsal fin (range 7–89 days; mean 31 days).

2. All individuals have equal probability of being captured within a sampling occasion. To ensure this assumption, attempts were made to photograph both sides of the dorsal fin of every dolphin during each encounter, and only 'excellent-quality' photographs were used in analyses. In addition, during dolphin encounters, explicit effort was made to photograph all the animals

present, despite their markings, proximity to the boat, or individual behaviour. Moreover, Pollock's robust design allows for heterogeneity of capture probabilities because the secondary sampling periods occur close together (Williams et al. 2002).

3. There is no behavioural response to the capture (i.e. no trap response). Boat-based photographic identification surveys did not induce significant behavioural changes or stress to the animals being studied. Moreover, the studied bottlenose dolphins are well habituated to human presence (marine traffic, aquaculture, and fishing activities).

4. All individuals have equal probability of survival. To ensure this assumption, only adult bottlenose dolphins were included in mark–recapture analyses. The presence of transient individuals is commonly reported in cetacean studies based on photographic identification data (Silva et al. 2009; Speakman et al. 2010). Ignoring the presence of transients can produce negatively biased survival estimates because transients do not return to the study area (Hines et al. 2003). Program U-Care (R. Choquet, A. M. Reboulet, J. D. Lebreton, O. Gimenez and R. Pradel, CEFE, Montpellier, France) was used to test and confirm the presence of transient individuals. The data were adjusted for transience following an ad hoc approach (Hines et al. 2003) by relying on individuals captured in more than one secondary period to provide direct estimates of survival rate for residents. The ad hoc approach yields unbiased estimated pertaining to residents (Pradel et al. 1997; Hines et al. 2003).

5. The sampling interval for a particular secondary sample is instantaneous. To ensure this assumption, secondary periods were completed within the shortest period of time possible.

6. The population is closed within primary periods. To ensure this assumption, primary periods were structured as seasons of the year rather than years. Moreover, because bottlenose dolphins are long-lived animals and the sampling period in the present study was short, demographic closure can be assumed. Furthermore, the CloseTest program (Stanley & Burnham 1999) was used to investigate population closure. Closure tests indicated population closure during all primary seasons (Stanley & Burnham 1999 closure test, $\chi^2 = 15.29$, d.f. = 12, $P = 0.23$; Otis closure test, z-value = 1.91, $P = 0.97$).

7. Captures are independent between individuals. This assumption may have been violated, which is a common characteristic of dolphin mark–recapture data, because most bottlenose dolphin populations show non-random social preferences (Connor et al. 2000; Díaz López & Shirai 2008; Nicholson et al. 2012). This potential violation may cause an extra binomial variation, which is unlikely to cause a bias in the estimates obtained in the present study; however, standard errors are likely to be underestimated to some extent (Williams et al. 2002).

3.3.5.2 Modelling procedures and model selection

Mark–recapture analysis was conducted using the MARK version 8.1 (White & Burnham 1999). Data were analysed by Pollock’s robust design model (Pollock 1982; Kendall et al. 1997). Closed captures and parameters were adjusted within the parameter index matrix (PIM) available in MARK. Estimated parameters within sampling periods included the abundance of distinctly marked adult individuals in the study area (\hat{N}), the probability of first capture (p) and the probability of recapture (c). Because capture should not affect recapture when using photographic identification methods adequately (Würsig & Jefferson 1990), robust models with a behavioural response were not fitted to the data. Therefore, p was set to equal c in all models. Estimated parameters between sampling periods included the probability of apparent survival (ϕ) and two temporary emigration parameters (γ' and γ'' ; Kendall et al. 1997); ϕ is defined as the probability that a bottlenose dolphin survives and stays in the study area scaled on a seasonal basis, γ' is defined as the probability of an individual being a temporary emigrant if the individual was absent in the previous sampling period and γ'' is defined as the probability of an individual being a temporary emigrant if the individual was present in the previous sampling period (Kendall et al. 1997).

A combination of different robust models, where parameters were either constant or were allowed to vary with time, were fitted for different temporary emigration patterns to look for a more parsimonious model. The models were no movement ($\gamma'' = 0, \gamma' = 1$), no temporary emigration ($\gamma'' = \gamma' = 0$), random emigration ($\gamma'' = \gamma'$), or Markovian emigration ($\gamma' \neq \gamma''$), as described in Kendall et al. (1997). A ‘no movement’ model assumes that unobservable individual bottlenose dolphins remain unobservable and that observable individuals always remain observable over all sampling occasions. No temporary emigration assumes that there is

no temporary emigration at all. The random emigration model assumes that an identified bottlenose dolphin emigrates out of the study area independent of whether or not it was present in the study area in the previous sampling period. The Markovian emigration model permits unequal emigration and immigration rates across sampling periods, assuming that bottlenose dolphins return to the study area based on a time-dependent function (Pine et al. 2003). When models contained time-varying survival, constraints were placed (i.e. $\gamma''_k = \gamma''_{k-1}$, $\gamma'_k = \gamma'_{k-1}$), so that all parameters could be identified (Kendall et al. 1997). Capture probability was modelled as time varying over primary periods because environmental conditions were not constant over the duration of the study. Furthermore, capture probability was modelled as either constant within primary periods ($p = c(t,.)$) or varying by secondary periods within primary periods ($p = c(t)$). Heterogeneity in capture probabilities was fitted to the data using mixture models with two mixtures of capture probability (Pledger 2000) only in models with no emigration because full-likelihood estimators have not yet been developed for temporary emigration models (Kendall et al. 1997).

There is no goodness-of-fit test for robust design models in MARK (White & Burnham 1999), so the overall model fit could not be evaluated and the models were not adjusted for overdispersion. The best fitting model was selected based on the lowest Akaike's information criterion corrected for small sample size (AICc; Burnham and Anderson 2004). Likelihood ratio tests (LRTs) were used to test for significant differences between nested models.

3.3.6 Total population size

Abundance estimates from the robust design models are based solely on the number of distinctly marked adult individuals ('well-marked' and 'marked' individuals). To obtain the total population size, \hat{N}_t , the estimated abundance of distinctly marked adult individuals (N_m) was divided by the estimated proportion of distinctly marked adult individuals ($\hat{\theta}$) for each primary period (Wilson et al. 1999). To calculate $\hat{\theta}$, the number of distinctly marked adult individuals was divided by the total number of adult individuals observed in each group (including 'poorly marked' and 'unmarked' adults), averaged over all encounters during each season of the year:

$$\hat{N}_t = \frac{Nm}{\hat{\theta}}$$

For this calculation, we selected only encounters in which all members of the group were photographed. The s.e. and lognormal 95% confidence intervals (CI) of the total population size (\hat{N}_t) were derived using the delta method (Williams et al. 2002).

3.4 Results

3.4.1 Survey effort, group size and datasets

In all, 170 daily boat-based surveys were completed from March 2014 to June 2016 in the study area (**Table 3.1**), with 25 months spent in the field, totalling 517 hours and 4 285 km.

Table 3.1. Annual observation effort, robust design periods, bottlenose dolphin encounters, encounter ratio, and the number of bottlenose dolphins identified included in the mark–recapture analysis.

The encounter ratio (ER) was calculated by dividing the total number of encounters by the total number of hours spent searching for dolphins

<i>Year</i>	Robust design		Observation effort				Number of group encounters	ER	Number of bottlenose dolphins identified
	Number of primary periods	Number of secondary periods	Months	Days	Hours	Kilometres			
<i>2014</i>	3	8	9	67	217	1 625	139	1.47	119
<i>2015</i>	4	9	10	63	191	1 646	151	1.88	137
<i>2016</i>	2	5	6	40	109	1 014	96	2.20	129
<i>Total</i>	9	22	25	170	517	4 285	386	1.77	190

Overall, 386 groups of common bottlenose dolphins (*Tursiops truncatus*) were encountered in 157 boat-based surveys (92% of total days at sea) and 309 groups were sampled and photographed (80% of the total number of groups observed). Most encounters (99.7%) were recorded inside the Ría de Arousa (**Figure 3.1**). Group size ranged from 1 to 64 individuals (mean 13.0 ± 0.6 dolphins; median 10 dolphins). Group composition showed that 87.7% of the observed bottlenose dolphins were considered adults; thus, the remaining 12.3% were categorised as dependent calves (11% immature and 1.3% newborn dolphins). Calves were present in 66% of the groups observed. Group size was positively correlated with the presence of dependent calves in the group (Spearman $\rho = 0.64$, $P < 0.001$). Likewise, the number of individuals in the group was significantly higher in the presence of dependent calves (median with and without calves 13 v. 3 respectively; Mann–Whitney, $P < 0.001$).

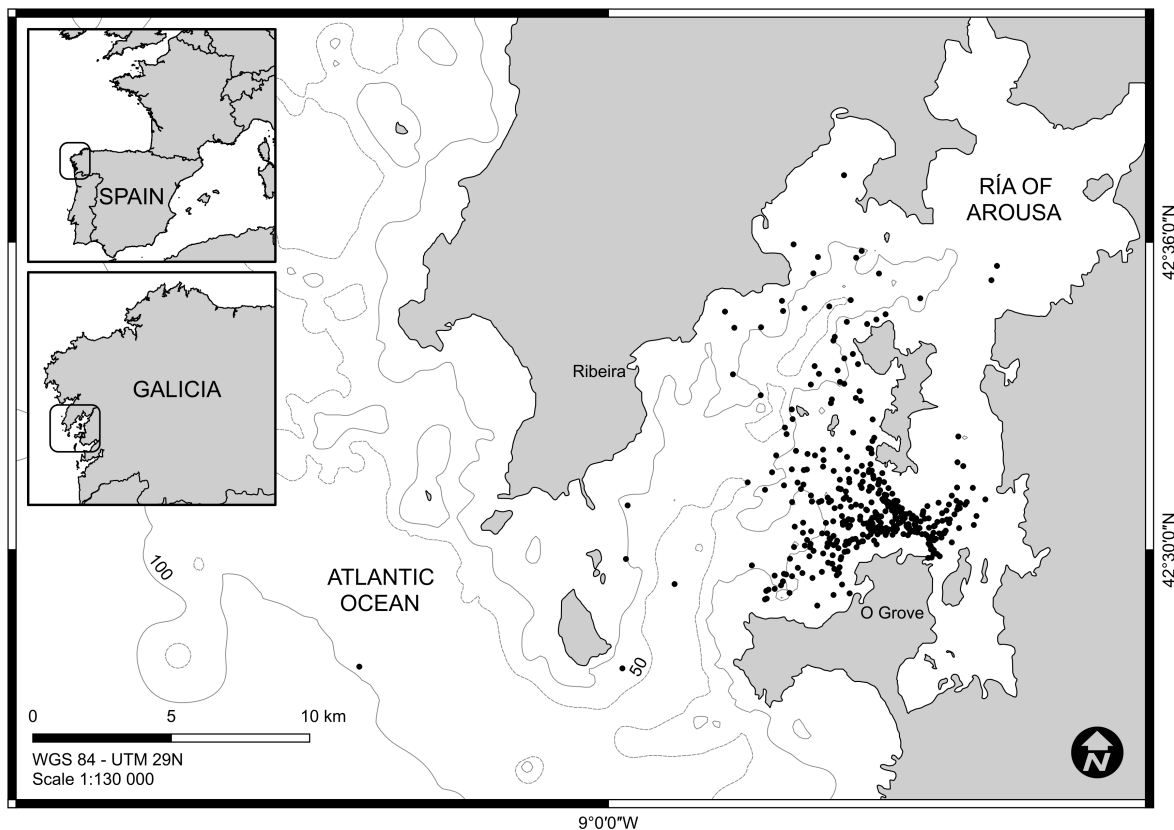


Figure 3.1. Map of the study area (Ría de Arousa and surrounding waters, North-West Spain) including the 50 and 100 isobaths. Bottlenose dolphin encounters are indicated by filled circles.

3.4.2 Relative frequency of occurrence

The mean ER of groups of bottlenose dolphins in the study area was 1.77. The ER did not exhibit any differences between the nine primary sampling periods (Kruskal–Wallis, $P > 0.05$). Similarly, seasonal fluctuations in ER were not observed (when pooled by the four seasons of the year; Kruskal–Wallis, $P > 0.05$).

3.4.3 Photographic identification data

The photographic identification catalogue used in the analysis contained 190 distinctly marked adult bottlenose dolphins. Of these, 57 were documented as female (30%), 40 were documented as male (21%) and 93 (49%) were of unknown sex. The proportion of distinctly marked adult bottlenose dolphins within each primary period ranged between 0.68 and 0.92 (mean 0.77 ± 0.01), exerting a moderate effect on the total abundance estimate. The number of encounters with identified individual bottlenose dolphins ranged from 1 to 101 (mean 16 ± 2) across the duration of the study. The number of primary sampling periods an identified individual bottlenose dolphin was photographed ranged from 1 to 9 (mean 3.6 ± 0.2). The number of encounters fluctuated across secondary sampling periods from 1 to 21 (mean 6.0 ± 0.4). Overall, 134 bottlenose dolphins (71% of the total catalogue) were identified in more than a single primary sampling period. Of these dolphins, 22 (4 females, 18 males) were identified during all the 9 primary sampling periods and in more than 75% of the secondary sampling periods. Conversely, 49 individuals (26% of the total catalogue) were only seen during a single secondary sampling period. All the individuals sighted during two or more secondary sampling seasons (141 dolphins) were only encountered inside the Ría de Arousa (a 240-km² area). During the study, only two groups of bottlenose dolphins were encountered outside the Ría de Arousa and included individuals that have never been recaptured (three identified individuals).

3.4.4 Robust design model selection

The best-fitting model, determined by the lowest AICc value, showed a constant apparent survival rate (rather than varying with time), seasonal Markovian temporary emigration (with time variation in emigration parameters ψ'' and ψ') and a different capture probability for each primary and secondary sampling occasion (**Table 3.2**). The LRT rejected the models with no movement, no emigration, random emigration, mixture proportion, Markovian emigration with

variable survival rate and Markovian emigration with constant probability of capture in favour of the first model with a Markovian emigration process and constant apparent survival rate (Chi-Square, $P < 0.001$).

Table 3.2. Capture–recapture models fitted to the capture histories of bottlenose dolphins to estimate parameters for population size (\hat{N}), apparent survival (ϕ), emigration probabilities (γ'' , γ') and capture probability (p).

The notation ‘(.)’ indicates that a given parameter was kept constant and ‘(t)’ indicates that a given parameter was allowed to vary with time. Emigration pattern notations follow Kendall et al. (1997). c , recapture probability; γ' , probability of an individual being a temporary emigrant if the individual was absent in the previous sampling period; γ'' , probability of an individual being a temporary emigrant if the individual was present in the previous sampling period; π_i , mixture proportion; AICc, Akaike’s information criterion corrected for small sample size.

Ran k	Model	Emigration pattern	AICc	Δ AICc	Model likelihood	AICc weight	Parameters	Deviance
1	(.), $\gamma' (t)$ $\gamma'' (t), p(t) = c(t)$	Markovian	-1447.2	0.00	1.0000	0.999	47	1524.0
2	(t), $\gamma' (t)$ $\gamma'' (t), p(t) = c(t)$	Markovian	-1432.6	14.6	0.0007	0.001	52	1527.6
3	(.), $\gamma' (t)$ $\gamma'' (t), p(t,.) = c(t,.)$	Markovian	-1378.1	69.1	0.0000	0.000	34	1621.2
4	(t), $\gamma' (t)$ $\gamma'' (t), p(t,.) = c(t,.)$	Markovian	-1361.3	85.8	0.0000	0.000	38	1629.4
5	(t), $\gamma' (t) = \gamma'' (t), p(t) = c(t)$	Random	-1328.9	118.3	0.0000	0.000	46	1644.5
6	(.), $\gamma' (t) = \gamma'' (t), p(t) = c(t)$	Random	-1321.3	125.9	0.0000	0.000	40	1665.1
7	(t), $\gamma' = \gamma'' = 0, \pi_i(t), p(t)$	No emigration	-1312.7	134.4	0.0000	0.000	38	1678.0
8	(t), $\gamma' = \gamma'' = 0, \pi_i(.), p(t)$	No emigration	-1293.0	154.2	0.0000	0.000	36	1702.0
9	(t), $\gamma' (t) = \gamma'' (t), p(t,.) = c(t,.)$	Random	-1259.9	187.3	0.0000	0.000	33	1741.5
10	(.), $\gamma' (t) = \gamma'' (t), p(t,.) = c(t,.)$	Random	-1252.8	194.4	0.0000	0.000	27	1761.3
11	(t), $\gamma' = \gamma'' = 0, p(t) = c(t)$	No emigration	-1112.9	334.3	0.0000	0.000	39	1875.6
12	(t), $\gamma' = 1, \gamma'' = 0, p(t) = c(t)$	No movement	-1112.9	334.3	0.0000	0.000	39	1875.6
13	(.), $\gamma' = 1, \gamma'' = 0, p(t) = c(t)$	No movement	-1092.7	354.5	0.0000	0.000	32	1910.8
14	(.), $\gamma' = \gamma'' = 0, p(t) = c(t)$	No emigration	-1092.7	354.5	0.0000	0.000	32	1910.8
15	(t), $\gamma' = 1, \gamma'' = 0, p(t,.) = c(t,.)$	No movement	-1069.2	377.2	0.0000	0.000	26	1947.0
16	(t), $\gamma' = \gamma'' = 0, p(t,.) = c(t,.)$	No emigration	-1069.2	377.9	0.0000	0.000	26	1947.0
17	(.), $\gamma' = 1, \gamma'' = 0, p(t,.) = c(t,.)$	No movement	-1048.9	398.3	0.0000	0.000	19	1981.9
18	(.), $\gamma' = \gamma'' = 0, p(t,.) = c(t,.)$	No emigration	-1048.9	398.3	0.0000	0.000	19	1981.9

3.4.5 Abundance estimation

For the best-fitting model, the estimated seasonal abundance of Nm varied between a minimum of 46 (95% CI 45.2–54.6) in spring 2015 and a maximum of 122 (95% CI 113.1–140.7) in winter 2015. The $\hat{N}t$ ranged from 56 (95% CI 55.2–66.4) in autumn 2014 to 144 (95% CI 133.1–165.6) in winter 2015 (Table 3.3). Bottlenose dolphin abundance estimates were not significantly related to the ER (Spearman ρ , $P > 0.05$). Seasonal changes in abundance were most evident (+ 155%) between autumn 2014 (56 dolphins) and winter 2015 (144 dolphins) and between winter 2015 and spring 2015 (- 60%).

Table 3.3. Seasonal abundance estimates of bottlenose dolphins in the study area.

\hat{N} , estimation of the marked population; $\hat{\theta}$, proportion of distinctly marked adult individuals; $\hat{N}t$, total population size; CI, confidence interval.

Year	Season	Number of dolphins identified	\hat{N}	s.e.	$\hat{\theta}$	$\hat{N}t$	95% CI
2014	Spring	73	76	2.8	0.68	111	107–125
	Summer	100	85	3.0	0.69	123	118–138
	Autumn	37	50	1.8	0.89	56	55–66
2015	Winter	115	122	6.7	0.85	144	133–166
	Spring	46	46	1.8	0.81	57	56–67
	Summer	82	68	1.2	0.88	77	76–84
	Autumn	40	61	3.5	0.92	66	62–78
2016	Winter	84	87	3.3	0.75	116	110–130
	Spring	114	110	4.0	0.79	139	133–153

3.4.6 Survival rates, temporal emigration patterns and capture probabilities

The model that best fitted the data gave a constant apparent survival rate of 1.0 ± 0.0 . Temporary emigration rates were higher from summer to autumn and lower from autumn to winter. The probability of being a temporary emigrant if the individual bottlenose dolphin was absent in the previous season (γ') was high, with a mean value of 0.68 ± 0.12 . Conversely, the probability of being a temporary emigrant if the individual bottlenose dolphin was present in

the previous season (γ'') was low, with a mean of 0.23 ± 0.07 (Table 3.4). Mean capture probabilities among seasons were moderate (0.65 ± 0.03), with the highest obtained in spring 2015 (0.80 ± 0.02) and the lowest during spring 2016 (0.56 ± 0.09). Temporal emigration rates (γ' and γ'') and capture probabilities did not show significant differences between seasons (Kruskal–Wallis, $P > 0.05$).

Table 3.4. Mean seasonal temporary emigration rates for the best fitting Markovian model.

Data are the mean \pm s.e. γ' , probability of an individual being a temporary emigrant if the individual was absent in the previous sampling period; γ'' , probability of an individual being a temporary emigrant if the individual was present in the previous sampling period.

<i>Season</i>	Temporary emigration rates	
	γ'	γ''
<i>Winter–spring</i>	0.73 ± 0.27	0.34 ± 0.26
<i>Spring–summer</i>	0.75 ± 0.00	0.14 ± 0.08
<i>Summer–autumn</i>	0.89 ± 0.04	0.37 ± 0.08
<i>Autumn–winter</i>	0.38 ± 0.28	0.08 ± 0.04
<i>Overall</i>	0.68 ± 0.12	0.23 ± 0.07

3.5 Discussion

This study presents the first robust estimates of abundance and demographic parameters of resident common bottlenose dolphins (*T. truncatus*) in a highly affected coastal ecosystem along the north-eastern Atlantic. Further, these results provide baseline information for future comparisons with other populations of similar characteristics under the pressure of human activities (i.e. marine traffic, fisheries and aquaculture), which may become of increasing importance as anthropogenic activities affect coastal dolphin populations.

Bottlenose dolphins are present year-round and with a high degree of occurrence inside the Ría de Arousa, an area highly affected by human activities, but also a highly productive estuarine system. This area not only produces an important amount of commercially valuable shellfish as a result of the aquaculture industry (Rodríguez et al. 2011), but the epifaunal community associated with the shellfish production also supports the substantial production of fish and megabenthos compared with other coastal and estuarine areas (Chesney & Iglesias 1979). Similar abundance estimates in terms of the number of individuals present have been obtained in other studies, performed using other mark–recapture methods rather than the robust design model, of north-east Atlantic bottlenose dolphin populations living in rich coastal environments, such as Moray Firth, Scotland (Wilson et al. 1999) and the Shannon Estuary, Ireland (Berrow et al. 2012).

This study reports seasonal fluctuations in abundance as observed in other bottlenose dolphin populations (Smith et al. 2013; Sprogis et al. 2016b). Although there may be different factors playing a key role in bottlenose dolphin distribution to some extent, the observed changes in abundance and emigration rates most likely reflect seasonal fluctuations in the abundance of prey species in this area. Bottlenose dolphins in Galicia eat a wide range of demersal fish species (Santos et al. 2007). These fish species are a resident component of the Ría de Arousa (Fariña et al. 1997) and a possible explanation for the estimates of bottlenose dolphin abundance and observed large group size compared with other coastal populations (Bearzi et al. 1997; Díaz López et al. 2013; Santostasi et al. 2016). Thus, the winter season, with the highest abundance and lowest emigration rates of bottlenose dolphins observed in this study, is characterised by a peak in numbers of demersal fish species inside the Ría de Arousa (Chesney & Iglesias 1979).

Moreover, the derived return rate ($1 - \gamma'$) of temporary emigrants (Sprogis et al. 2016b) indicated that bottlenose dolphins had a high probability of returning to the Ría de Arousa from autumn to winter.

The estimated apparent survival rate is high and constant, suggesting no mortality and no permanent emigration of individuals during the duration of the study. These results are common for long-lived species with slow growth rates and low fecundity, and have been reported in other bottlenose dolphin populations (Nicholson et al. 2012; Sprogis et al. 2016b).

The results of the present study show seasonal fluctuations in the temporary emigration rates. Temporary emigration rates for dolphins that were absent in the previous period were higher (0.38–0.89) than those for dolphins that were present (0.08–0.37), suggesting different levels of site fidelity. Some individuals (18 males, 4 females) showed a strong preference for the study area (being present in all primary periods), so there is a core of resident bottlenose dolphins in the Ría de Arousa with some other dolphins coming in and out of the study area for different periods of time. The age and sex of each individual, as well as its ecological and social preferences, could explain the differences in the residence patterns observed (Bearzi et al. 1997). In these waters, resident males may have a smaller home range than females, showing a stronger site fidelity to the Ría de Arousa. Different reasons could help explain the observed differences in site fidelity, such as different tolerances to human disturbance or different prey preferences. The latter is supported by a study about the diet of bottlenose dolphins in the region that indicated differences in diet between males and females (Santos et al. 2007). In contrast with other areas where females stay in sheltered waters for protection from predation, showing strong site fidelity (Nicholson et al. 2012; Smith et al. 2013), the absence of natural predators in the present study area may not constrain females to a small home range. Moreover, area defence by individuals or social groups could also help explain the observed differences in site fidelity and temporal occurrence rates observed in the present compared with other studies (Díaz López 2012).

Previous studies of wild populations of dolphins have documented avoidance of highly affected ecosystems where humans are present (Dawson & Slooten 1993; Bejder et al. 2006; Bearzi et al. 2009, 2008a, 2008b; Rako et al. 2013), although others have reported continued use of

valuable habitat areas despite high levels of human disturbance (Ingram & Rogan 2002; Bearzi et al. 2008b; Díaz López 2012). In highly affected and highly productive coastal ecosystems, like the Ría de Arousa, where human impact levels are consistently high primarily due to fisheries and aquaculture activities, some bottlenose dolphins may have become habituated to these predictable disturbance levels and continued to use this affected, but rich, habitat. Indeed, previous studies in the Ría de Arousa reported a relationship between the occurrence of bottlenose dolphins and mussel aquaculture zones as a result of higher densities of higher-quality prey for dolphins than in areas outside the mussel farm zones (Díaz López & Methion 2017).

The presence of bottlenose dolphins in the Ría de Arousa should not be assumed to mean that human disturbance has no effect on these bottlenose dolphins. The effects of human activities on bottlenose dolphins could differ between individuals because of individual variability in site fidelity. Future research that compares home range, social structure and reproductive success of bottlenose dolphins would help reveal individual level effects of human disturbance, should they exist.

Chapter 4. Dolphin group dynamics as an indicator of environmental change

Article submitted

Authors

Séverine Methion, Bruno Díaz López, Thierry Corrège

Personal contribution

I conceived and designed the study with BDL and TC. I collected the data. I analysed the data with input from BDL. I interpreted the results and implication with BDL. I produced the figures. I wrote the paper with input from BDL and TC.

4.1 Abstract

Because marine top predators are often large and long-lived, characteristics of their populations can potentially serve to understand the effects of ecosystem change over a range of spatial and temporal scales. Cetaceans often form groups to increase access to resources. Since the abundance and distribution of their prey is influenced by environmental conditions, environmental variation could remain a cause of intra-specific variation in group size. Using a long-term (five years) and year-round dataset, the main objective of the present study was to investigate the influence of multiple environmental factors (water temperature, water salinity, fluorescence intensity, and dissolved oxygen) on the fluctuations of bottlenose dolphin group size in a coastal area subject to intense anthropogenic activities (Ría de Arousa, North-West Spain). The findings indicated that environmental conditions (chlorophyll-a and dissolved oxygen) influence the spatio-temporal aggregation patterns of bottlenose dolphins. The observed link between these environmental variables and dolphin group size may be associated to changes in the availability of dolphin food resources. The present study provides valuable information on how dolphin group dynamics are influenced by fine-scale environmental changes in coastal ecosystems and suggests that dolphin group dynamics could act as a useful indicator of environmental change in coastal ecosystems. The results highlight the importance of considering the interaction of multiple environmental variables on fine temporal and spatial scales in ecological studies. Further studies with larger temporal and spatial scales would allow to understand dolphin distribution patterns associated with broader environmental changes.

4.2 Introduction

Changes in environmental parameters occur at different spatial and temporal scales and are a major source of uncertainty in ecological research (Heuvelink 1998; Diniz-Filho et al. 2009). Environmental conditions determine the distribution and abundance of marine top predators both directly, by altering their physiology (Kitagawa et al. 2000; Yeates & Houser 2008), and indirectly, by affecting the availability of their prey (Harlin-Cognato et al. 2007). In coastal ecosystems, anthropogenic activities induce significant environmental changes causing marine coastal environments to become some of the most vulnerable and severely degraded habitats (Halpern et al. 2008a). Because marine top predators are often large and long-lived, characteristics of their populations can potentially serve to understand the effects of ecosystem change over a range of spatial and temporal scales (Iverson et al. 2006). As such, they can serve as indicators of ecosystem health (Bowen et al. 2006). Therefore, studying the link between top predators' ecology and variability of environmental features in coastal ecosystems is becoming increasingly important.

Predicting the biological effects of environmental changes on marine top predators, such as cetaceans, is complex and arises in part from uncertainties about how individual species and local populations might respond to changes in the marine environment (Hobday et al. 2015). Cetaceans commonly form groups to increase access to resources and mating opportunity, and reduce predation risk (Alexander 1974; Díaz López et al. 2018b). Since those situations may be influenced by environmental conditions, environmental variation could remain a cause of intra-specific variation in group size and, hence, in sociality (e.g. Baird & Dill 1996; Janson & Goldsmith 1995; Macdonald 1983). Therefore, understanding the environmental factors that are responsible for the group dynamics of local populations is fundamental to comprehend how species respond to changes in their environment.

Several species of dolphins (e.g. bottlenose dolphins, *Tursiops spp.*; dusky dolphins, *Lagenorhynchus obscurus*; humpback dolphin, *Sousa spp.*) live in societies with flexible grouping patterns (i.e. fission-fusion dynamics) (Connor et al. 2000; Pearson 2009; Parra et al. 2011). Within this flexible social system, individuals associate in groups that change in composition to limit or enhance the effect of intra-group competition (Smith et al. 2008).

Thereby, while they limit the effect of competition through group splits during periods of high competition (Dunbar 1992), they enhance cooperative effects through group cohesion when the ecological costs of aggregating are low or when the benefits of grouping are high (Takahata et al. 1994; van Schaik 1999). Fluctuations in cetacean group size can therefore be indicative of the characteristics of the environment on which a local population relies for food (Foster et al. 2012). Studying such fluctuations is also important to understand and predict the influence of environmental variation on a population (Lusseau et al. 2004). Long-term datasets are of key importance to assess and detect cetaceans' responses to environmental variations, yet few are available because of logistical difficulties and financial costs (Foster et al. 2012; Díaz López 2019).

An understanding of the effect of environmental variables on grouping pattern in coastal cetaceans is becoming increasingly important since anthropogenic activities (e.g. fisheries and aquaculture) induce significant environmental changes in marine coastal waters (Díaz López 2019). Bottlenose dolphins are long-lived, marine top predators that inhabit a wide range of habitats due to their extreme behavioural plasticity (Connor et al. 2000). They adapt to a variety of marine and estuarine habitats, and frequently enter harbours, bays, lagoons, and rivers (Connor et al. 2000). They feed on locally abundant prey species (mainly demersal and pelagic fish, and cephalopods) (Santos et al. 2007) and live in fission-fusion societies (Wells et al. 1987; Smolker et al. 1992; Connor et al. 2000). This species therefore provides an adequate framework for analysing the effect of environmental variables on coastal cetaceans' group size. Previous research into the effects of environmental variation on bottlenose dolphins highlighted that environmental variables, linked to food availability (e.g. sea surface temperature), can influence their grouping patterns and abundance (e.g. Lusseau et al. 2004; Sprogis et al. 2018). In spite of this, little is known about the influence of environmental factors on bottlenose dolphin group dynamics and, in particular, in coastal waters under the pressure of intense anthropogenic activities.

Resident, coastal common bottlenose dolphins (*Tursiops truncatus*, hereafter referred to as bottlenose dolphins) inhabit the Ría de Arousa (North-West Spain) (Díaz López & Methion, 2017; Methion & Díaz López 2018). This area is an important feeding ground for bottlenose dolphins (Methion & Díaz López 2019a) where the distribution and abundance of their prey is

indirectly influenced by intense upwelling events (Evans & Prego 2003), land runoff (Varela et al. 2005), and the presence of one of the world's most important shellfish farming industry (Rodriguez et al. 2011; Chesney & Iglesias 1981). Using a long-term (five years) and year-round dataset, the main objective of the present study is to investigate the influence of multiple environmental factors (water temperature, water salinity, fluorescence intensity, and dissolved oxygen) on the fluctuations of bottlenose dolphin group size in a coastal area subject to intense anthropogenic activities (Ría de Arousa, North-West Spain). Through this framework, we aim to further our understanding of the effect of spatio-temporal variability in coastal environments on marine top predators' ecology.

4.3 Methods

4.3.1 Study area

The study was performed along the North-Western coast of the Iberian Peninsula, specifically in the largest of the Galician rías (which are ancient drowned tectonic valleys that were taken over by the sea), the Ría de Arousa (240 km²) (North-West Spain) (Evans & Prego 2003; Prego et al. 1999) (**Figure 4.1**). Water circulation in the ría is driven by the tide, wind regime over the continental shelf, wind regime over the ría, freshwater discharge, air temperature, and upwelling events (Otto 1975; Alvarez et al. 2005). The ría is divided into zones under an external oceanic influence (exposed to oceanic processes, deeper) and zones under an internal estuarine influence with important tidal range (exposed to fluvial processes, shallower and secluded areas) (Evans & Prego 2003). The internal estuarine area is more exposed to changes in salinity and temperature due to the input of freshwater (Alvarez et al. 2005). This ría is an estuarine coastal embayment with a large tidal range (between 1.1 m and 3.5 m during neap and spring tides respectively) (Álvarez et al. 2005). Residence time of water in the Ría de Arousa is 5 to 10 days (Alvarez-Salgado et al. 1996). The frequent upwelling of cold and dense Eastern North Atlantic Central Water (ENACW) results in nutrient enrichment of the water, making this area one of the most productive oceanic regions in the world (Santos et al. 2011). Oceanographic patterns in the region are modulated by the seasonal cycle of wind direction, where the prevalence of north-eastern winds between May and October is the main cause of coastal upwelling events that significantly increases primary production (Álvarez et al. 2011). The ría behaves as a partially mixed estuary where the partial stratification is maintained by the river discharge in winter, and by solar heating and coastal upwelling in summer (Alvarez et al. 2005). Under upwelling conditions, nutrient-rich subsurface ENACW enter the ría by positive estuarine circulation (Prego & Fraga 1992). The rest of the year, there is a dominance of downwelling conditions (Figueiras et al. 2002), during which warmer, nutrient-depleted surface waters move inshore and downward reducing the strength of exchange flow (Alvarez et al. 2005). The main freshwater input is located in the innermost part of the ría and comes from two rivers: the Ulla River (river flow = 79.3 m³/s) and the Umia River (river flow = 16.3 m³/s) (Alvarez et al. 2005). These rivers show a high seasonal variability in river flow, with the highest value in winter and the lowest in summer, following the rainfall pattern (Alvarez et al. 2005).

Around 2 370 shellfish cultivation rafts (about 500 m² each) are located in the Ría de Arousa (Rodríguez et al. 2011), covering approximately 17% of the area (Díaz López & Methion 2017). Bottlenose dolphins are present year-round in this ría (Díaz López & Methion 2017) and their seasonal abundance ranges from 56 to 144 individuals (Methion & Díaz López 2018). The ría is used as a main foraging area for resident bottlenose dolphins (Methion & Díaz López 2019a, b), with a predominance of foraging activities inside shellfish farm areas (Methion & Díaz López 2019a).

4.3.2 Data collection

Boat-based surveys were conducted year-round from March 2014 to November 2018. The Ría de Arousa was monitored onboard a research vessel during daylight hours at a constant speed of 6 kn. The minimum number of experienced observers and vessel speed remained consistent during the study period. While the surveyed area and daily routes were designed to cover the study area equally, the spatial distribution of the effort varied according to weather conditions and time constraints throughout the study period (Methion & Díaz López 2018). Surveys were carried out when the sea conditions were no greater than 3 on the Douglas sea force scale (approximately equivalent to the Beaufort wind force scale) and visibility was not reduced by rain or fog (Díaz López & Methion 2017). A group of bottlenose dolphins was defined as one or more individuals observed within a 100 m radius and, if more than one, interacting with each other and engaging in the same behavioural activity (Methion & Díaz López 2018). Upon a bottlenose dolphin group encounter, searching effort ceased and the vessel slowly manoeuvred towards the animals in order to minimise disturbance during the approach. A suite of data including, the initial time, Global Positioning System (GPS) location, depth (depth at the first position of the group encounter), the group size, and group composition were recorded for each bottlenose dolphin group encounter. Digital photographs were taken using DSLR cameras equipped with 35–300 mm telephoto zoom lens. Group size was later verified with photographs taken during each encounter by increasing the number of individuals present if more individuals were photograph (Methion & Díaz López 2019b). The age of individuals was classified as either adults or dependent calves (including new-born dolphins < 1.5 m, swimming in the infant position, and immature dolphins, < 2/3 length of an adult, in association with an adult) based on behavioural cues and visual assessment of the size (following Methion & Díaz

López 2018, 2019b). On return to shore, the minimum distance between the first position of each group of dolphins and the coastline (Distance to the coast) was calculated from the GPS position via spatial analyst tools using QGIS software (www.qgis.org).

4.3.3 Environmental data

Environmental data were obtained from the weekly records of oceanographic data provided by INTECMAR observation network from a set of 11 sampling stations distributed in the Ría de Arousa (<http://www.intecmar.gal>) (**Figure 4.1**). Data obtained included weekly measurements at each station of vertical profiles of four oceanographic parameters: water temperature (WT, in degree Celsius, °C), salinity (WS, in practical salinity unit, PSU), dissolved oxygen (O₂, in mL/L), and water fluorescence intensity (FL, in mg/m³, as an indirect measure of chlorophyll-a concentration) using a portable CTD instrument sensor and a fluorometer. These variables were collected along the water column, every week, at each station, during the full study period. The high frequency of sampling (weekly) and the high number of stations (11) distributed along the Ría de Arousa provide a thorough understanding of the oceanographic conditions in the area. These variables were explored to detect errors of measurements with two packages of the software R (R Development Core Team 2011). The package 'lubridate' was used to work with dates and the package 'dplyr' was used for data manipulation (to filter and summarize the data). For each of the variables, at each station, for each sampling day, the average values for the water column was calculated. A monthly average value, per variable, per station was also calculated. To take into account the spatio-temporal variability of each variable and to link the oceanographic data previously obtained from IntecMar to bottlenose dolphin presence-absence data and sightings, the oceanographic data were transformed to raster format. QGIS 2.18 was used to create the raster files, to extrapolate the monthly spatial variation across the study area, and for each one of the oceanographic variables. A monthly raster for each variable was therefore created by interpolating the values of each station using the inverse distance weighted (IDW) interpolation in QGIS. One raster was created for each of the oceanographic variables, for each month of the study period, from the 11 sampling stations. The maps were created by interpolating each variable (of each station, of each month) using the inverse distance weighted interpolation. IDW is a spatial interpolation method that assumes that values of nearby points are more similar than values of more distant points (Li &

Heap 2008). Hence, it estimates values at unknown locations by giving a heavier weight to closer sampled points (Li & Heap 2008; Lu & Wong 2008). IDW is a spatial interpolation method that has been widely used to predict environmental variables (Li & Heap 2008). The ‘point sampling’ tool in QGIS was then used to extract the raster values (environmental variables) from multiple layers at each bottlenose dolphin encounter position in order to link the group size with environmental variables.

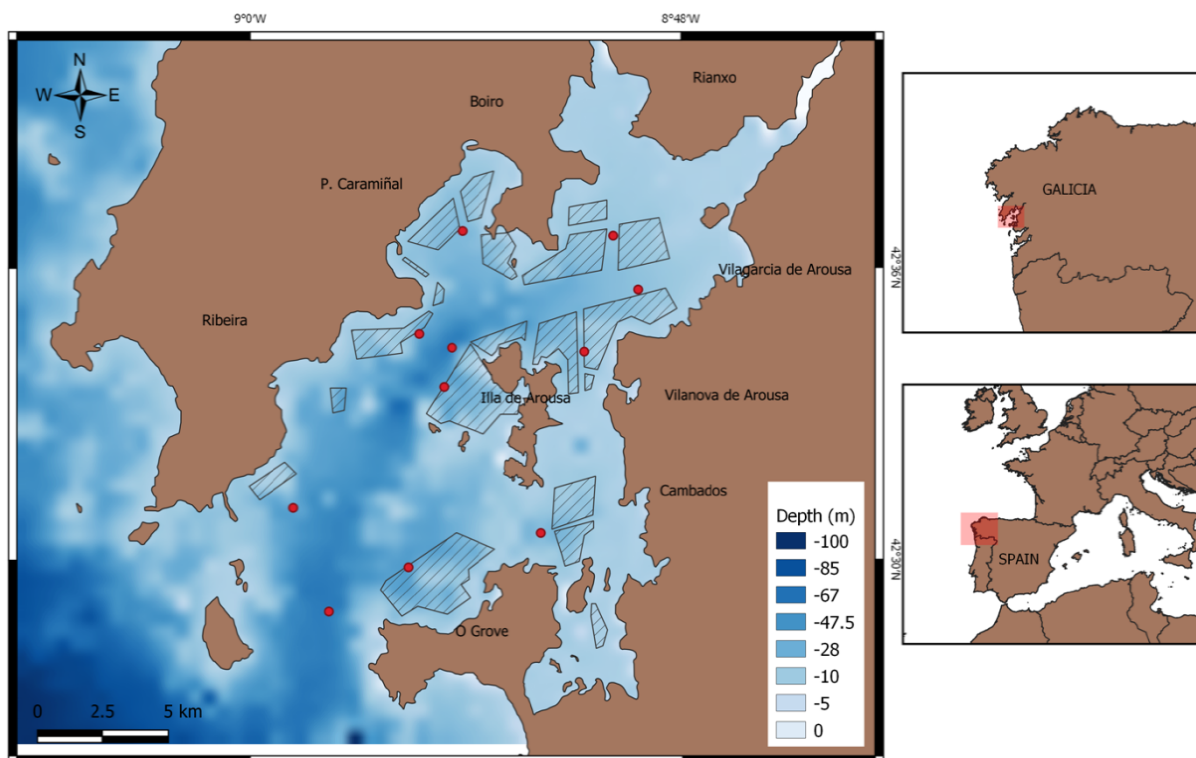


Figure 4.1. The Ría de Arousa (North-West Spain) where bottlenose dolphin distribution and abundance surveys were conducted from 2014 to 2018.

The red circles represent the 11 oceanographic stations from which environmental data (fluorescence intensity, water temperature, water salinity, and dissolved oxygen) were collected. The polygons represent the shellfish farms.

4.3.4 Data analysis and modelling framework

Six environmental predictors (depth, distance to the coast, water temperature, water salinity, dissolved oxygen, and fluorescence intensity) were initially considered to have potential ecological significance and were available for each group of dolphins observed. Date was not included as covariate, because it was related with environmental variables that show seasonal changes (i.e. water temperature, water salinity) (Díaz López & Methion 2018a) which were

included instead due to their biological interpretability (Forney 2000), and to prevent over-parameterization (Burnham & Anderson 2002). Likewise, latitude and longitude were not included in further analysis, because they were related with environmental variables that show spatial changes within the ría (i.e. depth and water salinity) (Alvarez et al. 2005).

Generalized additive models (GAMs) were used to explore the variables that might have affected bottlenose dolphin group size. GAMs are widely-used for interpreting ecological interactions and are particularly well-suited for the type of non-linear responses that are expected in species-environment relationships (Hastie & Tibshirani 1990). Data exploration protocols described by Zuur et al. (2010) were used to identify outliers, data variability, and relationships between environmental variables and the bottlenose dolphin group size (response variable). Modelling was initiated using a full General Linear Model (GLM), which included all six environmental variables that could potentially drive group size: depth, distance to the coast, water temperature, water salinity, dissolved oxygen, and fluorescence intensity. Before model fitting, variance inflation factors (VIFs) were calculated to assess multicollinearity with all values below a cut-off level of 5 (Dormann et al. 2013). To find a set of explanatory variables that does not contain collinearity, variables were removed one at a time and then the VIF values were recalculated. Following this procedure, 'distance to the coast' was excluded before starting the GAM fitting. Bottlenose dolphin group size was modelled using a GAM with a negative binomial distribution and logarithmic link function. The negative binomial distribution is appropriate for overdispersed count data such as group size, in which the variance is larger than the mean. The smooth functions were constructed as cubic splines and their optimal shape was estimated by minimizing the general cross validation (GCV) criterion (Wood 2006). To limit relationships to plausible simple forms and limit the risk of overfitting we reduced the number of knots in the smooth functions to 5. The optimal model was selected using a combination of backward and forward model selection procedures based on the Akaike Information Criteria (AIC) and covariate interaction terms were not considered as the primary aim was to identify a potential 'bottlenose dolphin group size' – 'environment' relationships, instead of maximising explained deviance (Beekmans et al. 2010). Model assumptions were checked by visual inspection of the residuals and regression fits were examined using plots of residuals against fitted values. The Durbin-Watson test (from the R package "lmtest", Zeileis & Hothorn 2002) and auto-correlation functions (ACF) were used to check for serial correlation,

both in our raw data and in the residuals from the models. The final model was the model with the lowest AIC given that effects of all explanatory variables retained in the model were statistically significant and there were no clear patterns in the residuals (Hastie & Tibshirani 1990). The GAMs results and diagnostic information about the fitting procedure were implemented from the *mgcv* (Wood 2006) and *MASS* (Venables & Ripley 2002) packages in v. 1.8.1. of the statistics and graphics tool R (R Development Core Team 2011). Partial predictions with 95% confidence intervals were plotted for each covariate included within the final model. The data are presented as means \pm standard error (s.e.).

4.4 Results

4.4.1 Survey effort and bottlenose dolphin group dynamics

Overall, 340 daily boat surveys over a period of 51 months of research and covering 7 495 nm were undertaken between March 2014 and November 2018. In total, 1 340 h were spent in satisfactory conditions (up to 3 on the Douglas sea force scale and absence of rain or fog). During the study, 846 bottlenose dolphin groups were encountered (**Figure 4.2**). A total number of 9 009 bottlenose dolphins were observed on 313 different days at sea (92% of total number of daily surveys) over 51 different months. This species was encountered all over the Ría de Arousa and in all months of the year.

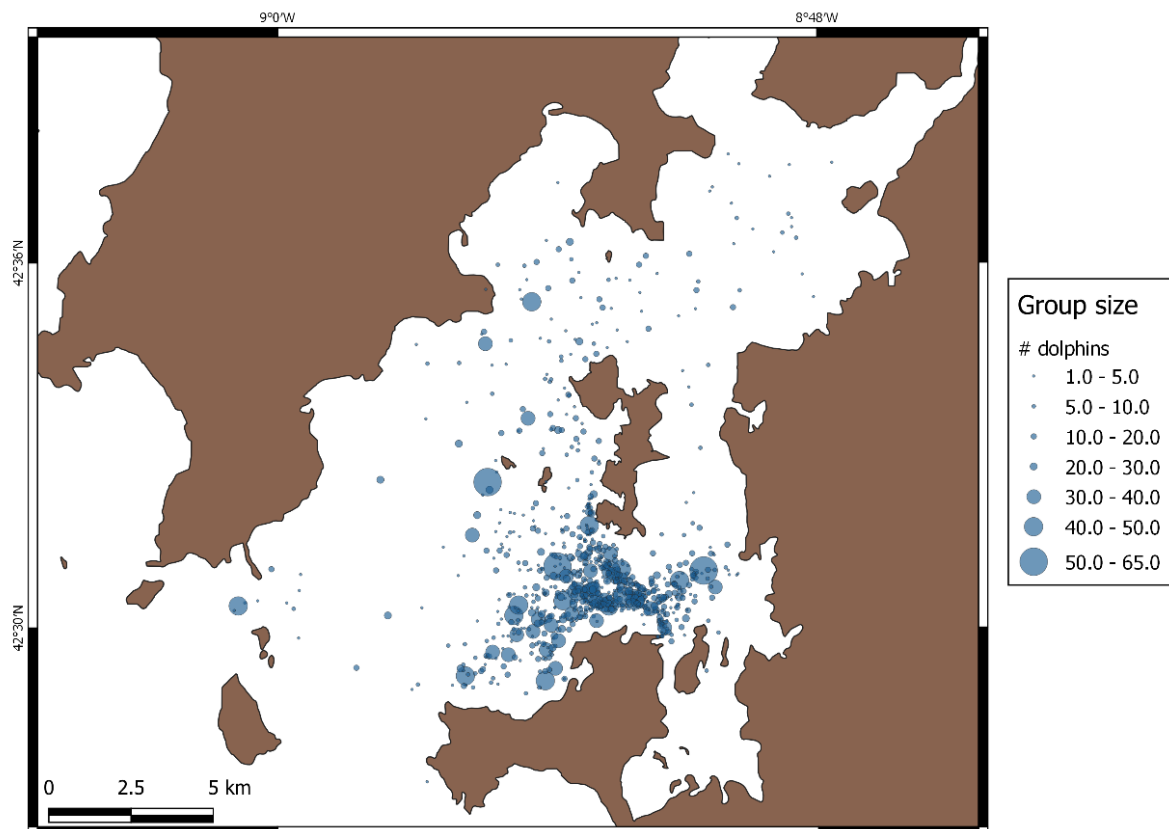


Figure 4.2. Bottlenose dolphins encounters in the Ría de Arousa, from 2014 to 2018.

The size of the circles represents the size of the groups.

Group size ranged from 1 to 64 dolphins (mean = 10.6 ± 0.3 , median = 7) with the majority (78% of the groups) containing 15 or less individuals. The groups were composed of 88% of adults and 12% of dependent calves (of which 1.7% were new-born dolphins younger than 1 year-old). Dependent calves were present in 55% of the observed groups. New-born dolphins were present in 11% of the observed groups and were observed from June to September.

There were annual fluctuations in the group size, with larger groups mostly present during the first three years of research and smaller groups during the last two years (Kruskall-Wallis, $P < 0.01$) (**Table 4.1**). However, there were no seasonal fluctuations in the group size (Kruskall-Wallis, $P > 0.05$) (**Table 4.2**).

Group size was significantly related with the number of dependent calves in the group (Spearman rho = 0.59, $P < 0.001$). Likewise, the size of the aggregations was significantly higher in presence of dependent calves (mean with calves = 14.6 ± 0.5 vs. mean without calves = 6.0 ± 0.3 ; Mann-Whitney, $P < 0.001$).

Table 4.1. Yearly variation in bottlenose dolphin group size and associated environmental factors, between 2014 and 2018, in the Ría de Arousa.

WT: water temperature (°C). WS: water salinity (PSU). FL: fluorescence intensity (mg/m³). O2: dissolved oxygen (mL/L). Depth: (m).

	Mean group size	WT	WS	FL	O2	Depth
<i>2014</i>	12.89 ± 1.0	17.01 ± 0.14	34.50 ± 0.05	2.15 ± 0.04	5.62 ± 0.03	15.70 ± 0.86
<i>2015</i>	11.63 ± 0.81	15.10 ± 0.16	34.69 ± 0.07	3.69 ± 0.07	3.00 ± 0.21	14.55 ± 0.79
<i>2016</i>	13.60 ± 0.82	15.26 ± 0.10	33.96 ± 0.16	1.00 ± 0.06	5.41 ± 0.04	16.33 ± 0.74
<i>2017</i>	8.07 ± 0.49	15.61 ± 0.10	34.78 ± 0.05	2.17 ± 0.09	5.32 ± 0.03	13.41 ± 0.64
<i>2018</i>	7.07 ± 0.48	15.25 ± 0.16	33.95 ± 0.15	1.63 ± 0.07	4.54 ± 0.03	15.69 ± 0.87
<i>Overall</i>	10.65 ± 0.34	15.60 ± 0.06	34.38 ± 0.05	2.06 ± 0.04	4.85 ± 0.05	15.1 ± 0.34

Table 4.2. Seasonal variation in bottlenose dolphin group size and associated environmental factors, between 2014 and 2018, in the Ría de Arousa.

WT: water temperature (°C). WS: water salinity (PSU). FL: fluorescence intensity (mg/m³). O2: dissolved oxygen (mL/L). Depth: (m).

	Mean group size	WT	WS	FL	O2	Depth
<i>Winter</i>	10.71 ± 0.85	12.83 ± 0.05	32.89 ± 0.17	1.91 ± 0.12	5.55 ± 0.06	15.26 ± 0.85
<i>Spring</i>	10.41 ± 0.61	15.70 ± 0.07	33.97 ± 0.08	2.31 ± 0.08	5.23 ± 0.08	15.56 ± 0.62
<i>Summer</i>	10.86 ± 0.52	16.93 ± 0.06	35.28 ± 0.02	2.14 ± 0.07	4.28 ± 0.10	14.32 ± 0.52
<i>Autumn</i>	10.44 ± 1.04	15.41 ± 0.10	34.93 ± 0.06	1.25 ± 0.08	4.50 ± 0.05	16.17 ± 1.10
<i>Overall</i>	10.65 ± 0.34	15.60 ± 0.06	34.38 ± 0.05	2.06 ± 0.04	4.85 ± 0.05	15.1 ± 0.34

4.4.2 Effects of environmental conditions on the bottlenose dolphin group size

Table 4.1 and **Table 4.2** displays the average environmental conditions across the 5 years of research and across seasons, respectively. Based on AIC scores, the most parsimonious model included fluorescence intensity, dissolved oxygen, and water temperature as explanatory variables of bottlenose dolphin group size. Yet, water temperature did not contribute significantly to the observed variation in group size ($P > 0.05$). The number of bottlenose dolphins in a group was predicted to be mostly influenced by the concentration of chlorophyll-a (fluorescence intensity) and dissolved oxygen in the water. Group size showed a linear relationship with the fluorescence intensity, with the number of dolphins decreasing within the group with more intense fluorescence conditions (**Figure 4.3**, **Figure 4.4a**). Dissolved oxygen showed a non-linear relationship with the number of bottlenose dolphins present in each group (**Figure 4.3**, **Figure 4.4b**). A decrease of 1 mg/m^3 in average fluorescence intensity increased the group size by 11.6% (from 8.38 ± 0.46 to 9.35 ± 0.51), while an increment of 1 mL/L in average dissolved oxygen resulted in an 38.1% (from 8.38 ± 0.46 to 11.57 ± 0.66) increase in group size.

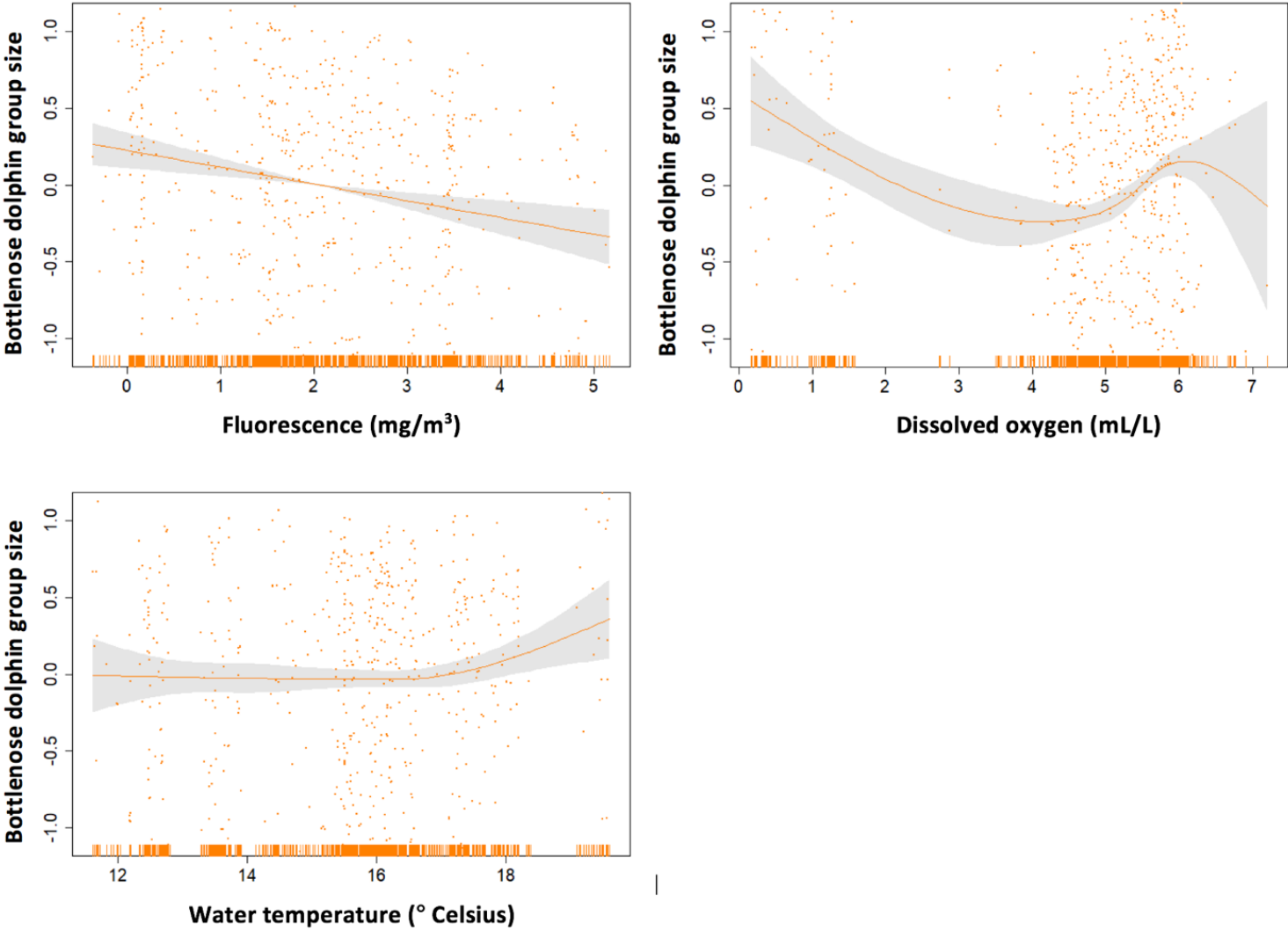


Figure 4.3. Averaged predictions of the number of bottlenose dolphins in each group for each significant covariate in the final model. The 95% confidence limits are represented, when all other variables are fixed on their mean value.

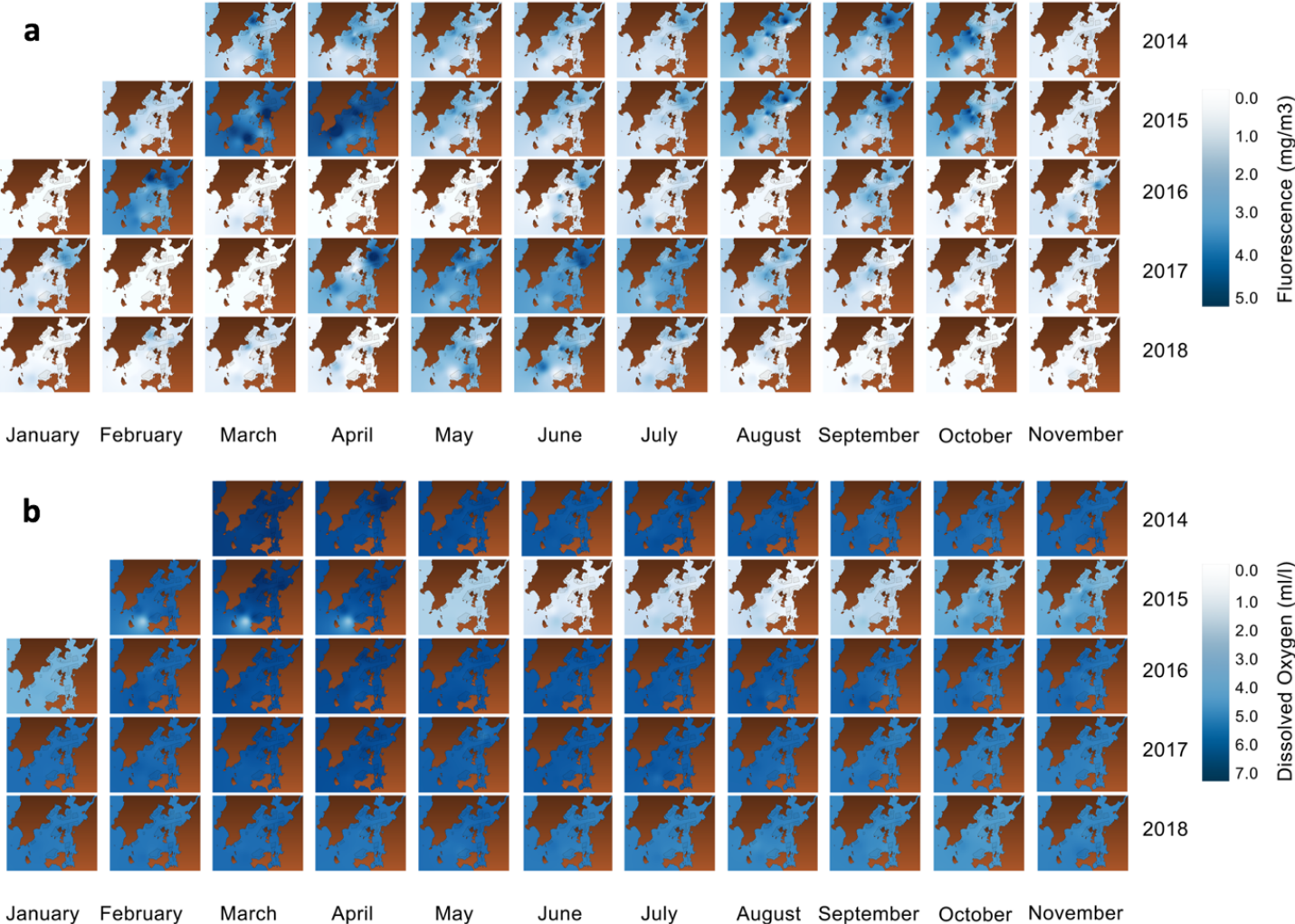


Figure 4.4. Monthly average of (a) fluorescence (mg/m³) and (b) dissolved oxygen (mL/L) in the Ría de Arousa, from 2014 to 2018.

4.5 Discussion

A comprehensive 5-year, year-round, dataset was used to investigate the relationship between environmental variability in coastal waters and the group size of a marine top predator, the bottlenose dolphin. This study indicates that environmental conditions influence the spatio-temporal aggregation patterns of bottlenose dolphins in a highly affected coastal ecosystem. Fluctuations in bottlenose dolphins' group size was indeed linked with concentration of chlorophyll-a and dissolved oxygen in the water column. The observed link between these environmental variables and dolphin group size may be associated to changes in the availability of dolphin food resources.

Environmental variables (i.e. chlorophyll-a, measured as fluorescence intensity values, and dissolved oxygen) seem to be a key mechanism in shaping the availability of bottlenose dolphins' prey and therefore the group dynamics of bottlenose dolphins. The concentration of chlorophyll-a and dissolved oxygen play a fundamental role in fish dynamics in coastal ecosystems (Ware & Thomson 2005; Stevens et al. 2006). Dissolved oxygen is an important factor affecting the distribution and abundance of both demersal and pelagic fish communities (Howell & Simpson 1994), with fish diversity and abundance increasing in areas of high oxygen levels (Mas-Riera et al. 1990; Howell & Simpson 1994). Therefore, the large groups of dolphins observed in higher concentration of dissolved oxygen (**Figure 4.3**) might be related to a higher availability of prey for bottlenose dolphins. Fluctuations in primary production (chlorophyll-a concentration) could be responsible of short-term changes in bottlenose dolphin prey availability. Primary production in the Ría de Arousa is mainly stimulated by subsequent increases in total nitrogen and phosphorus from continental inputs (Alvarez-Salgado et al. 1996) and by nutrient enrichment from upwelled offshore waters (Fraga 1981). The observed link between the concentration of chlorophyll-a in the water and bottlenose dolphin group size (**Figure 4.3**) does not necessarily imply a direct relationship. The fluorescence intensity values (i.e. chlorophyll-a concentration), associated to large groups of bottlenose dolphins, could be interpreted as a period of phytoplankton decay, mediated by zooplankton grazing, and therefore a high abundance of plankton-feeding fish species (Díaz López & Methion 2019).

Bottlenose dolphin grouping patterns are, at least partially, dependent on habitat features (Connor et al. 2000; Lusseau et al. 2004). Previous studies indicated that bottlenose dolphins, in the Ría de Arousa, were capable of developing different foraging strategies, including cooperative feeding techniques, which involve a high degree of social organisation and behavioural adaptation (Methion & Díaz López 2019a,b). Therefore, when environmental conditions (high fluorescence intensity values and low concentration of dissolved oxygen; **Figure 4.3**), in specific zones of the ría, lead to a low availability of prey (plankton-feeding fish species) (Santos et al. 2007), bottlenose dolphins could form smaller groups while foraging to reduce competition (Methion & Díaz López 2019b). Smaller groups may indeed be advantageous when prey items occur singly, and cooperative or coordinated foraging is inefficient (e.g. Heithaus & Dill 2002; Mann & Sargeant 2003). In contrast, bottlenose dolphins could increase prey-finding and capture abilities by forming large groups when the environmental conditions (low fluorescence intensity values and high concentration of dissolved oxygen; **Figure 4.3**) facilitate a higher availability of fish species (i.e. the entrance of large schools of pelagic fish species in the ría). Fishery catch (landings) of plankton-feeding fish species (clupeidae) in the Ría de Arousa indeed did follow a similar temporal pattern to the ones observed with bottlenose dolphin group size, with a peak in 2016 (1085 tonnes) and a minimum in 2018 (259 tonnes) (official catches for the Ría de Arousa, Galician Institute for Statistics, 2018). Changes in prey availability, in relation to large-scale ocean climate variation, were indeed previously associated to fluctuation in bottlenose dolphin grouping behaviour (Lusseau et al. 2004).

Several environmental factors may interact and influence the observed patterns in dolphin group size. The presence of intensive shellfish aquaculture activities in the Ría de Arousa, which introduces a large biomass of filter-feeders, may also alter the local environmental conditions (Chesney & Iglesias 1979). Indeed, suspended bivalve culture activities divert primary production and energy flow from planktonic food webs by producing faeces and pseudofaeces, which are a source of changes in the physical and chemical characteristics of the ecosystem (Alonso Perez et al. 2010). Therefore, shellfish aquaculture could also influence the distribution of dolphin food resources (Díaz López & Methion 2017), which may promote fluctuations in dolphin group size (as a response to fluctuations in prey availability).

Bottlenose dolphin group dynamics is likely to be driven by multiple factors, and other variables such as behaviour, parental care, and protection from predators and conspecifics (Gowans et al. 2007) may act synergistically with environmental parameters. The observed influence of dependent calves (presence and number) on bottlenose dolphin group dynamics is in concordance with previous studies reporting larger groups in presence of dependent calves (Wells et al. 1987; Díaz López 2012). Although the mechanisms that led to the link between group size and presence of calves have not been analysed in this study, such relationship might be mainly explained by parental care and protection from conspecifics, as several cases of infanticide have been reported in this area (Díaz López et al. 2018b: annex 1). Further studies about parental care and predation risk could therefore help the understanding on grouping patterns in bottlenose dolphins.

Findings of this study highlight the importance of long-term monitoring to identify possible environmental factors affecting marine top predators over differing spatial and time scales. The long-term, year-round dataset used in this study allowed for both monthly and yearly fluctuations to be analysed, highlighting the effect of environmental variables on the group dynamics of coastal bottlenose dolphins. Continued monitoring of this population will be important as coastal resident dolphins are at risk from anthropogenic stressors, including aquaculture activities (Methion & Díaz López 2019a; Díaz López 2012), fisheries (López et al. 2002; Díaz López et al. 2018a), and marine traffic (Nowacek et al. 2001).

The present study provides valuable information on how dolphin group dynamics are influenced by fine-scale environmental changes in coastal ecosystems and suggests that dolphin group dynamics could act as a useful indicator of environmental change in coastal ecosystems. The findings highlight the importance of considering the interaction of multiple environmental variables on fine temporal and spatial scales in ecological studies. The observed fluctuation in dolphin group size could also be driven by unmeasured oceanographic events occurring at different temporal and spatial scales than the ones monitored in this study (e.g. outside the Ría de Arousa and in periods of time previous to the research). Further studies with larger temporal and spatial scales would allow to understand dolphin distribution patterns associated with broader environmental changes.

Chapter 5. The impact of shellfish farming on common bottlenose dolphins' use of habitat

Article published

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Personal contribution

I conceived and designed the study with BDL. I collected the data with BDL. I interpreted the results and implication with BDL. I contributed to data analyses. I reviewed the manuscript.

5.1 Abstract

Shellfish farming is an expanding segment of marine aquaculture, but the impact of this industry on coastal cetacean species is only beginning to be considered. The interaction between mussel farming and coastal cetaceans in one of the world's leading producers of this bivalve (Galicia, NW Spain) was studied. Specifically, the habitat use of common bottlenose dolphins (*Tursiops truncatus*) was evaluated in relation to environmental, geographical, and anthropogenic variables. Over a period of 22 months spent in the field, 154 daily boat surveys and 353 common bottlenose dolphin encounters were done. Results of this study confirm that areas of mussel production are frequently utilized by common bottlenose dolphins. Of the investigated factors, shellfish farms appeared to have a clear effect, with increased bottlenose dolphin occurrence at mussel farm locations and in waters close to the aquaculture zones. These observations contrast with previous studies where the occurrence and distribution of coastal cetacean species decreased in association with shellfish aquaculture representing a source of habitat loss and causing potentially negative effects. These differences suggest that the interactions between shellfish aquaculture and cetaceans are affected by the culture method and cetacean species involved. The positive relationships between dolphins' occurrence and mussel aquaculture zones are presumably the result of large aggregations of fish species around mussel rafts, which provide high densities of high-quality prey for dolphins. This study provides new insights into the understanding of how shellfish aquaculture influences coastal dolphins and hence support the design of policies aimed at implementing ecosystem management principles.

5.2 Introduction

Marine aquaculture, that is, the farming of plant and animal species from the sea, has shown a large worldwide expansion over the last years (FAO 2014). An increasing demand for seafood products, declining wild stocks, together with globalization of trade and economic incentives, have resulted in this rapid growth in fish and shellfish farming (Naylor et al. 2000; Bostock et al. 2010). According to the latest available statistics collected globally by FAO (2014), world aquaculture production attained an all-time high of 90.4 million tonnes in 2012 (US\$144.4 billion).

Shellfish farming is an important sector of the industry (representing the 23% of the total production) and, like other forms of aquaculture, is expanding (FAO 2014). Consistent with this global trend, shellfish aquaculture has increased rapidly in Galician waters (Spain) since the 1940s (Miguez et al. 2009). Mussel production volume in Galician waters (300 000 tonnes annual production) represents 98% of the total Spanish production, approximately 50% of the European production and almost 13% of the world mussel production (FAO 2014). This Spanish region is the third largest mussel producer in the world behind China and Thailand (Fuentes et al. 2000; Rodriguez et al. 2011).

The development of aquaculture industry has been accompanied by an increase in environmental impacts (reviewed by Pillay 2008). Concerns related to shellfish aquaculture have centred around the introduction of nonindigenous species, habitat alteration, changes to community structure or function (Chesney & Iglesias 1979; Iwama 1991; McKindsey et al. 2011), and effects on bird and mammal populations (Price & Nickum 1995; Würsig & Gailey 2002). Only a relatively small number of studies have evaluated the effects of shellfish aquaculture on cetacean species (Indo-Pacific bottlenose dolphin, *Tursiops aduncus* Watson-Capps & Mann 2005; Dusky dolphin, *Lagenorhynchus obscurus*; Markowitz et al. 2004; Pearson et al. 2012; Chilean dolphin, *Cephalorhynchus eutropia*; Ribeiro et al. 2007). These previous studies showed that shellfish farming restricts cetaceans from using the available space, reducing the extent of coastal areas used for potentially important biological and social activities.

Common bottlenose dolphins (*Tursiops truncatus*) are particularly likely to interact with human activities (Würsig & Gailey 2002; Díaz López 2006b, 2012, 2017; Bearzi et al. 2009). Most of the previous studies about bottlenose dolphins and aquaculture have been focused on the interaction with finfish farms (Díaz López et al. 2005; Díaz López 2006b, 2012, 2017; Díaz López & Shirai 2008). However, there are no previous studies about the impact of shellfish aquaculture on this species. Likewise, the relationship between mussel cultivation in Galicia, which constitutes one of the world's leading producers of this bivalve (Fuentes et al. 2000), and habitat use by cetacean species has never been analysed. As observed in other cetacean species, shellfish aquaculture could negatively affect this species through habitat transformation or exclusion, entanglement risk, or by disturbance arising from farming activities and boat traffic (Würsig & Gailey 2002). As the hazards can already be identified, information on habitat use is a critical missing piece of the equation that can be used to determine the impact shellfish aquaculture may have on common bottlenose dolphins.

The aims of this study are (i) to assess the type of impact caused by shellfish aquaculture on bottlenose dolphins' presence and distribution and (ii) to describe habitat selection patterns of common bottlenose dolphins in this important area for shellfish farming, while identifying potential anthropogenic and environmental features responsible for fine-scale habitat use.

5.3 Methods

5.3.1 Study area

Galicia is a region situated in the northwest of Spain with 1 195 km of coastline, on which there are a series of ancient drowned tectonic valleys taken over by the sea (also referred to as “rías”) (Evans & Prego 2003). The rías are important areas for shellfish aquaculture, and more particularly for the production of mussels (*Mytilus galloprovincialis*) due to the high primary production enhanced by intense upwelling events in the area (Perez Camacho et al. 1991; Prego et al. 1999).

The Ría of Arousa (where the present study was performed; **Figure 5.1**), located in southern Galicia (Spain), is the largest of the Galician rías (approximately 33.1 km long, 10 km wide at the mouth, and covering an area of 239 km²) (Prego et al. 1999). The average depth of the ría is 19 m. The entire system is subjected to a semidiurnal and mesotidal tide regime, with a tidal range of 1.1 and 3.5 m during neap and spring tides, respectively (Alvarez et al. 2005).

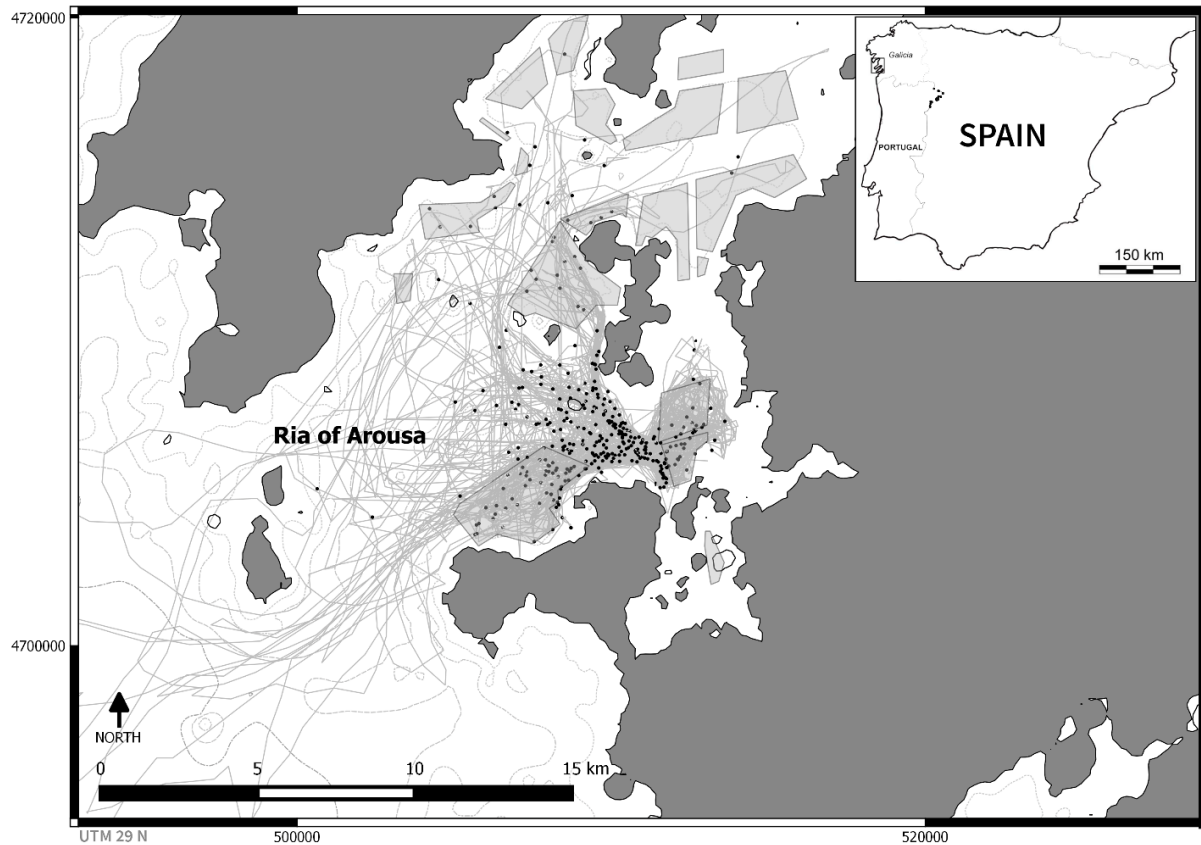


Figure 5.1. Geographical location of the Ría of Arousa (Galicia, NW Spain) including 50 and 100 isobaths with index map of the Iberian Peninsula. Survey effort is indicated by grey track lines. Dolphin encounters are indicated by small circles. Filled polygons indicate location of mussel aquaculture zones.

The system of shellfish production employed in Galicia is the floating raft (named “batea”), which is in contrast with other traditional systems of production such as longlines, stake cultivation, or beach mussel farming (Perez Camacho et al. 1991). The rafts are floating mussel platform farms configured in a rectangular shape. They are usually made of eucalyptus trusses bound together, from which ropes are suspended for the mussel cultivation. The rafts keep afloat with a system of floating devices that are also bound by chains to a block of concrete resting on the sea floor. These rafts have a maximum surface area of about 500 m² and a maximum of 500 ropes with a length no longer than 12 m for the cultivation of mussels (Fuentes et al. 2000). There are 3 386 mussel cultivation rafts in the Galician rías, of which about 70% (2 000 floating rafts) are situated in the Ría of Arousa (Rodríguez et al. 2011).

While the use of habitat and the status of the common bottlenose dolphin population in Galician waters remain poorly known, this is the most frequent cetacean species along the

coast, and more particularly inside of the Galician rías (López 2003; Pierce et al. 2010; Louis et al. 2014).

5.3.2 Data collection

Data for this study were collected as part of a longitudinal study of common bottlenose dolphins inhabiting the Galician coast. We conducted boat-based surveys in the Ría of Arousa between April 2014 and May 2016 using a 12-m vessel, powered by two 180 hp inboard engines. In all, 22 months were spent in the field. Because of poor weather conditions during December, we were unable to complete surveys in this month.

The Ría of Arousa was surveyed during daylight hours at a constant speed, between 6 and 8 knots, with at least three experienced observers, stationed on the flying bridge, scanning 360° of the sea surface in search of bottlenose dolphins (with the naked eye and/or 10 × 50 binoculars). The minimum number of observers and vessel speed remained constant during the study period, making data suitable for the comparative analysis of encounter rates. Boat-based observations were done when the visibility was not reduced by rain or fog, and sea conditions were < 3 on the Douglas sea scale (approximately equivalent to the Beaufort wind force scale). The survey area and track were selected based on sea conditions and time constraints on each day. Surveys were attempted to equally cover all parts of the study area, although the geographic distribution of effort could vary according to weather conditions. Upon sighting a group of bottlenose dolphins, searching effort ceased and the vessel slowly manoeuvred towards the group in order to minimize disturbance during the approach. During observation sessions, bottlenose dolphin groups were monitored for extended periods of time, often during the course of several hours. After the end of an encounter, the searching effort generally continued along the previously planned route.

On each boat survey, the time, position, speed (knots), presence of dolphins, and environmental and anthropogenic data were recorded every 20 min (following Díaz López 2017). These 20-min sets were used to summarize field conditions and distribution of the survey effort irrespective of dolphins' presence. Sets were designed to collect records for dolphin groups using one-zero sampling (Altmann 1974), for which an observer records the

presence or absence of bottlenose dolphins at the beginning of each 20-min sample. We also recorded potentially confounding variables that were beyond the control of the observers but which may have influenced the presence or sightability of the bottlenose dolphins.

The environmental variables used to predict bottlenose dolphin presence comprised date, time, position, bathymetry, bottom slope gradient (the maximum rate of change in depth in a given grid cell and expressed as percent slope), bottom slope aspect (the compass orientation of the slope, ranging from -180° to $+180^{\circ}$ with respect to true north), tide level, sea surface temperature (SST), sea surface salinity (SSS), wind speed and direction, and distance to the coast (metres). The anthropogenic variables comprised distance to mussel aquaculture zones (metres, value zero when the group of dolphins was inside the aquaculture zone), number of recreational vessels, number of fishing vessels, and number of mussel farm boats in the area.

The date, time (UTC), position (UTM coordinates), bathymetry (depth in metres), speed of travel (knots), and SST (in degree Celsius) were obtained by a GPS-Plotter Map Sounder (Garmin) associated with an echo-sounder. The wind speed (m/s) and direction (degrees) were measured, when the vessel was stationary, by a cup anemometer and compass situated 4 m above the sea level. Tide level (metres) was obtained for the harbour of Vilagarcia de Arousa from the Galician weather service: <http://www.meteogalicia.gal>. Bottom slope gradient and slope aspect were computed from the bottom depth obtained from the General Bathymetric Chart of the Oceans (GEBCO08, <http://www.gebco.net>) dataset. This dataset was converted to a raster format and then interpolated using QGIS software (<http://www.qgis.org>) terrain analysis tools. All distances to coast and mussel aquaculture zones were minimum distances from the GPS position of each 20-min point sample to the perimeter of the feature, taking into account the coastal and shellfish aquaculture zones' profile and calculated via spatial analyst tools using QGIS software.

A group of bottlenose dolphins was defined as one or more common bottlenose dolphins observed within a radius of 100 metres. When a group of dolphins was sighted, dolphin aggregations and composition were estimated based on the initial count of individuals observed at one time in the area. Individual dolphins were classified according to age within each group at the time of the sighting (Scott et al. 1990). Age class definitions followed those

by Mann & Smuts (1998), Mann et al. (2000), and Díaz López (2006b), where bottlenose dolphins were classified as follows: (1) Newborns are dependent dolphins smaller than 1.5 m (in relation to the mother) with foetal folds or lines. Newborns were also determined on the basis of uncoordinated surfacing behaviour and swimming in infant position (underneath the mother lightly touching her abdomen). (2) Immatures are dolphins with few rake marks and skin lesions and two-thirds or less the length of adults, often observed in close association with an adult but never observed in the infant position. (3) Adults are full-grown (longer than 2.5 metres) marked or unmarked animals with darker skin colouration.

5.3.3 Data analysis and modelling framework

The target sample size was arbitrarily set at 50 randomly selected instantaneous 20-min sets searching for dolphins (on-effort) for each season across the study period. During the study, four seasons were defined (Díaz López & Shirai 2007): Winter (January to March), Spring (April to June), Summer (July to September), and Autumn (October to December). By selecting data at random, the lack of independence arising from consecutive samplings was limited, avoiding the influence of variations in the observation effort and limiting any pseudoreplication problems.

The relative frequency of occurrence of common bottlenose dolphins (ER) was computed as $ER = N_s/Eff$ where N_s is the number of 20-min sets (on-effort) with the presence of *T. truncatus* and Eff is the total number of 20-min sets searching for dolphins as a measure of the effort. A non-parametric Mann–Whitney test was used to investigate the equality of medians of group size samples (i.e. groups observed inside and outside the shellfish aquaculture zones).

Since the shapes of relationships with explanatory variables were unknown, a generalized additive modelling (GAM) framework was used to investigate the factors affecting the occurrence of common bottlenose dolphins throughout the Ría of Arousa. GAMs allow for flexible relationships between the response variable (presence/absence of common bottlenose dolphins) and explanatory variables (Hastie & Tibshirani 1990). The GAMs were implemented from the library *mgcv* (Wood 2006) in v. 1.8.1. of the computer package R (R Development Core Team 2012).

We initially attempted to model the presence–absence of common bottlenose dolphins as a binomial GAM with a logistic link function. For the binomial model, the following hypotheses of control were tested: environment-based (persistent and non-persistent environment), geographical, and anthropogenic variables. Therefore, four different models— each with a set of related variables—were generated. To reduce multicollinearity and eliminate redundant information, we selected a set of explanatory variables to enter in the GAM analysis by eliminating those variables that were highly correlated with each other ($r > 0.70$) and exhibited low tolerance statistics (< 0.3) in ordinary least squares regression analysis (OLS) (Dormann et al. 2013). Multicollinearity between model terms was tested by means of variance inflation factors (VIF; Neter et al. 1990).

Environment-based models (persistent and non-persistent environment) aim to relate observations of dolphin's presence to various attributes of the marine environment. Persistent environment models initially included depth, bottom slope gradient, bottom slope aspect, and distance to the coast. Non-persistent environment models initially included time of the day, month, season, wind speed and direction, SST, tide level, and SSS. Geographical models initially included continuous geographical coordinates (UTM longitude and UTM latitude). Anthropogenic models initially included distance to mussel farms, number of recreational vessels, number of fishing vessels, and number of mussel farm boats in the area. To account for a different probability of encountering common bottlenose dolphins depending on different survey efforts, a relative sampling effort index was included in all four models. This index was generated by calculating the number of 20-min sampling sets (on-effort) within stratified grid cells of 1 km² throughout the study area. This effort index was then simplified into a factor variable at the quartiles of the resulting values, generating categories of 'low', 'medium', 'high', and 'very high' survey effort (Bonizzoni et al. 2014). All four models also included initially the wind speed as a measure of the sea conditions to account for sampling bias and error.

The outcome of this multimodel inference may not always be the identification of a unique solution ("best model") but rather an ensemble of likely solutions (Planque et al. 2011). The technique, if used appropriately, can lead to robust predictions without the need to identify a unique best model (Araújo & New 2007). Akaike information criteria (AIC) with forward

stepwise selection was used to obtain the optimal set of predictor variables, where the lowest AIC value for every possible combination of explanatory variables was chosen (Pan 2001). To assist with the selection process, we used the 'basis = cs' option for fitting smoothers, which allows degrees of freedom for individual smoothers to fall to zero (a good indication of non-significance). We conservatively removed a variable in the model if it was clearly non-significant ($P \gg 0.05$). Partial predictions for significant predictors were plotted, and 95% confidence bands were constructed.

5.4 Results

5.4.1 Survey effort and presence of common bottlenose dolphins

The field effort within the coastal waters off the Ría of Arousa entailed two consecutive years of fieldwork from April 2014 to May 2016. The total area monitored was around 410 km². In all, 154 daily boat surveys over a period of 22 months were spent in the field, totalling 466 h and 3 788 km (**Table 5.1**). During this period, 1 428 instantaneous sets were recorded every 20 min (795 sets searching for dolphins (on-effort) and 633 with the group of dolphins (off-effort)).

Table 5.1. The seasonal observation effort, bottlenose dolphin encounters, and number of 20 min samples collected in relation to the two years of research.

<i>Seasons</i>	<i>Days</i>	<i>Observation effort (h)</i>	<i>Distance surveyed (km)</i>	<i>Number of bottlenose dolphin encounters</i>	<i>Total 20 min sets</i>	<i>On-effort 20 min sets</i>	<i>Off-effort 20 min sets</i>
<i>Winter</i>	31	94	763	85	289	165	124
<i>Spring</i>	47	138	1 129	99	423	234	189
<i>Summer</i>	61	200	1 661	146	613	336	277
<i>Autumn</i>	15	34	235	23	103	60	43
<i>Total</i>	154	466	3 788	353	1 428	795	633

During this time, there were 369 small cetacean encounters (353 with common bottlenose dolphins, 11 with harbour porpoises (*Phocoena phocoena*), 4 with common dolphins (*Delphinus delphis*), and 1 with Risso's dolphins (*Grampus griseus*)). Common bottlenose dolphins were the most commonly observed cetacean species in the area, seen on 141 days at sea (92% of total number of daily surveys). This species was encountered throughout the whole study area and in all months of the year. Bottlenose dolphins were the only cetacean species encountered inside of the aquaculture zones.

In order to limit the lack of independence arising from consecutive 20-min instantaneous set sampling and to control for seasonal variation, a total of 200 randomly selected samples were used. The relative frequency of occurrence (ER) of bottlenose dolphins in relation to the spatial distribution inside or outside of the aquaculture polygons is summarized in **Table 5.2**.

Table 5.2. Frequency of occurrence of common bottlenose dolphins (ER) with respect to whether or not dolphins were present inside the mussel aquaculture zones.

	Total number of randomly selected (on-effort) 20 min sets	Number of randomly selected (on-effort) 20 min sets with presence of <i>T. truncatus</i>	ER
Inside	45	22	0.49
Outside	155	47	0.30
Total	200	69	0.35

Common bottlenose dolphin group size and composition were examined for 353 independent groups monitored during 245 h (corresponding to 1 270 km). Each group was observed during an average of 42 ± 2 min (3.7 ± 2 km). Group size ranged from 1 to 64 individuals (mean = 13.0 ± 0.6 ; **Table 5.3**). The most observed were aggregations of three dolphins (8% of the encounters) followed by couple of individuals (7%), and with most encountered groups (81%) containing less than 20 animals. Group composition showed that 87% of the observed common bottlenose dolphins were considered adults; thus, the remaining 13% were categorized as dependent calves (here considered together as immature dolphins (12%) and newborn dolphins (1%)). Group size did not exhibit any spatial variations between groups observed inside

and outside the mussel farm zones (Mann–Whitney test, $P > 0.05$). Likewise, the number of dolphins of a given age category did not show spatial fluctuations between inside and outside the mussel farm zones (Mann–Whitney test, $P > 0.05$).

Table 5.3. Mean number of dolphins \pm standard error with respect to whether or not bottlenose dolphins were present inside the mussel aquaculture zones.

Presence	Number of encounters	Group size	Adults	Immatures	New-borns
Inside	106	13.2 \pm 1.1	11.7 \pm 1.0	1.3 \pm 0.1	0.10 \pm 0.04
Outside	247	13.0 \pm 0.7	11.3 \pm 0.6	1.5 \pm 0.1	0.18 \pm 0.04
Total	353	13.0 \pm 0.6	11.4 \pm 0.6	1.5 \pm 0.1	0.16 \pm 0.03

5.4.2 Models output: environmental (persistent and non-persistent), geographical, and anthropogenic variables

The summary of the values of the selected variables in the presence and absence of common bottlenose dolphins is given in **Table 5.4**. For all four final models, the effect of sea state and the effect of relative sampling effort were never significant. Therefore, these variables did not affect the probability of bottlenose dolphin encounters.

Table 5.4. Summary of the variables retained by the final selected models (persistent environment, geographical, and anthropogenic models) for presence and absence of common bottlenose dolphins.

In all cases, the sample size (N) corresponds with the number of randomly selected 20-min sets.

<i>Model / Significant variable</i>	Presence			Absence			Overall		
	N	Mean \pm s.e.	Min - max	N	Mean \pm s.e.	Min - max	N	Mean \pm s.e.	Min - max
<i>Persistent environment / Depth (m)</i>	69	16.7 \pm 1.6	4.2 – 94.1	131	20.7 \pm 1.8	2.9 - 118	200	19.3 \pm 1.3	2.9 - 118
<i>Geographical / Longitude (UTM X) (km)</i>	69	509.8 \pm 0.4	491 - 514	131	508.7 \pm 0.4	491 - 516	200	509.1 \pm 0.3	491 – 516
<i>Anthropogenic / Distance from mussel rafts (km)</i>	69	0.73 \pm 0.2	0 - 14	131	1.33 \pm 0.2	0 - 17.9	200	1.12 \pm 0.16	0 -17.9

Once these results were taken into account, within the final persistent environment model only depth was retained as a predictor of *T. truncatus* presence (**Figure 5.2**). The persistent environment model explained 21.5% of deviance in bottlenose dolphin presence. In this case, the model can be considered satisfactory. The response curve for depth indicates that dolphin presence was higher in waters shallower than 30 m. Within the non-persistent environment model, all the variables were non-significant. Within the geographic model, longitude was retained as a predictor of *T. truncatus* presence (**Figure 5.3**). The response curve for longitude indicates that dolphin occurrence was lower in western portions of the Ría of Arousa (at the mouth of the ría). This model explained 20.3% of deviance in bottlenose dolphin presence and is thus relatively good. For the anthropogenic model, the distance to mussel farms affects the probability of bottlenose dolphin encounters. Bottlenose dolphin occurrence was higher in areas within 1 km of mussel farms and lower at distances greater than 6 km (**Figure 5.4**). The explanatory power of the distance to mussel farms (19% of deviance, not accounted for the effects of variables related to observation effort and efficiency) can be considered satisfactory.

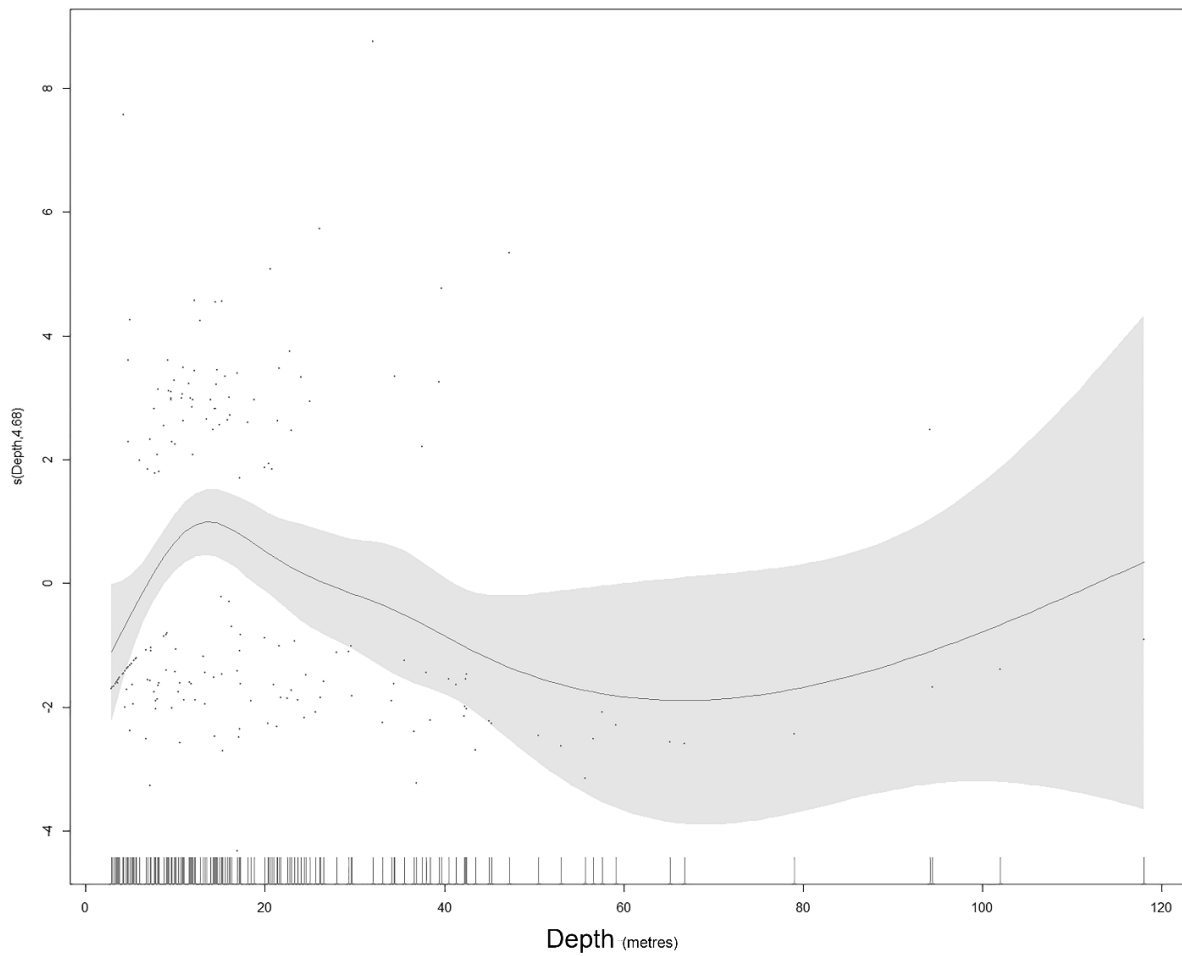


Figure 5.2. Common bottlenose dolphin presence modelled as a smooth function of depth. The AIC of the best permanent environment model was 230 (corresponding $R^2 = 0.2$) and $P < 0.01$. Shaded areas represent 95% CIs. A rug plot with the actual data values is also shown.

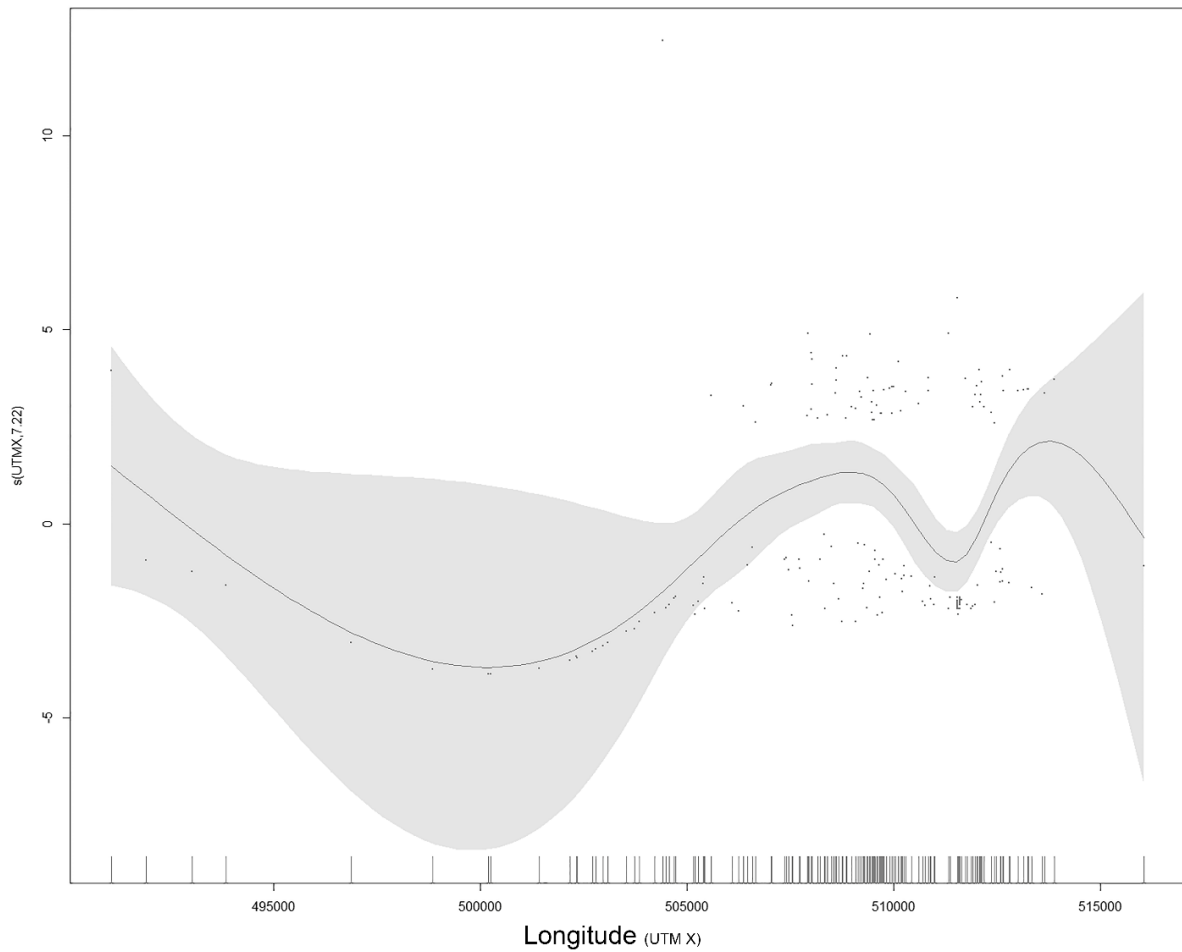


Figure 5.3. Common bottlenose dolphin presence modelled as a smooth function of longitude (UTM X, grid 29N). The AIC of the best geographic model was 229 (corresponding $R^2 = 0.19$) and $P < 0.01$. Shaded areas represent 95% CIs. A rug plot with the actual data values is also shown.

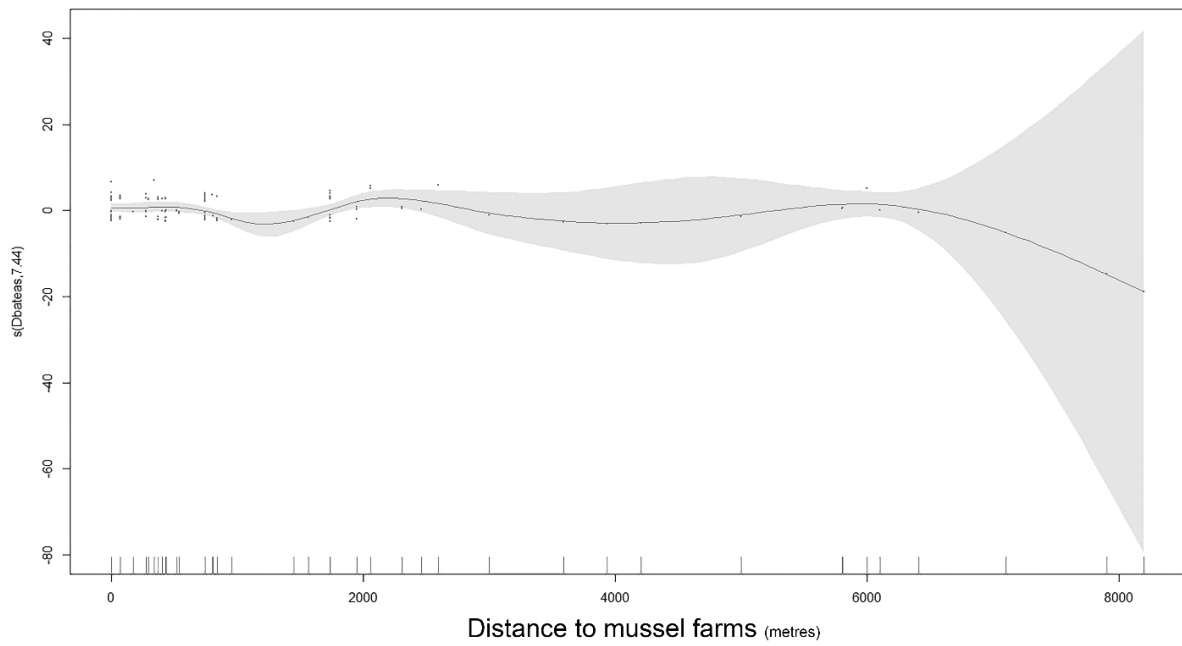


Figure 5.4. Common bottlenose dolphin presence modelled as a smooth function of distance to mussel farms. The AIC of the best anthropogenic model was 237 (corresponding $R^2 = 0.14$) and $P < 0.05$. Shaded areas represent 95% CIs. A rug plot with the actual data values is also shown.

5.5 Discussion

The interaction between top predators and aquaculture, and the consequences of this interaction, is of great importance for coastal and aquaculture management (Díaz López 2012). Since marine aquaculture activities are restricted to shallow, near-shore waters, there is an important overlap with the distribution of coastal cetacean species in several areas around the world (Würsig & Gailey 2002; Jefferson & Hung 2004; Markowitz et al. 2004; Watson-Capps & Mann 2005; Visser 2007; Ribeiro et al. 2007; Pearson 2009; Pearson et al. 2012; Díaz López 2012, 2017; Díaz López et al. 2013; Bonizzoni et al. 2014).

Observations during this study suggest that areas of shellfish production are frequently utilized by common bottlenose dolphins. These results contribute to extend the scant information available about the impact of aquaculture on marine top predators. The unequal use of available habitat, concentrated in the vicinity of shellfish aquaculture zones, and in shallow waters inside of the Ría of Arousa, showed that bottlenose dolphins presented a fine-scale pattern of habitat selection. Of the investigated factors, shellfish farm appeared to have a clear effect, with increased bottlenose dolphin occurrence at shellfish farm locations and in waters close to the farm zones. While mussel farms comprised just around 17% of the total area in the Ría of Arousa, they appear to represent a preferred area of distribution for *T. truncatus*.

These observations contrast with previous studies where the occurrence and distribution of cetacean species decreased in association with shellfish aquaculture representing a source of habitat loss by excluding cetacean species and causing potentially negative effects. In Admiralty Bay, New Zealand, dusky dolphins spent significantly less time than expected inside shellfish farm zones (Markowitz et al. 2004; Pearson et al. 2012). In Shark Bay, Australia, Indo-Pacific bottlenose dolphins used habitat inside shellfish farms significantly less than they used an ecologically similar habitat without shellfish farms (Watson-Capps & Mann 2005). In Yaldad Bay, Chile, Chilean dolphins avoided using areas that were covered by shellfish farms (Ribeiro et al. 2007). In the Marlborough Sounds, New Zealand, killer whales (*Orcinus orca*) avoid entering shellfish farm areas (Visser 2007). In Chinese waters, Indo-Pacific humpback dolphins' (*Sousa chinensis*) use of habitat was also influenced negatively by the presence of shellfish farms (Jefferson & Hung 2004). These differences suggest that the interactions between shellfish

aquaculture and cetaceans seem to be affected very significantly by the culture method and cetacean species involved, being fundamental to study the impacts on a case-by-case basis in more detail. The type of bivalve culture technique used in Galician waters, characterized by mussel rafts (Perez Camacho et al. 1991), differs from the longline system described in the previous studies about interactions between cetaceans and shellfish aquaculture.

Although predator avoidance, interspecific competition, and reproductive strategies all play a key role in cetacean distribution to some extent, habitat preference is assumed to be determined primarily by food availability (Stevick et al. 2009). The positive relationships between dolphins' occurrence and mussel aquaculture zones are presumably the result of large aggregations of fish species around mussel rafts, which in turn provide higher densities of higher quality prey for dolphins than in areas outside the mussel farm zones. Bottlenose dolphins in Galicia eat a wide range of fish species, the most important numerically and in terms of biomass being pelagic and demersal fish species (Santos et al. 2007). The physical structure of mussel rafts, acting as "fish aggregation devices" (Rountree 1989), together with the cascading effect from the presence of an associated high epifaunal biomass (McKindsey et al. 2011), enhances the biomass of bottlenose dolphin preys. Effects on wild fish species have been investigated in the Ría of Arousa, indicating a considerable increase in pelagic and demersal fish species abundance and biomass in the immediate vicinity and inside of mussel aquaculture zones (Chesney & Iglesias 1979). Many of these fish species (i.e. families Gadidae, Mullidae, and Carangidae) were described as the most important prey species of *T. truncatus* in Galician waters (Santos et al. 2007). Behavioural observations of groups of bottlenose dolphins conducted during this study were consistent with the hypothesis of mussel rafts playing a key role in their distribution, as dolphin groups were repeatedly observed catching fish and performing long dives around the floating platforms. By reducing the time spent searching for prey, common bottlenose dolphins reduce the energy required to feed and possibly increase the quantity and quality of the food consumed (Díaz López 2006a). This effect has been associated in other *T. truncatus* populations with opportunistic feeding due to concentrated resource of food in a coastal environment characterized by a patched distribution of food resources (Díaz López 2012, 2017).

Management of shellfish farms with regard to how they affect marine mammals is currently a pressing issue. Modelling cetaceans' distribution is a valuable tool for conservation, in particular in terms of identifying relationships between the environment and species habitat selection (Pirotta et al. 2011). In essence, distribution models are restricted to modelling species response to the environment but environmental forcing alone cannot be expected to fully explain the spatial distribution of bottlenose dolphin populations, unless such forcing is so strong that it over-rides all other drivers. This study suggests that other mechanisms such as the impact of human activities, and more particular shellfish farming, affect the spatial distribution of common bottlenose dolphin populations.

This study provides new insights into the understanding of how shellfish aquaculture influences common bottlenose dolphins' ecology, and hence supports the design of policies aimed at implementing ecosystem management principles. This also contributes to the growing body of literature addressing environmental consequences of suspended shellfish aquaculture, particularly the effects on coastal cetaceans, which have rarely been evaluated. A better understanding of the preferred behaviour associated with the observed habitat preferences will improve management and conservation efforts by providing a context for interpreting the present and future anthropogenic effects on bottlenose dolphin populations and their distribution.

Chapter 6. Natural and anthropogenic drivers of foraging behaviour in bottlenose dolphins: influence of shellfish aquaculture

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Personal contribution

I conceived and designed the study with BDL. I collected the data. I analysed the data with input from BDL. I produced the figures. I interpreted the results and implication with BDL. I wrote the paper with input from BDL.

6.1 Abstract

In the coastal environment, marine mammals are exposed to one of the fastest growing food production sectors; namely, the shellfish farming industry. Identification of critical habitats, such as foraging grounds in highly human-impacted areas, is essential to species conservation. Therefore, understanding the variables that influence a species' foraging behaviour is important for their conservation, especially for long-lived mammals such as cetaceans. The aims of this study were (a) to identify and quantify the environmental and anthropogenic drivers of wild bottlenose dolphin (*Tursiops truncatus*) foraging behaviour, and (b) to investigate whether the shellfish farming industry influences the behaviour of this species. Behavioural observations were conducted along the north-western coast of Spain, an area affected by intensive human activities, particularly the shellfish aquaculture industry. A multi-modelling approach highlighted the importance of shellfish farm areas as a foraging ground for bottlenose dolphins. Dolphins were predicted to be more likely found foraging inside shellfish farm areas than outside (57% vs. 43%). Variability in bottlenose dolphin behaviour is likely a result of the interactions of environmental and anthropogenic drivers with prey availability and the physiological needs of the dolphins. Although shellfish farm areas provide high prey density for dolphins, they can also pose threats in a number of ways (i.e. collisions with vessels, entanglement with ropes, habitat loss, noise and water pollution). From a conservation perspective, aquaculture management should consider the presence of dolphins foraging and minimize the associated risks that this industry may pose to these coastal cetaceans.

6.2 Introduction

Human-induced behavioural disturbance of wild animals can lead to the reduction of foraging efficiency, therefore affecting energy intake with potential implications for individuals and possibly populationlevel fitness (Ashe et al. 2010). Foraging behaviour is driven by multiple stressors, including environmental variables (as indicators of prey availability) and, in certain conditions, anthropogenic variables (Patterson et al. 2009; Yirga et al. 2017). Human activities have been linked to alteration in mammal foraging behaviour in the literature; for example, black bears *Ursus americanus* (Beckmann & Berger 2003), chimpanzees *Pan troglodytes verus* (Hockings et al. 2012), European hedgehogs *Erinaceus europaeus* (Dowding et al. 2010), key deer *Odocoileus virginianus clavium* (Harveson et al. 2007), stonemarten *Martes foina* (Herr et al. 2010), and killer whales *Orcinus orca* (Williams et al. 2006). Likewise, some studies point out that anthropogenic food resources affect the foraging behaviour of several generalist mammal species; for example, bottlenose dolphins *Tursiops truncatus* (Díaz López 2006b, 2012, 2018) and spotted hyenas *Crocuta crocuta* (Yirga et al. 2012). For instance, some species are able to persist at high human densities and to capitalize on human activities, taking advantage of the availability of food resources in a human-dominated landscape; for example, racoon *Procyon lotor* (Prange et al. 2004) and spotted hyenas and African golden wolf *Canis anthus* (Yirga et al. 2017). Conversely, mammals being attracted by high food availability in anthropogenic areas face many threats, such as direct persecution (Yirga et al. 2017), loss of natural food resources (Oriol-Cotterill et al. 2015), habitat loss and modification (Rogala et al. 2011), accidental mortality (Díaz López 2012), and pollution (Kannan et al. 1996). Therefore, identifying and quantifying the factors that influence a species' foraging behaviour is essential to implement appropriate future conservation measures.

In the marine environment, marine mammals are exposed to multiple human activities, such as marine traffic (Constantine et al. 2004), fisheries (Read et al. 2006), and aquaculture (Díaz López 2012). Marine aquaculture is one of the fastest growing food production sectors in the world and continues to expand globally (Food and Agriculture Organization of the United Nations [FAO], 2014). Shellfish farming, which is the culture of filterfeeding bivalves, is the main sector of this industry, comprising 60% of the marine aquaculture production (FAO 2014). Several studies (reviewed in Callier et al. 2017) suggest that the three-dimensional scale of

shellfish farming may reduce the coastal areas used by cetaceans for potentially important biological and social activities. Multiple species of dolphins in various locations around the world appear to avoid areas occupied by shellfish farming, indicating a potentially large impact of this industry on small cetaceans; for example, dusky dolphin *Lagenorhynchus obscurus* in New Zealand (Markowitz et al. 2004; Pearson 2009; Pearson et al. 2012), Chilean dolphins *Cephalorhynchus eutropia* in Chile (Ribeiro et al. 2007), and Indo-Pacific bottlenose dolphins *Tursiops aduncus* in Australia (Watson-Capps & Mann 2005). In contrast, a recent study carried out along the north-western coast of Spain demonstrated that common bottlenose dolphins (*T. truncatus*) are attracted by shellfish farm areas, suggesting that, depending on the culture method, these farms can provide an adequate foraging habitat for dolphins (Díaz López & Methion 2017).

Bottlenose dolphins show a high behavioural and ecological plasticity that allows them to live in coastal areas along with human activities (Díaz López 2006b, 2018; Scott et al. 1990). Bottlenose dolphins inhabit a very wide range of habitats and are generalist animals that feed on locally abundant prey species (mainly demersal and pelagic fish, and cephalopods) (Santos et al. 2007). Foraging behaviour in bottlenose dolphins is driven by a multitude of environmental and anthropogenic factors, and differs in different parts of their range and among individuals of the same population (Díaz López 2009; Sargeant et al. 2007; Torres & Read 2009). The bottlenose dolphin is an opportunistic species that is capable of developing, over its range, a multitude of adaptive strategies, including specialist feeding techniques, which involve a high degree of diet flexibility, social organization, and behavioural adaptation (Connor et al. 2000; Díaz López 2012, 2018; Díaz López & Shirai 2008). In different parts of the world, these strategies allow bottlenose dolphins to capitalize on human activities, such as gillnet and trawl fisheries and fin fish aquaculture (Chilvers & Corkeron 2001; Díaz López 2006b, 2012; Fertl & Leatherwood 1997). In spite of this, little is known about the factors that affect bottlenose dolphin behaviour and, in particular, about the influence of shellfish farming on bottlenose dolphin foraging behaviour.

The north-western coast of Spain, being one of the world's most important areas for shellfish farming (Rodríguez et al. 2011) and supporting a resident population of bottlenose dolphins (Methion & Díaz López 2018), exhibits the perfect conditions to carry out such a specific study.

Building upon the study of the influence of shellfish farming on the habitat use of bottlenose dolphins in these waters (Díaz López & Methion 2017), this present study attempted to investigate the influence of the shellfish aquaculture industry on the foraging behaviour of bottlenose dolphins. The aims of this study were to identify and quantify the environmental and anthropogenic drivers of wild bottlenose dolphin foraging behaviour and to investigate whether the presence of shellfish farms influences the behaviour of this species.

6.3 Methods

6.3.1 Study area

The north-western coast of the Iberian Peninsula (Galicia, Spain) lies at the northern edge of one of the major upwelling areas in the world, the eastern boundary system off north-west Africa and south-western Europe (Santos et al. 2011). The frequent upwelling of cold and dense North Atlantic Central Water results in nutrient enrichment of the water, making this area one of the most productive oceanic regions in the world (Santos et al. 2011). This coast is characterized by high biodiversity, productive fisheries, and important aquaculture activities, particularly the production of mussels (*Mytilus galloprovincialis*; Tenore et al. 1995). Shellfish farming has occurred in Galicia since the late 1940s (Miguez et al. 2009) and has developed over the years, making this area the European leader in this sector (FAO 2014). Galicia produces an average of 300 000 tonnes of mussels per year, making it the third most important producer in the world after China and Thailand (Fuentes et al. 2000; Rodríguez et al. 2011) with 13% of the world's mussel production (50% of Europe and 98% of Spain; FAO 2014). In Galicia, the shellfish are grown on rectangular floating platforms, which is in contrast to other systems of production, such as long-lines or poles (Perez Camacho et al. 1991). The rafts are generally made of wood, and the bivalves are grown on ropes tied to the platforms. Each individual raft has a maximum of 500 ropes (no longer than 12 m) and covers an area of up to 500 m² used for shellfish cultivation (Fuentes et al. 2000).

The current study was conducted in the largest of the Galician rías, the 239 km² Ría de Arousa (Prego et al. 1999; **Figure 6.1**). The ría is exposed to a semidiurnal, mesotidal regime, with the tidal range varying between 1.1 m and 3.5 m during neap and spring tides respectively (Alvarez et al. 2005). Around 2 370 mussel cultivation rafts are situated in the Ría de Arousa (Rodríguez et al. 2011), covering approximately 17% of the area (Díaz López & Methion 2017). Bottlenose dolphin (*T. truncatus*) abundance ranges from 56 to 144 individuals in the Ría de Arousa (Methion & Díaz López 2018). In this ría, bottlenose dolphins are frequently found in shellfish farm areas (Díaz López & Methion 2017).

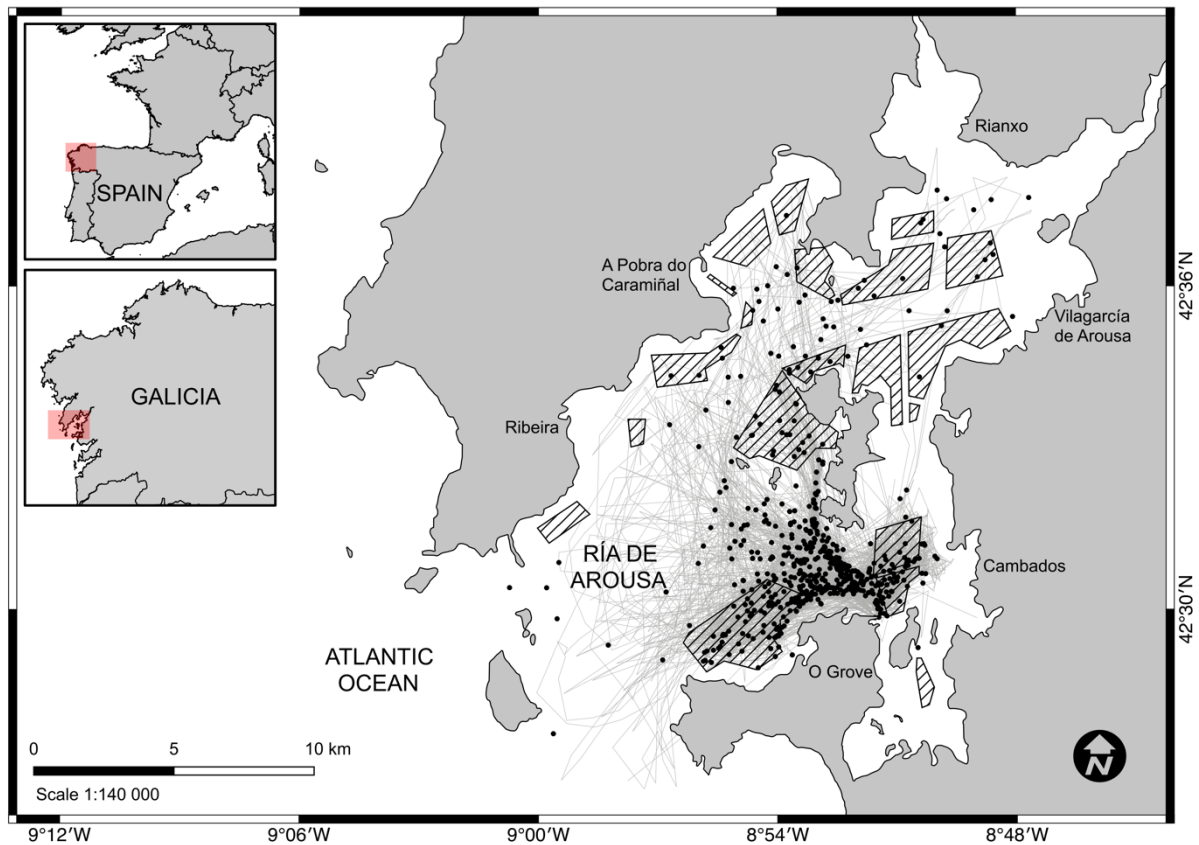


Figure 6.1. Map of the study area (Ría de Arousa, North-West Spain) with survey tracks, bottlenose dolphin encounters (indicated by filled circles), and polygons representing the shellfish farm areas.

6.3.2 Data collection

Boat-based surveys were conducted between March 2014 and November 2017. The study area was monitored onboard a 12 m research vessel during daylight hours at a constant speed of 6 kn. At least three experienced observers were stationed on the flying bridge (4 m above sea level), scanning 360° of the sea surface in search of bottlenose dolphins (with the naked eye or 10 × 50 binoculars). The minimum number of experienced observers and vessel speed remained consistent during the study period. Surveys were carried out when the sea conditions were no greater than 3 on the Douglas sea force scale (approximately equivalent to the Beaufort wind force scale) and visibility was not reduced by rain or fog (Díaz López & Methion 2017). The surveyed area and daily routes were designed to cover all parts of the study area equally (Figure 6.1; Methion & Díaz López 2018).

Upon sighting a group of bottlenose dolphins the vessel slowly manoeuvred towards them in order to not alter their behaviour during the approach. A group of bottlenose dolphins was defined as one or more individuals observed within a 100 m radius, and if more than one, interacting with each other and engaging in the same behavioural activity (Methion & Díaz López 2018). Group size and composition were estimated before, during, and after the bottlenose dolphins had been approached. Individual dolphins were classified according to age at the time of the encounter (Scott et al. 1990). Age class definitions followed those of Díaz López & Methion (2017), whereby bottlenose dolphins were classified as either dependent calves or adults. Individuals were considered dependent calves when they were about two-thirds the length of an adult and were observed in close association with an adult. Individuals were considered adults when their length was more than 2.5 m.

The behavioural state of a group was determined every 5 min based on the activity performed by at least 50% of the individuals present in the group for at least 50% of the duration of the 5-min sample (predominant group activity sampling) (Altmann 1974; Karniski et al. 2015). The behavioural states were classified into four categories: foraging, resting, socializing, and travelling (**Table 6.1**). As the determination of cetacean behaviour from surface observation can be challenging, several parameters were considered to assess the behavioural state in order to reduce potential bias: behavioural events, dive duration, swimming speed and direction, interindividual distance, and contact among individual dolphins (following Díaz López 2006a). To eliminate inter-observer variability, the behavioural state was determined by the same observer during the full study period. All encounters continued until the group composition changed, the group was lost, or until weather conditions became unfavourable.

Table 6.1. Description of the behavioural states observed in bottlenose dolphins in the Ría de Arousa (North-West Spain).

<i>Behavioural state</i>	Description
<i>Foraging</i>	<p>Solitary or aggregation of bottlenose dolphins swimming in different directions in the same area. Dolphins usually stay in the same area, involve carrousel and cross swimming. If large group, the group can be split into two or more subgroups spread over a large area (100 m); or the individuals can be completely spread between each other.</p> <p>Surface-feeding: includes fast surfacing (chase prey close to the surface), feeding rush towards the surface or towards obstacles (e.g. rocks, shellfish platforms), catching prey, fish kicking or tossing, ventral swimming.</p> <p>Deep diving: sequence of regular dives followed by steep dives (tail-stock or flukes-up dives), and then long dives (> 60 seconds) (Díaz López et al. 2008b).</p>
<i>Resting</i>	<p>Solitary or aggregation of bottlenose dolphins surfacing at a slow and constant speed (< 2kn). Group is tight (< 1 body length, 3 metres). Surfacing usually involves synchronous dive behaviour between two or more individuals and floating at the surface. Most of the ventilations are regular and the dives are short (< 60 seconds), with absence of steep dives. When this behavioural state finishes, there is a drastic change of behaviour (important changes of speed, direction, dive interval and behavioural events).</p>
<i>Socialising</i>	<p>Aggregation of bottlenose dolphins interacting at the surface and underwater with one other or, several other, dolphins. Can include synchronous dives, body contact, biting, rolling, charging, chasing, somersault, mating, genital inspections, tail slaps, leaps, bows, and breaches. Individuals change position in the group and swimming direction varies. The group can be split into small subgroups spread over a large area. The dive interval is short (< 60 seconds).</p>
<i>Travelling</i>	<p>Solitary or aggregation of bottlenose dolphins regularly surfacing (constant dive intervals) (< 60 seconds) at a constant speed (> 2 kn) and one goal direction. If there are several individuals in the group, the group is generally cohesive and the inter-individual distance is usually less than 3 bodies (approximatively 9 metres).</p>

The following variables were initially considered to have potential significance on bottlenose dolphin foraging behaviour, and were available for each 5-min sample recorded during the study: time (UTC), group size, presence of dependent calves, number of dependent calves, depth (metres), sea surface temperature (SST in degree Celsius), sea surface salinity (SSS in parts per thousand), wind speed (metres per second), bottom slope gradient (hereafter slope gradient—the maximum rate of change in depth in a given area of grid cell and expressed as per cent slope), tide level (metres), tidal cycle (flood; ebb), distance to the coast (metres), and the presence of the group of bottlenose dolphins inside or outside the shellfish farm areas.

The date, time, position (UTM longitude and UTM latitude, WGS 84 UTM Zone 29 N), depth, SST, SSS, wind speed, and the presence of the group of bottlenose dolphins inside or outside the shellfish farm areas were collected in situ along with the behavioural state of the group as an instantaneous point sample every 5 min.

Supplementary variables were extracted and linked to each behavioural state: slope gradient, tide level, tidal cycle, and distance to the coast. Tide level and tidal cycle categories were obtained from the Galician weather service (<http://www.meteogalicia.gal>). Slope gradient was computed from the bottom depth obtained from a bathymetric chart dataset (following Díaz López & Methion 2018a). All distances to the coast were minimum distances in metres from the Global Positioning System position of each 5-min sample to the coastline and calculated via spatial analyst tools using QGIS software.

Data collection in the present study complied with current laws of Spain, the country in which the study was performed.

6.3.3 Data selection

As reported in other areas (Díaz López 2012), given the long-term nature of the study, the process of field data collection was not expected to cause significant behavioural changes to the animals studied. Following Díaz López (2009), at least 10 min of observation are needed to assess the behaviour of wild bottlenose dolphins. Consequently, all encounters with a duration of 10 min or less were discarded and only the third behavioural sample (corresponding to the interval between minutes 10 and 15 of observation) of each encounter was selected for further analysis. By downsampling the data, the autocorrelation and pseudoreplication arising from consecutive samples was limited (Díaz López & Methion 2018a).

6.3.4 Data analysis

Explanatory variables were tested for multicollinearity by examining the variance inflation factor (VIF), and the variable was discarded when $VIF > 5$ (Dormann et al. 2013). Following this procedure, tide level, number of calves, and distance to the coast were excluded from the analyses. Coordinates were not included as covariates because they were correlated with SST, SSS, presence of shellfish farms, and depth, which were included instead due to their biological interpretability (Díaz López & Methion 2018a; Forney 2000). As a result, 10 predictor variables were selected: group size, presence of dependent calves, time, depth, SST, SSS, slope gradient, tidal cycle, wind speed, and whether the dolphins were inside or outside the shellfish farm areas.

A generalized additive modelling (GAM) framework was used to study variables correlated to the foraging behaviour of bottlenose dolphins. Presence–absence of foraging behaviour was modelled as a binomial GAM (presence of foraging behaviour scored as 1; or absence of foraging behaviour, i.e. resting, socializing, and travelling, scored as 0) with a logistic link function. The smooth functions were represented by cubic regression splines (Wood 2006). The amount of smoothing was not fixed to a preset value; rather, cross-validation was used to estimate the optimal amount of smoothing (Wood 2006). The *mgcv* package (Wood 2006) in the software R (R Development Core Team 2011) was used to perform the GAM. Model assumptions were checked by visual inspection of the residuals, and regression fits were examined by using residual plots against fitted values. The Durbin–Watson test (from the

package *lmtest*; Zeileis & Hothorn 2002) and autocorrelation functions were used to check for serial correlation, both in the raw data and in the residuals from the models. The optimum final model (hereafter referred to as the global model) was selected based on the lowest unbiased risk estimator, and there were no clear patterns in the residuals (following Díaz López & Methion 2018a). A multimodel inference approach (referred as model averaging, i.e. several models used at once for making predictions; Grueber et al. 2011) was used for model simplification and selection, because of the large number of potential combinations of predictor variables. Model averaging can lead to robust predictions accounting for uncertainty in model selection by making inferences from an assemblage of possible solutions (Burnham & Anderson 2002). Model averaging was used to calculate the relative importance of predictor variables. The R package *MuMIn* (Barton 2011) was used to produce a candidate model set consisting of all simplified versions of the global model and compared them based on their Akaike information criterion corrected for small sample sizes (AICc; Grueber et al. 2011). To ensure that the most parsimonious models were maintained within the best supported model set, the models with $\Delta\text{AICc} < 2$ were used to identify the relative importance of each model term in predicting the response variable and to estimate the effect sizes of the predictors (Burnham & Anderson 2002). Models were ranked from best to worst using the difference in AICc and the relative importance of a predictor variable (relative variable importance, RVI) was calculated as the sum of the Akaike weights over all of the models in which the predictor appeared (Burnham & Anderson 2002). Partial predictions with 95% confidence intervals were plotted for each covariate included within the best supported model set.

6.4 Results

6.4.1 Survey effort, group size, and behavioural samples

From 2014 to 2017, 273 boat-based observations were carried out for a total of 1 015 hr, covering 9 416 km (Figure 6.1). Overall, 712 groups of bottlenose dolphins (*T. truncatus*) were encountered. The behaviour of the bottlenose dolphins was sampled for a total of 445 hours and 2 566 km. The mean duration of encounters was 38.0 ± 1.3 min (median 25 min, minimum 1 min, maximum 253 min).

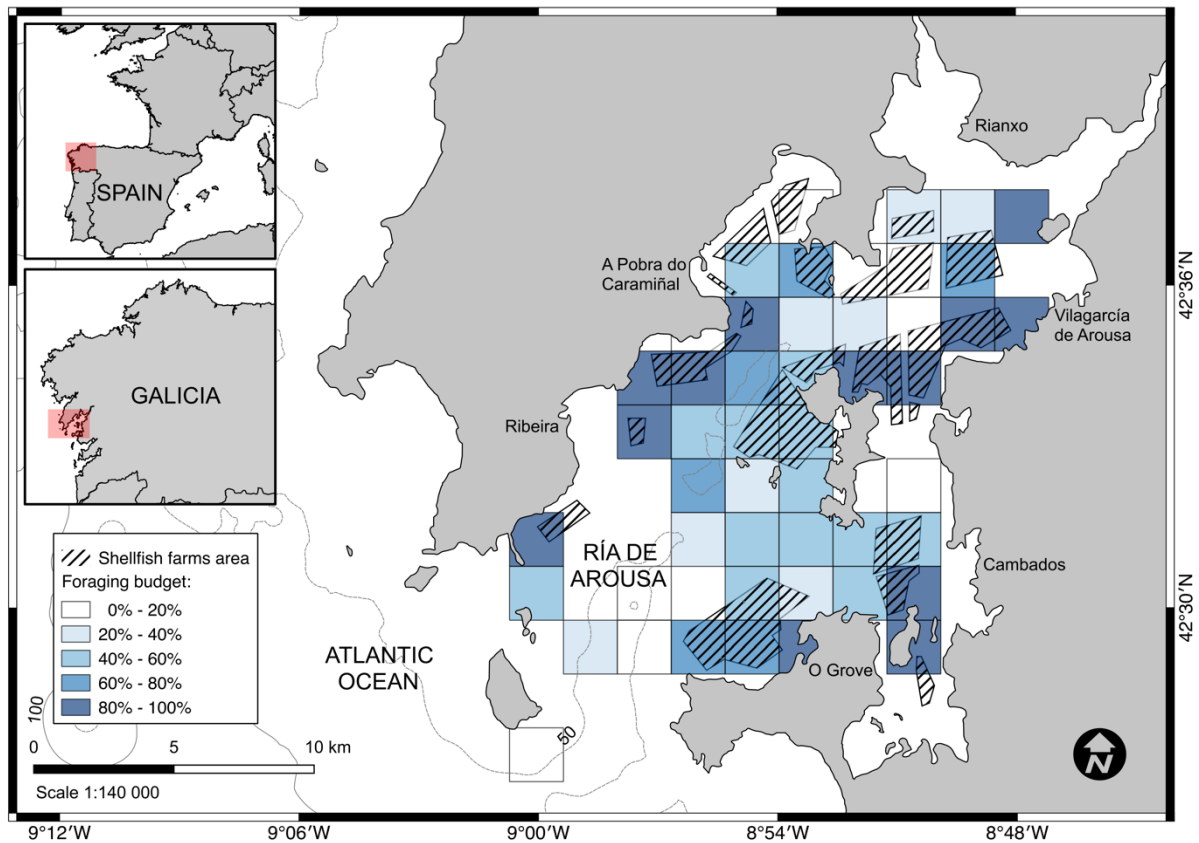


Figure 6.2. Map of the study area with grid representing bottlenose dolphin foraging budget and polygons representing the shellfish farm areas.

Group size ranged from 1 to 90 individuals (mean 11.87 ± 0.44 ; median 8). The groups were composed of 88% adults and 12% dependent calves. Dependent calves were present in 56% of the groups. The group size, presence of dependent calves, and number of dependent calves

did not vary for groups present inside or outside the shellfish farm areas (Mann–Whitney test, $P > 0.05$).

Overall, 5 299 of the 5-min behavioural samples were collected (of which 2 481 foraging, 148 resting, 675 socializing, and 1 995 travelling samples). A final dataset of 574 samples (~11% of the total samples) was generated for further analysis.

6.4.2 Behavioural budget

Of the 574 selected behavioural samples, 282 were foraging samples (49.1%), 220 were travelling samples (38.3%), 51 were socializing samples (8.9%), and 21 were resting samples (3.7%). The frequencies of occurrence of the four behavioural states were not distributed uniformly inside and outside shellfish farm areas, with a predominance of foraging activities inside shellfish farm areas (contingency table $\chi^2 = 10.1$, 3 df, $P < 0.05$; **Figure 6.2**). On the contrary, resting and travelling behaviour occurred more frequently outside shellfish farm areas (**Figure 6.3**). Social behaviour was not related to any area in particular.

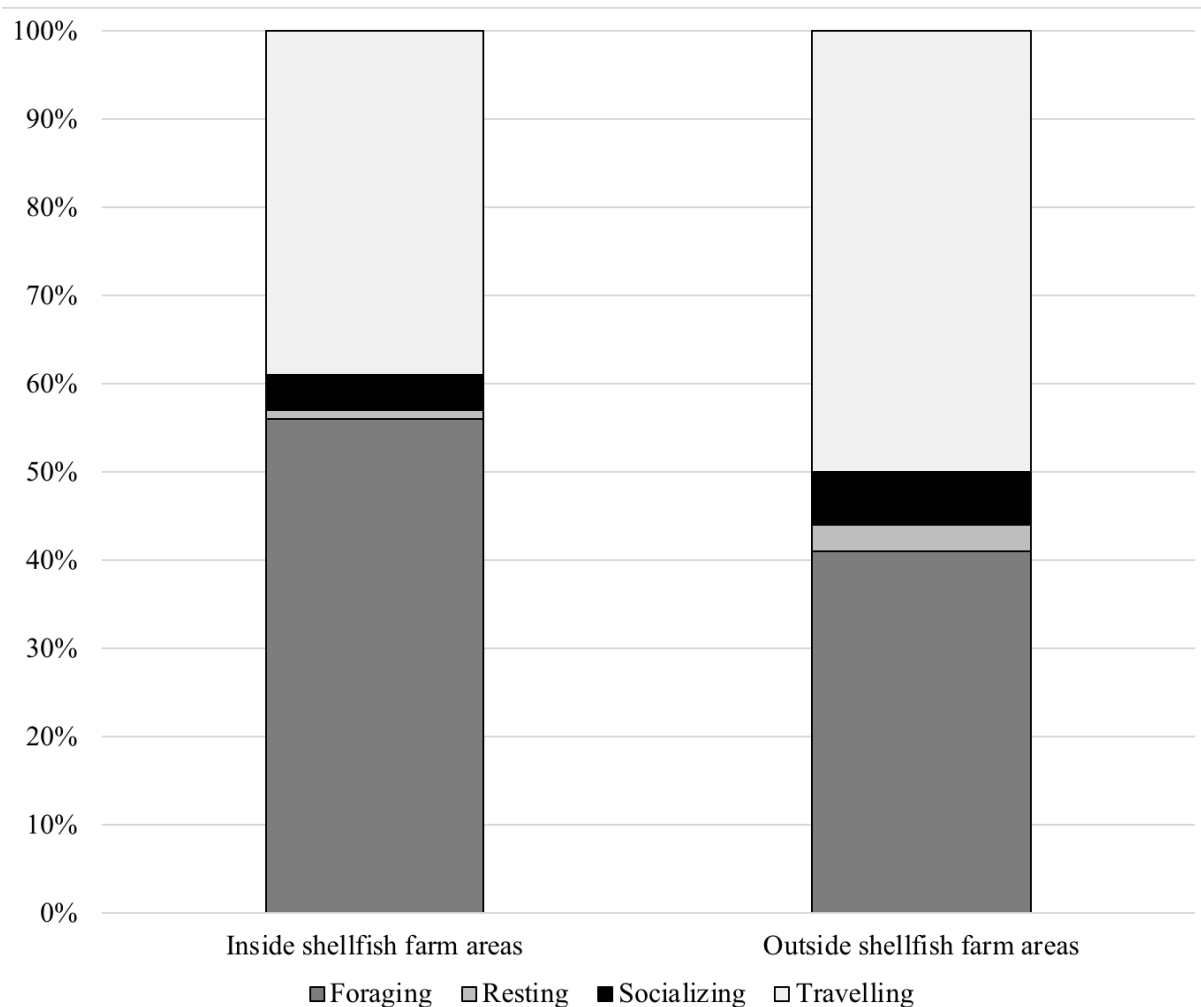


Figure 6.3. Bottlenose dolphin behavioural budget inside and outside shellfish farm areas.

6.4.3 Factors influencing bottlenose dolphin foraging behaviour

A candidate model set was produced with all 1 024 simplified versions of the global model, and the models were compared based on their AICc. Five models with $\Delta AICc < 2$ were used to produce model averaged parameter estimates (**Table 6.2**). The shellfish farm areas, SST, and time were retained in each model within the candidate model set and had an RVI = 1 in the final average model (**Table 6.3**). The slope gradient was retained in five top models within the candidate model set and had an RVI = 0.89. The wind speed (as a measure of the sea state), group size, tidal cycle, and SSS were only retained in one of the top models with an RVI ≤ 0.20 (**Table 6.3**). Depth and presence of dependent calves were not present in the top model set, indicating that these covariates were not important predictors of bottlenose dolphin foraging behaviour. Bottlenose dolphin foraging activity was predicted to be driven by environmental

variables (predominantly at low SST and during morning hours) and anthropogenic variables (higher inside shellfish farm areas [$57 \pm 5\%$] than outside shellfish farm areas [$43 \pm 4\%$]; **Figure 6.4, Table 6.3**).

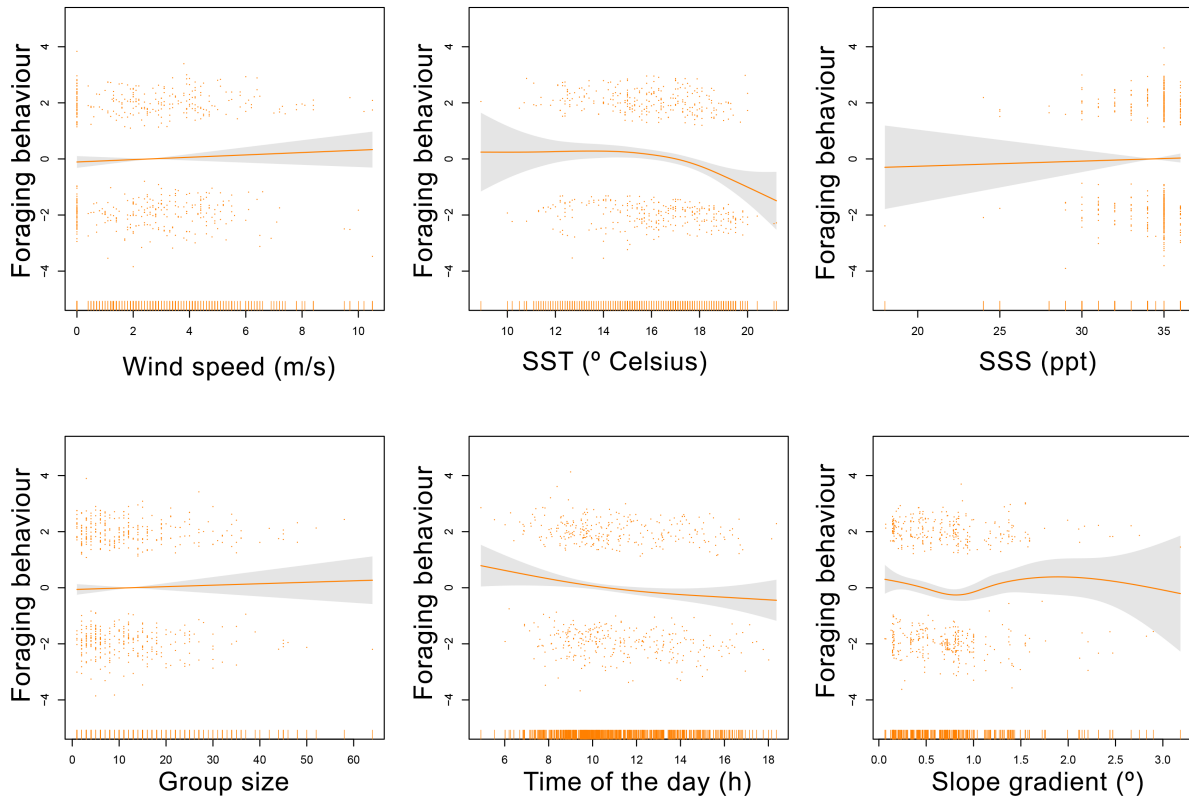


Figure 6.4. Averaged predictions of bottlenose dolphin foraging behaviour for each covariate present in the confidence set of models and their 95% confidence limits when all other variables are fixed on their mean value.

Table 6.2. Summary of the 6 best-supported models of bottlenose dolphin foraging behaviour.

Only six most candidate models ($\Delta_i \leq 2$) of the 1 024 are presented. *df* degrees of freedom, Δ_i difference in AIC between the particular model and the first-ranked model, w_i Akaike weight showing the relative support of a given model compared to the others, SF shellfish farms, S slope gradient, SST sea-surface temperature, T time, W wind speed, G group size, TC tidal cycle, and SSS sea surface salinity.

<i>Models</i>	<i>df</i>	<i>logLik</i>	<i>AICc</i>	Δ_i	w_i
<i>SF + SST + T + S</i>	9.53	-379.36	778.14	0.00	0.30
<i>SF + SST + T + S + W</i>	10.65	-378.60	778.93	0.79	0.20
<i>SF + SST + T + S + G</i>	10.57	-379.04	779.66	1.51	0.14
<i>SF + SST + T + S + TC</i>	10.47	-379.18	779.73	1.59	0.13
<i>SF + SST + T</i>	5.83	-384.14	780.07	1.92	0.11
<i>SF + SST + T + S + SSS</i>	10.44	-379.40	780.11	1.97	0.11

Table 6.3. Model-averaged relative variable importance (RVI) estimated by a generalized additive model to determine the effects of shellfish farms (SF), sea surface temperature (SST), time (T), slope gradient (S), wind speed (W), group size (G), tidal cycle (TC), and sea surface salinity (SSS) on bottlenose dolphin foraging behaviour ($n = 574$).

	RVI
<i>SF (Yes)</i>	1
<i>SST</i>	1
<i>T</i>	1
<i>S</i>	0.89
<i>W</i>	0.2
<i>G</i>	0.14
<i>TC (Flood)</i>	0.13
<i>SSS</i>	0.11

6.5 Discussion

Integrating behavioural studies into conservation strategies is an important step for the protection of wildlife and contributes to reducing the consequences of human disturbances (Buchholz 2007; Sutherland 1998). Identification and protection of critical habitats, such as foraging grounds, are particularly difficult tasks and essential to the conservation of species in the marine environment. Therefore, defining the variables that influence the foraging behaviour of a marine top predator, such as the bottlenose dolphin, can help with the protection, management, and conservation of this potentially vulnerable species.

This study provides additional understanding on the environmental and anthropogenic factors that drive bottlenose dolphin foraging behaviour in a highly human-impacted area. The results highlight the importance of shellfish farm areas as potential foraging grounds for this species. The model-averaged parameter estimates revealed that foraging behaviour is correlated to both environmental (SST and time of the day) and anthropogenic (shellfish farm areas) variables. Variability in bottlenose dolphin behaviour is likely a result of the interactions of these drivers with prey availability and physiological needs of the dolphins. The observed influence of environmental parameters (such as the SST and time of the day) on foraging behaviour may in fact be related to temporal changes in abundance of pelagic and demersal fish species. Indeed, pelagic and demersal fish species, which are the most important prey species of bottlenose dolphins in the region (Santos et al. 2007), show clear temporal changes (seasonal and circadian) in abundance and distribution inside of the Ría de Arousa (Chesney & Iglesias 1979; Tenore et al. 1995). As a result, during seasons characterized by low sea surface water temperature, dolphins might tend to increase the time spent foraging because of their higher energy requirements (Bräger 1993; Díaz López 2012; Shane 1990).

The observed preference that bottlenose dolphins show for foraging inside shellfish farm areas contrasts with other studies claiming that dolphins avoid shellfish farm areas; for example, Hector's dolphins in New Zealand (Würsig & Gailey 2002), Indo-Pacific bottlenose dolphins in Australia (Watson-Capps & Mann 2005), and Chilean dolphins in Chile (Ribeiro et al. 2007). The difference in these results might be due to differing shellfish culture methods used (i.e. floating rafts vs. long-lines). In Galicia, the use of square floating rafts with a concentration of ropes in

the same area in the water has introduced spatial habitat complexity (Chesney & Iglesias 1979; Iglesias 1981). Indeed, shellfish aquaculture has fragmented bottlenose dolphin habitat in the Ría de Arousa, causing certain areas to become more attractive to dolphins (Díaz López & Methion 2017). Shellfish farms lead to a variation in food resource distribution and abundance in the form of modified habitat that is favourable for bottlenose dolphin foraging activity (high diversity and abundance of fish species and physical space for the dolphins to move in between the rafts). The rafts provide a physical structure acting as a fish aggregating device, thus increasing the abundance of fish species within shellfish farm areas relative to adjacent areas (Chesney & Iglesias 1979; Romero et al. 1982; Tenore & Gonzalez 1976). Consequently, the pelagic and demersal fish species concentrated in the aquaculture areas, feeding directly on the shellfish-line-associated community or using the structures as resting sites (Freire & González-Gurriarán 1995; Iglesias 1981), provide bottlenose dolphins with an important source of food. Similar results have been found in studies on the interaction between bottlenose dolphins and finfish aquaculture (Bonizzoni et al. 2014; Díaz López 2006a, 2012). In Mediterranean waters, bottlenose dolphins feed more efficiently in areas with a high concentration of prey around finfish cages, allowing them to shorten their dive time and consequently giving them more flexibility with speed and swimming mode as a result of higher oxygen availability (Díaz López 2009). In this way, dolphins reduce the proportion of time spent searching for food and increase the quantity of food consumed (Díaz López 2012).

Previous studies have shown that interaction between dolphins and marine aquaculture can cause damage to both the aquaculture industry (i.e. damage to gear, depredation of farmed fish) and to dolphins (i.e. fatal entanglement, habitat loss and degradation, introduction of diseases) (Díaz López 2012; Würsig & Gailey 2002). While dolphins around finfish farm areas can feed on both wild and farmed fish, often causing damage to the equipment and the stock (Díaz López 2006a), dolphins in shellfish farm areas only feed on wild prey, thus not affecting the aquaculture product. Therefore, attempts to dissuade bottlenose dolphins, through the use of predator nets or acoustic harassment devices, are not necessary in shellfish aquaculture. Nevertheless, shellfish aquaculture can pose threats to bottlenose dolphins in a number of ways: (a) increased mortality as a result of fatal collisions with vessels working in the area (Ribeiro et al. 2007) or entanglement with ropes; (b) habitat loss (Watson-Capps & Mann 2005); (c) increased levels of noise pollution due to the high number of vessels in the area; and (d)

water pollution due to the use of antifouling paint biocides containing toxic compounds (i.e. lead, arsenic, mercury, copper, cuprous oxide, organotin compounds such as tributyltin), associated with the maintenance of the floating rafts and working vessels (Terlizzi et al. 2001). These biocides diffuse at the paint–water interface and wash away with time. Some authors have claimed that the accumulation of biocides may cause bottlenose dolphin mortality by suppressing their immune system (Kannan et al. 1996).

From a conservation perspective, aquaculture management should consider the presence of bottlenose dolphins foraging in shellfish farm areas and minimize the associated risks that this industry may pose to these coastal cetaceans. Management action for the shellfish industry threats listed in this study should be implemented following the European Union legal obligations under the Habitats Directive to protect bottlenose dolphins, a species listed under Annexes II and IV (species in need of strict protection and which require the designation of Special Areas of Conservation). Speed regulations for vessels operating inside the shellfish farm areas and control of antifouling paints containing biocides used for the floating rafts could minimize the potential impacts of this industry on bottlenose dolphins. In addition, the implementation of shellfish farms in areas of particular ecological importance for bottlenose dolphins should be regulated.

Chapter 7. Individual foraging variation drives social organization in bottlenose dolphins

Article published

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Personal contribution

I conceived and designed the study with BDL. I collected the data. I carried out the photo-identification analyses. I analysed the data with input from BDL. I produced the figures. I interpreted the results and implication with BDL. I wrote the paper with input from BDL.

7.1 Abstract

Identifying foraging variation within a population and assessing its relationship with social structure is essential to increase knowledge about the evolution of social systems. Here, we investigated individual foraging variation in bottlenose dolphins and its potential influence on their social organization. We used generalized affiliation indices and applied social network analysis to data collected over four consecutive years of research in a coastal area subject to significant use and pressure by humans. Our findings revealed variation in foraging behavior among individual bottlenose dolphins, which in turn shapes their social organization. Our results indicated that individuals that frequently foraged within human-altered areas (i.e. shellfish farms) exhibited weaker Strength, Reach, and Affinity compared to others. These bottlenose dolphins profit from a reliable and easily located food source, which may increase their energy intake and inter-individual competition. In contrast, individuals that foraged less frequently within the shellfish farms occupied a central position within the network and exhibited strong associations. These individuals may benefit from increased cooperation and reduced intragroup competition, thus increasing learning and information-sharing, as they may face a patchy and irregular distribution of prey. We also demonstrated that bottlenose dolphins preferred to affiliate with other individuals with similar foraging strategies (i.e. homophily), which could promote, through time, a segregation of the population into behaviorally distinct groups. These findings provide valuable insight into the evolution of bottlenose dolphin social systems and their response to human-induced changes in the marine environment.

7.2 Introduction

Animals commonly form groups to reduce predation risk, increase mating opportunity and access to resources (Alexander 1974). Yet, grouping is also associated with costs, such as intraspecific competition for food (Clark & Mangel 1986; Krause & Ruxton 2002). Societies with flexible grouping patterns limit the effect of within-group competition through group splits during periods of low resource availability and enhance cooperative effects through group cohesion when the ecological costs of aggregating are low (Chapman 1990; van Schaik 1999). Several group-living mammal species exhibit such fission-fusion dynamics (e.g. chimpanzee, *Pan troglodytes*: Lehmann & Boesch 2004; African elephant, *Loxodonta africana*: Fishlock & Lee 2013; giraffe, *Giraffa Camelopardalis*: Muller et al. 2018; zebra, *Equus spp.*: Sundaresan et al. 2007; bottlenose dolphin, *Tursiops spp.*: Connor et al. 2000; Bechstein's bat, *Myotis bechsteinii*: Kerth et al. 2011).

To balance the effect of competition for resources, individuals within a population can also differ substantially in resource use (Svänback & Bolnick 2006). Foraging variation may arise from differences in sex, age, or morphology (Gustafsson 1988). Alternatively, foraging variation may arise from individual specialization, with individuals differing in prey preferences, habitat use, or foraging behavior (Bolnick et al. 2002; Robertson et al. 2014), independently of environmental or phenotypic variation (Estes et al. 2003). Individual foraging variation has been documented in several mammals with dynamic grouping patterns including macaques, *Macaca fascicularis* (Maria & Van Schaik 1986), African elephants (Woolley et al. 2009), and bottlenose dolphins (Sargeant et al. 2007; Díaz López 2012) and has important ecological implications. Previous studies reported that individual foraging variation can alter the structure of animal societies (Chilvers & Corkeron 2001; Díaz López & Shirai 2008; Ansmann et al. 2012), which in turn may influence population fitness (Formica et al. 2012), reproductive success (Cameron et al. 2009), genetic structure (Altmann et al. 1996), and transmission of learned behavior (Whitehead 2010) and pathogens (Keeling & Eames 2005). Given such broad implications, identifying foraging variation within a population and assessing its relationship with population social structure is essential to increase knowledge about the evolution of social systems (Cantor & Farine 2018).

Social network analyses have been increasingly used to accurately describe animal societies (Farine & Whitehead 2015). A common challenge when analyzing social network, is distinguishing true affiliations from other structural variables (e.g. sex; gregariousness: Godde et al. 2013; sample size: Farine & Strandburg-Peshkin 2015) that may influence the association patterns among individuals (Whitehead & James 2015). The incorporation of structural variables into social network analysis is important for revealing true association patterns, and a growing number of studies on animal societies take these into account (e.g. Muller et al. 2018; Diaz-Aguirre et al. 2019; Hunt et al. 2019; Machado et al. 2019). Generalized affiliation indices, which have been recently developed, enable control of structural variables in social network analyses (Whitehead & James 2015), therefore providing an encouraging approach for understanding complex animal societies.

Exhibiting social systems characterized by fission-fusion dynamics, bottlenose dolphins provide a useful framework for analyzing variation in social relationships within a population. In various locations around the world, bottlenose dolphins associate in temporary groups of variable size and composition yet also show long term association among individuals within these fluid groups (Connor et al. 2000). Multiple variables may play a role in shaping bottlenose dolphin societies including predation risk (Heithaus & Dill 2002), mating opportunity (Möller et al. 2001), access to resources (Gowans et al. 2007), human activities (Díaz López & Shirai 2008), sex (Diaz-Aguirre et al. 2018), and kinship (Wiszniewski et al. 2010).

Bottlenose dolphins display numerous foraging techniques that vary substantially among and within populations (e.g. mud plume feeding: Lewis & Schroeder 2003; fish herding: Gazda et al. 2005; benthic feeding: Rossbach & Herzing 1997; sponge feeding: Sargeant et al. 2007). In some areas, bottlenose dolphins have adapted their foraging techniques to maximize their energy intakes, capitalizing on anthropogenic activities such as fisheries (e.g. trawler fisheries: Corkeron et al. 1990; Bearzi et al. 2009; gillnet fisheries: Read et al. 2003; Díaz López 2006) and aquaculture (e.g. finfish aquaculture: Díaz López, 2009; shellfish aquaculture: Methion & Díaz López 2019a). Such interactions influence bottlenose dolphin social structure: in Australia, bottlenose dolphins feeding in association with trawlers were part of a different social community than the ones not using this feeding technique (Chilvers & Corkeron 2001); in Brazil, bottlenose dolphins cooperating with beach-casting fishermen were socially segregated from

non-cooperative dolphins (Daura-Jorge et al. 2012); and in Italy, the level of association between individuals was significantly lower for bottlenose dolphins engaged in opportunistic feeding activities in finfish farm areas than during not-opportunistic feeding activities (Díaz López & Shirai 2008; Díaz López 2019).

Along the northwestern coast of Spain (Galicia), shellfish aquaculture leads to a variation in resource distribution and abundance. Shellfish are grown on floating rafts with a concentration of ropes in the same area, submerged in the water, increasing the abundance of fish species within shellfish farm areas relative to adjacent areas (Chesney & Iglesias 1979), thus providing high prey density for common bottlenose dolphins (*Tursiops truncatus*) (Díaz López & Methion 2017). When foraging in shellfish farms, bottlenose dolphins swim around the floating rafts to herd school of fish, rush toward the ropes, and feed (Methion & Díaz López 2019). Although bottlenose dolphin habitat-use and foraging behavior have previously been associated with shellfish aquaculture areas, potential variation in the frequency with which individuals use shellfish farms as foraging grounds and its influence on social interactions have never been studied.

In light of the above considerations, we used behavioral and photo-identification data to investigate individual foraging variation in bottlenose dolphins and its potential influence on their social organization (affiliation indices and network metrics). First, we evaluated whether individual bottlenose dolphins varied in the frequency with which they use human-altered areas (i.e. shellfish farms) as foraging grounds. Second, we evaluated whether this variation was linked to individual associations and social structure characteristics using generalized affiliation indices (Whitehead & James 2015) and social network analysis (Lusseau et al. 2003; Whitehead 2008). Given the findings of previous research (Díaz López & Methion 2017; Methion & Díaz López 2019a), we expected that the concentration of food resources associated with shellfish aquaculture would induce individual foraging variation, with some individuals foraging more frequently within shellfish farms than others. Subsequently, we expected that this foraging variation would influence bottlenose dolphin social organization, with weaker associations between individuals showing foraging preferences for high food availability areas, where inter-individual competition is higher (Holekamp et al. 2012). Through this framework,

we aimed to further our understanding of individual foraging variation driving social organization in bottlenose dolphins.

7.3 Methods

7.3.1 Study area

The present study was conducted in the Ría de Arousa (Galicia, North-West Spain) (**Figure 7.1**). Intense upwelling events occur in the area, leading to high biodiversity, productive fisheries, and important aquaculture activities, particularly the production of shellfish (Tenore et al. 1995). Shellfish farming has occurred in Galicia since the late 1940s (Miguez et. 2009) and has developed over the years. Shellfish are grown on ropes suspended from wooden floating rafts which cover approximately 17% of the study area (**Figure 7.1**) (Díaz López & Methion 2017). The rafts act as fish aggregation devices, increasing the abundance of fish species within shellfish farm areas compared to adjacent areas (Chesney & Iglesias 1979). Bottlenose dolphins are present year-round in the Ría de Arousa (Díaz López & Methion 2017; Methion & Díaz López 2018) and frequently use the shellfish farm areas as foraging grounds (Methion & Díaz López 2019a).

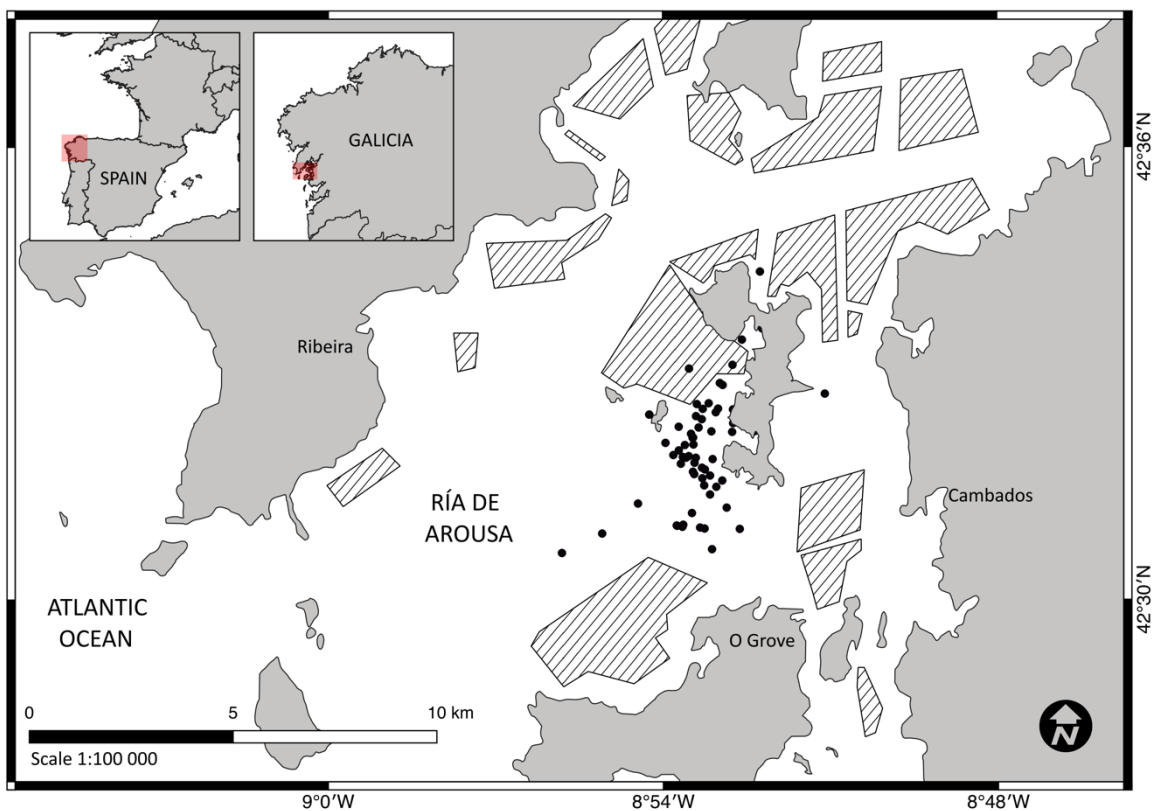


Figure 7.1. Map of the study area (Ría de Arousa, North-West Spain) showing the minimum convex polygon centroids for each of the 66 bottlenose dolphins studied. Polygons represent shellfish farm areas.

7.3.2 Data collection

Boat-based surveys were conducted on-board a 12 m research vessel between April 2014 and November 2017. The study area was monitored during daylight hours when the sea conditions were no greater than 3 on the Douglas sea force scale and visibility was not reduced by rain or fog (Díaz López & Methion 2017). A group of bottlenose dolphin was defined as one or more individuals observed within a 100-m radius, interacting with each other, and engaging in the same behavioral activity (Methion & Díaz López 2019a). All encounters continued until the group composition changed, the group was lost, or until weather conditions became unfavorable. Upon sighting a group of bottlenose dolphins, the date, time, and GPS location were recorded, and group size and composition were estimated. The presence of the group of bottlenose dolphins inside or outside the shellfish farm areas was also recorded. Photographs were taken for photo-identification purposes using digital single lens reflex cameras equipped with a 35-300-mm telephoto zoom lens. Attempts were made to photograph both sides of the dorsal fin of every dolphin present in the group, regardless of the degree of marking, age class, or behavior. Bottlenose dolphins were identified based on natural markings on their dorsal fin from high-quality photographs (Würsig & Jefferson 1990). Only individuals with distinctive marks (referred as identified individuals) were included in the analysis to avoid misidentification. Details on the photo-identification procedure can be found in Methion & Díaz López (2018). The predominant behavior of the group was assessed and classified into four categories: foraging, resting, socializing, and travelling (detailed in Methion & Díaz López 2019a). The age of individuals was classified as either dependent calves or adults based on behavioral cues and visual assessment of the size (following Methion & Díaz López 2019a). All males were sexed by the observation of an erection or by the gap (> 2.5 cm) between the genital and anal slits, with photographs of the genital area (N = 37). Females were sexed either (1) by the observation of mammary slits and absence of gap between the genital and anal slits, with photographs of the genital area (N = 20), or (2) by the repeated observation with a newborn swimming in infant position (a minimum of seven consecutive sampling days, N = 9). Data collection complies with the current laws of Spain, the country in which the study was performed.

7.3.3 Individual foraging variation and spatial distribution

Individual foraging variation was assessed through the difference in use of shellfish farm areas as foraging grounds. To explore the use of shellfish farm areas as foraging grounds by an individual bottlenose dolphin, a “farm foraging rate” was calculated for each individual. The farm foraging rate was defined as the number of times an identified individual was observed foraging in the shellfish farm areas as a proportion of the total number of times the same individual was observed foraging. The farm foraging rate was then used as a continuous measure in further analysis.

Spatial distribution of the sightings for each individual was plotted using a geographical information system (QGIS software, <http://www.qgis.org>). Minimum convex polygon was used to compare space-use between individuals (Burgman & Fox 2003). Space-use overlap between each pair of individuals was determined by using the vector overlay features in QGIS. The central tendency of an individual space-use was represented by the centroid of the minimum convex polygon of all sightings of the individual (**Figure 7.1**).

7.3.4 Defining association and estimating affiliation indices

Bottlenose dolphins identified within the same group during a single day were considered associated. To ensure accurate behavioral assessment and individual identification, only groups monitored for at least 15 min and where at least 75% of the estimated group size were reliably photographed were included in the analysis. In order to reduce inaccuracies and biases associated with small sample size, analyses were further limited to individual bottlenose dolphins observed (1) foraging more than six times (greater than the median number of sightings in which individuals were observed foraging) and (2) in at least three calendar years. Dependent calves were not included in the analysis because of their dependent relationship with their mothers (Mann & Smuts 1998).

Social and network analyses were carried out in Socprog 2.8 (Whitehead 2009). Daily sampling periods were used to remove possible demographic effects occurring during the study period (Whitehead 2008). A matrix of association was generated based on the half-weight index (HWI) to reduce biases due to sampling techniques (Cairns & Schwager 1987).

The coefficient of variation of the true association indexes (S) was estimated to measure the social differentiation of the observed HWI using maximum likelihood (Whitehead 2008). Coefficient of variation S values greater than 0.5 indicate well differentiated societies (Whitehead 2008). The correlation between true and estimated association indices (r) was calculated to assess whether the observed association accurately described the social structure (Whitehead 2008). Values of the correlation coefficient, r , close to 1 indicate a good representation of social structure.

The generalized affiliation index (GAI) was used as a measure of strength of the association between dyads (Whitehead & James 2015). The GAI was used to account for the effects of confounding structural factors that might influence the affiliation pattern between individuals (Whitehead & James 2015). The multiple regression quadratic assignment procedure (MRQAP) was used to test the correlation between the association indices (HWI; response variable) and four predictor variables: sex similarity, gregariousness, space-use overlap, and cumulative number of sightings for each pair of individuals. The correlations were calculated for each predictor variable while controlling for the others. GAIs were calculated as the residuals of a generalized linear model, where the dependent variable was the association index (HWI), and the structural factors were the predictor variables (Whitehead & James 2015).

7.3.5 Analysis of affiliation patterns

To assess whether observed associations occurred at random, a Monte Carlo simulation test was conducted, where association matrices were randomly permuted until the P-value stabilized (Bejder et al. 1998; Whitehead 2009). To account for non-independence of group membership, randomizations permuting associations among groups within each sampling period were carried out (Whitehead 2009). A significantly higher standard deviation (SD) of observed affiliation indices compared to that of randomly permuted data indicated the presence of non-random associations (Whitehead 1999).

To assess whether affiliation patterns (mean and maximum GAI) were related to the farm foraging rate, a non-parametric Spearman's correlation test was performed using the psych package in v. 1.8.1. of the statistics and graphics tool R (R Development Core Team 2011).

Additionally, to test whether individuals preferred to affiliate with other individuals having a similar farm foraging rate, an arbitrary threshold using the mean value was fixed and individuals were pooled in two foraging classes: (1) "Frequent Farmers", individuals with a farm foraging rate equal to or higher than the mean and (2) "Occasional Farmers", individuals with a farm foraging rate lower than the mean. A two-tailed Mantel test was then run to compare affiliation indices within and between the two foraging classes (Whitehead 2008).

7.3.6 Network metrics and social structure

A social network approach was used to investigate the social association patterns. Social network was modeled as weighted networks based on the association matrices defined by the GAI among individuals. We calculated five egocentric network measures (Whitehead 2008) to investigate differences in centrality of individuals: (1) the Strength, which is a measure of gregariousness and is the sum of the GAI of each individual (Barrat et al. 2004); (2) the Eigenvector Centrality, which is a measure of an individual's importance in the network and is determined as the distance from other central individuals relative to all others in the network (Newman 2004); (3) the Reach, which is a measure of indirect connectedness in the network (Whitehead 2008); (4) the Clustering Coefficient, which describes how well associated an individual associates are (Holme et al. 2007); and (5) the Affinity, which is a measure of how strongly an individual is associated to other individuals with high strength (Barthélemy 2005).

To assess whether network metrics were related to the farm foraging rate, non-parametric spearman's correlation tests were performed.

A social network diagram was drawn using the program Netdraw (Borgatti et al. 2002), with lines (edges) representing GAI between individuals (nodes).

Potential subgrouping within the network was explored using the clustering algorithm and eigenvector-based approach of Newman (2006) to select the community partition that maximizes the modularity coefficient (Q) (implemented in Socprog 2.8; Whitehead 2009). To define the most parsimonious clustering step, the social network is iteratively divided into clusters until a peak in Q is reached (Newman 2006). Q values above 0.3 are generally considered to present a meaningful delineation of the data (Newman 2004).

7.4 Results

During the study period, 265 groups of bottlenose dolphins were encountered and 171 individual dolphins were identified. Of the groups containing two or more adult individuals, 84% were mixed-sex. Of the total number of identified individuals, 66 met the restriction criteria including 37 males and 29 females. Total sightings per selected individual ranged from 7 to 82 (mean \pm SE = 32 ± 1.83 , median = 28).

7.4.1 Individual foraging variation and spatial distribution

Individual farm foraging rate varied from 0.00 to 0.57 (mean \pm SE = 0.30 ± 0.01 , median = 0.30). Males and females did not show significant differences in farm foraging rate (males: mean \pm SE = 0.32 ± 0.02 , median = 0.30; females: mean SE = 0.28 ± 0.02 , median = 0.30) (Mann-Whitney U test with 10000 permutations, $P > 0.05$).

7.4.2 Association patterns, network metrics, and social structure

The coefficient of variation of the true association indexes indicated a well-differentiated society ($S = 0.81 \pm 0.02$ SE). The correlation between the true association indexes and estimated association indexes indicated that the association data had good power to detect the true social system within the population ($r = 0.86 \pm 0.02$ SE).

MRQAP tests indicated a significant correlation of associations with sex similarity, gregariousness, space-use overlap, and cumulative number of sightings for each pair of individuals (**Figure 7.1**) and were, therefore, included in GAI analyses. The SD of the mean of the observed matrix was significantly higher than the one from random data (observed SD = 0.090, random SD = 0.085) (1 000 permutations, 1 000 trials per permutations, $P < 0.001$).

The mean and maximum GAI were negatively correlated to the farm foraging rate (Spearman's rho, $P < 0.01$) (**Figure 7.2**). Likewise, the analysis indicated a negative relationship between the network metrics and the farm foraging rate. Indeed, Strength, Reach, and Affinity were negatively related to the farm foraging rate (**Figure 7.2**).

Table 7.1. Significance of predictor variables on association indices using multiple regression quadratic assignment procedures (N = 66 individuals).

<i>Predictor variable</i>	Partial correlation coefficient	P
<i>Sex similarity</i>	0.1016	< 0.01
<i>Gregariousness</i>	0.3915	< 0.001
<i>Cumulative number of sightings per pair of individuals</i>	0.3293	< 0.001
<i>Space-use overlap</i>	0.3004	< 0.001

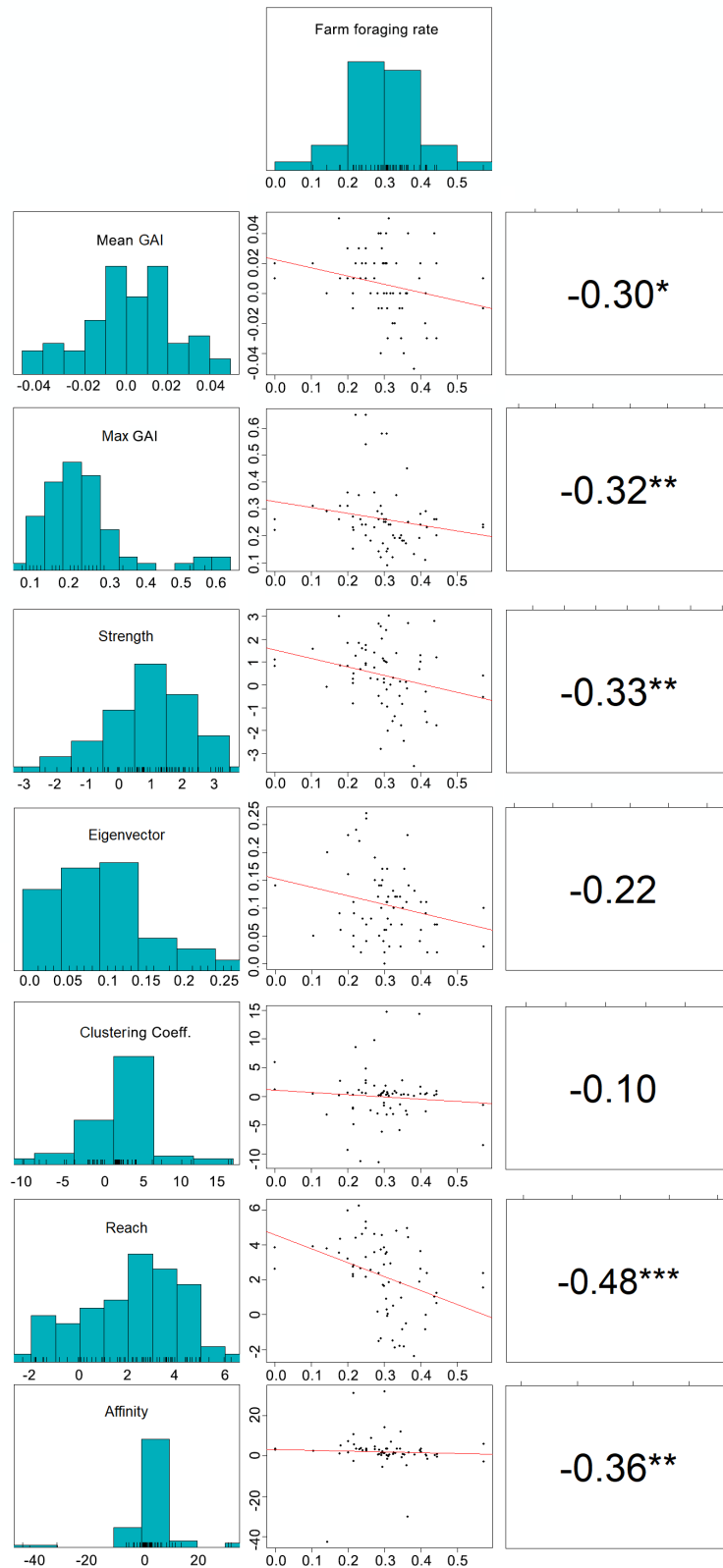


Figure 7.2. Scatter plot with fitted line and Spearman rho coefficient between farm foraging rate (x-axis) and each affiliation (mean GAI and max GAI) and network metrics (Strength, Eigenvector Centrality, Clustering Coefficient, Reach, and Affinity) (y-axis). Histograms with rug plot are provided for each variable. Significance codes: * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

Both the network analysis and the network diagram (**Figure 7.3**) indicated the rather peripheral positions of those individuals with higher foraging rates and emphasized the central role of individuals that forage less frequently between mussel rafts.

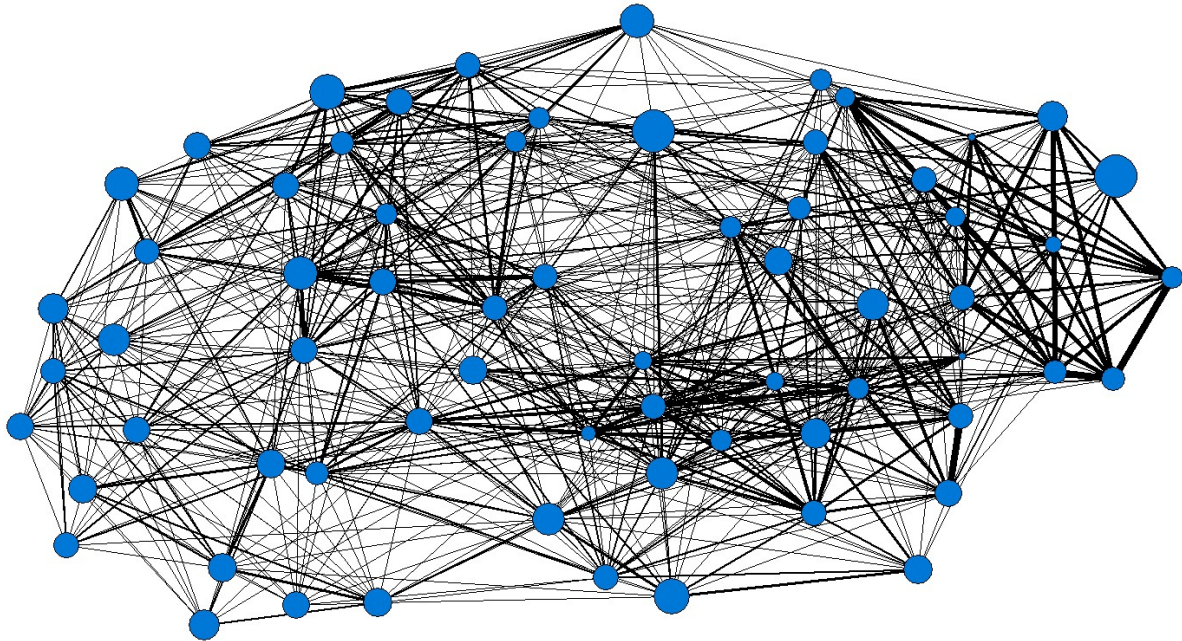


Figure 7.3. Social network of bottlenose dolphins in the Ría de Arousa (North-West Spain). Each individual is represented by a node. Only edges with GAI greater than 0.02 are displayed. Node sizes represent the farm foraging rate of the individuals, and edge width is proportional to the strength of the affiliations.

Modularity analysis identified four social clusters that ranged in size from 12 to 23 individuals. However, analysis did not show conclusive partitioning into separated social units as the modularity of this assignment was 0.09 (Newman 2004).

Affiliations were significantly higher within foraging classes than between foraging classes (two-tailed Mantel test with 1 000 permutations, $t = 5.4$, matrix correlation = 0.12, $P < 0.01$) (within foraging classes: mean GAI \pm SD = 0.02 ± 0.04 ; between foraging classes: mean GAI \pm SD = 0.00 ± 0.03), indicating that individuals preferentially associate with individuals having a similar farm foraging rate. Thirty-nine dolphins were categorized as Frequent Farmers (including 24 males and 15 females) and 27 dolphins were categorized as Occasional Farmers (including 13 males and 14 females).

7.5 Discussion

The current study reveals that behavioral variation among individual bottlenose dolphins shapes their social organization. In particular, bottlenose dolphins that frequently foraged within human-altered areas (i.e. shellfish farms) exhibited weaker associations when compared to others. Furthermore, we demonstrated that bottlenose dolphins preferred to affiliate with other individuals with similar foraging strategies. These findings provide valuable insight into the evolution of bottlenose dolphin social systems and their response to human-induced changes in the marine environment.

Our results indicate that bottlenose dolphins used shellfish farm areas as foraging grounds with varying intensity. Individual variation in foraging behavior has been previously documented in other parts of the world for bottlenose dolphins (e.g. Sardinia, Italy: Díaz López & Shirai 2008; Florida, USA: Nowacek 2002; Torres & Read 2009; Shark Bay, Australia: Mann & Sargeant 2003, Sargeant et al. 2007, Sargeant & Mann 2009; Brazil: Simões-Lopes et al. 1998) as well as other social mammals (e.g. European badger, *Meles meles*: Robertson et al. 2014; mink, *Mustela spp*: Sidorovich et al. 2001; sea otter, *Enhydra lutris*: Estes et al. 2003). Behavioral variation may reduce competition between group members and facilitate a stable society, playing an important role in the evolution of the social system (Barta 2016). In Galicia, competition for food resources may motivate individual bottlenose dolphins to adopt different foraging strategies, and thus induce the observed differences in foraging behavior. The behavioral variation reported in this study, therefore, likely reflects differences in the utilization of distinct foraging strategies rather than differences in spatial distribution and between sexes.

Along the North-Western coast of Spain (Galicia), shellfish aquaculture has introduced spatial habitat complexity, leading to a variation in resource distribution and abundance (Chesney & Iglesias 1979) and has fragmented bottlenose dolphin habitat (Díaz López & Methion 2017). Certain individual bottlenose dolphins frequently used the shellfish farm areas as foraging grounds, using specific foraging strategies to catch prey in between the floating rafts (Methion & Díaz López 2019a). These individuals therefore profit from a reliable and easily located (i.e. lower energetic and time expenditure when foraging) food source, which may increase their energy intake (Díaz López 2012; Methion & Díaz López 2019a). A frequent interaction with

shellfish aquaculture may have led some individuals to have an intimate knowledge of the characteristics of these human-altered areas and be able to efficiently obtain the food resources concentrated within these structures.

Social network analyses reveal that the observed variation in foraging behavior among individual bottlenose dolphins was associated with their social organization. Network metrics including Strength, Reach, and Affinity were negatively correlated to the farm foraging rate. Bottlenose dolphins frequently foraging within the shellfish farm areas had a peripheral position within the network and exhibited weaker Strength, Reach, and Affinity compared to individuals with a lower foraging rate. The reliable, easily located, and large food source present within the shellfish farm areas may have made less necessary for dolphins to cooperate with a large number of conspecifics. The presence of concentrated food resources within these human-altered areas could increase the level of intraspecific competition between individuals (Díaz López 2019). In contrast, individuals that foraged less frequently within the shellfish farms occupied a central position within the network and had strong associations. These individuals may benefit from increased cooperation and reduced intragroup competition, thus increasing learning and information-sharing, as they may face a patchy and irregular distribution of prey. Cooperative foraging tactics, such as “carousel swim” (i.e. dolphins surrounding wild fish schools, forcing the fish to swim in a concentrated ball), have been described in bottlenose dolphins hunting wild prey (Díaz López 2009). By coordinating their behaviors, individuals that foraged less frequently within the shellfish farms may maximize their foraging efficiency, and presumably their overall fitness. Relationships between association patterns and foraging behavior have been suggested to be a result of individual adaptations to local ecological conditions. In Sardinia Island (Italy), association levels between bottlenose dolphins became weaker as a consequence of an increase in intragroup competition due to human-induced changes (i.e. finfish farming and coastal fisheries) in the marine environment (Díaz López 2019). In Australia, Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) were socially more connected after the reduction of commercial fisheries (Ansmann et al. 2012). In Kenya, associations between spotted hyenas (*Crocuta crocuta*) were weakest when competition for resources was most intense (Holekamp et al. 2012).

Our findings indicate that bottlenose dolphins preferred to affiliate with other individuals that foraged within shellfish farms at similar frequencies. Homophily based on foraging strategies has been previously shown in other bottlenose dolphin populations (e.g. sponge foraging in Australia: Mann et al. 2012; foraging in interaction with fishermen in Brazil: Daura-Jorge et al. 2012; Machado et al. 2019; “Feeding associates” interacting with finfish farm in Italy: Díaz López & Shirai 2008). The observed tendency to associate with similar individuals (i.e. homophily) may influence a range of social processes in this population of bottlenose dolphins, including social segregation (Best et al. 2013), social contagion (i.e. spread of behavior patterns in a group through imitation) (Sah et al. 2018), and the evolution of cooperation (Massen & Koski 2014). As social bonds take investment of time, energy, and trust, maintaining associations with individuals that are more trustworthy is beneficial (Massen & Koski 2014). By associating with individuals of similar foraging preferences, bottlenose dolphins may facilitate the cooperation and the transmission of information (i.e. learning) within foraging groups rather than between foraging groups.

Efficient foraging requires knowledge of prey locations and foraging strategies, which may be learned by interacting with conspecifics (Sargeant et al. 2007; Díaz López 2009; Mann et al. 2012). The higher Strength, Reach (which has been associated with behavioral contagion; Flack et al. 2006), and Affinity observed in individuals foraging less frequently within the shellfish farm areas further suggest that these individuals play an important role in cooperation, communication, and social learning (Wey et al. 2008). Social learning is commonly used among mammals to acquire information about the environment and is a suggested process behind the development of individual foraging variation (e.g. meerkat, *Suricata suricatta*: Thornton & Malapert 2009; sea otter: Estes et al. 2003; bottlenose dolphin: Daura-Jorge et al. 2012; Mann et al. 2012). Given the observational learning skills of bottlenose dolphins (Kuczaj & Yeater 2006), the foraging strategies for capturing prey may be perpetuated by transmission of information between individuals (Rendell & Whitehead 2001). Learning through observation may help to maintain behavioral strategies by facilitating the transmission of behavior from one bottlenose dolphin to another (Kuczaj & Yeater 2006). In bottlenose dolphins, there is ample opportunity for social learning since mothers care for their offspring for several years (Mann & Smuts 1998), and since they exhibit social systems characterized by fission-fusion dynamics, allowing both vertical and horizontal transmission of behavior. The presence of females, which

had calves during the study period supports the fact that foraging strategies could be passed down from mother to offspring (vertical transmission). Bottlenose dolphins may also learn these foraging strategies from individuals within a generation (horizontal transmission). The flow of information could, therefore, be increased between individuals exhibiting similar foraging behavior. This learning homophily could promote, through time, a segregation of the population into behaviorally distinct groups (Centola et al. 2007).

Given bottlenose dolphins' inconspicuous nature and the changing environment they inhabit, there are inherent difficulties in studying their behavior and social organization. Bottlenose dolphin social organization is likely to be driven by multiple factors acting synergistically, including behavior (Díaz López & Shirai 2008), reproductive state (Connor et al. 2000), sex (Mann et al. 2012), kinship (Wiszniewski et al. 2010), age (Gero et al. 2005), and environmental conditions (Díaz López 2019). Our analytical approach, taking into account adult individuals only and the effects of four structural variables (sex similarity, gregariousness, space-use overlap, and cumulative number of sightings for each pair of individuals) when estimating affiliation indices (GAI), provides reliable results when estimating social interactions (Whitehead & James 2015). Other variables may contribute to social interactions in this bottlenose dolphin population such as kinship (Parsons et al. 2003; Wiszniewski et al. 2010; Carter et al. 2013) and similarity of interaction partners in terms of consistent individual differences in behavior (i.e. "behavioral syndromes" or "personality"). Individual differences in personality have been documented for captive bottlenose dolphins (Highfill & Kuczaj 2007) and may potentially correlate with the observed differences in foraging behavior (i.e. risk-taking behavior). These factors, together with ecological pressures (Yamagiwa 1999; Belton et al. 2018; Díaz López 2019), may play important roles in the development of non-random and long-term associations among individual bottlenose dolphins.

In conclusion, this study highlights the relationship between individual foraging variation in bottlenose dolphin and their social organization. The observed foraging variation may have further implication for bottlenose dolphin ranging behavior (Cantor et al. 2018) and genetics (Estes et al. 2003). From a conservation perspective, individual bottlenose dolphins frequently foraging within human-altered areas (i.e. shellfish farms) may face higher risk of injury or death due to the interaction with human activities (i.e. boat strikes, entanglement, water pollution;

Methion & Díaz López 2019a) which could alter the population social dynamics and structure. Further information about the willingness to interact with human activities (i.e. risk-taking behavior) through specific studies on personality will be crucial to further understand the social organization and the emergence of specialized behaviors in wild bottlenose dolphins.

Chapter 8. General discussion

This chapter is divided in four main sections: summarized key scientific findings, conservation measures for bottlenose dolphins, as well as regulations for the shellfish farming industry, and lastly, limitations of this study and perspectives for future research.

8.1 Overview

As reviewed in Chapter 1, studying the ecology and behaviour of cetaceans to obtain baseline data is essential in order to identify the potential influence of anthropogenic activities and to take appropriate conservation and management actions (Whitehead et al. 2000). Given the global expansion of marine aquaculture, and the paucity of information regarding cetaceans and shellfish farming, the aim of this thesis was to investigate the ecology and behaviour of a marine top predator, the bottlenose dolphin, living in a coastal area subject to intense shellfish aquaculture activity.

The Galician rías, being one of the world's most important areas for shellfish farming and a place where bottlenose dolphins are regularly present (López et al. 2004), exhibited adequate conditions to study the potential influence of shellfish farming on bottlenose dolphin ecology and behaviour. Until now, research in Galician waters had mostly focused on data obtained from stranded bottlenose dolphins and observational data from either land-based or opportunistic platforms (e.g. López et al. 2002, 2004; Pierce et al. 2010; Fernández et al. 2011a, b, 2013; Spyrakos et al. 2011; Méndez-Fernández et al. 2012, 2013, 2014a, 2014b; Louis et al. 2014; Nykänen et al. 2019). Therefore, there was little to no understanding of coastal bottlenose dolphin's abundance, site fidelity, grouping dynamics, habitat use, foraging behaviour, or social organisation. Likewise, the potential influence of shellfish aquaculture on bottlenose dolphins had never been studied. As a consequence, there was a lack of conservation and management decisions for bottlenose dolphins in Galician waters.

Using behavioural and environmental data collected year-round, over five years in Galician waters (North-West Spain), this study provides baseline data on bottlenose dolphins' ecology and behaviour within an area that is highly affected by human activities (8.2) and furthers the understanding of the shellfish aquaculture influence on cetaceans (8.3). The outcomes of this study allow for the suggestion of appropriate management and conservation measures for bottlenose dolphins in this area (8.4), as well as regulations for the shellfish farming industry (8.5).

8.2 Ecology and behaviour of bottlenose dolphins in Galician waters

Distribution

The results presented in this thesis highlight that Galician waters, and in particular the Ría de Arousa, are of considerable importance for coastal bottlenose dolphins. The bottlenose dolphin was the most frequently recorded cetacean species in this coastal area. This finding is consistent with previous studies carried out from land-based observation (Pierce et al. 2010) and with the geographical distribution of bottlenose dolphin strandings along the Galician coast (López et al. 2002). Bottlenose dolphins were present year-round, with no seasonal fluctuations in terms of presence, and with a high degree of occurrence in the area (Chapters 3, 4, and 5). While most of the groups of bottlenose dolphins were found inside the Ría de Arousa, a few groups of bottlenose dolphins were also observed in external waters, within the continental shelf (Chapter 3) (**Figure 8.1**). These groups encountered outside the Ría de Arousa were comprised of transient individuals only that were never recaptured (Chapter 3), while the individuals encountered inside the Ría de Arousa were the only ones recaptured within the study period. These findings reinforce the idea of the existence of both the coastal and pelagic ecotypes in Galician waters, as previously reported by genetic and isotopic studies (Fernández et al. 2011a; Méndez-Fernández et al. 2013; Louis et al. 2014).

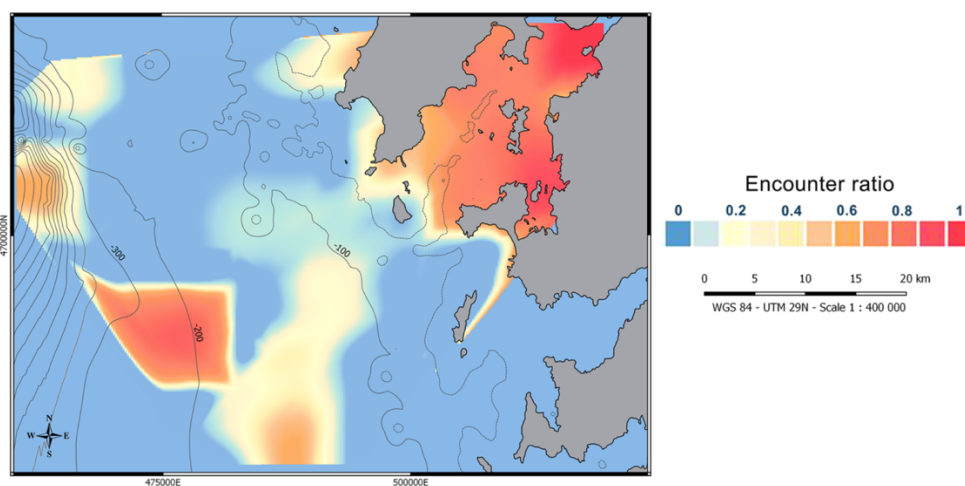


Figure 8.1. Spatial distribution of bottlenose dolphins in Galician waters.

Encounter ratio: number of samples with presence in each 2 nm x 2 nm cell of a grid divided by the total number of samples collected in each cell (source: Díaz López & Methion 2018a).

Results of Chapter 5 highlight that bottlenose dolphins present a fine-scale pattern of habitat selection, showing a preference for the inner part of the Ría de Arousa and for shallow waters (i.e. < 30 m). Bottlenose dolphins were often found in proximity to the shellfish farms, which act as fish aggregating devices (i.e. large aggregations of fish species around shellfish rafts compared to adjacent areas; Chesney & Iglesias 1979), thus providing a higher density of high-quality prey for dolphins. Although predator avoidance, interspecific competition, and reproductive strategies all play a key role in cetacean distribution to some extent (Stevick et al. 2009), habitat preference and relative density is assumed to be determined primarily by food availability. In Galicia, bottlenose dolphins feed on a wide range of fish species, the most important (numerically and in terms of biomass) being pelagic and demersal fish species (Santos et al. 2007). The observed influence of depth on bottlenose dolphin habitat use and their preference for the inner part of the ría may therefore be related to the availability of food resources (Tenore et al. 1995; Spyarakos et al. 2011). Chapter 6 findings indeed revealed that the ría is an important feeding ground for bottlenose dolphins, as they were observed foraging on almost half of the observations (49% of the time).

New-born dolphins were observed from June to September, indicating that the Ría de Arousa is used as a nursery area by bottlenose dolphins and that calving occurs mainly in summer. Evidence of three infanticides occurring in Galician waters during the summer month (July-September) with post-mortem examinations (Díaz López et al. 2018b: annex 1) supports this fact. This is consistent with findings from other studies; bottlenose dolphins usually give birth during the warmer season of the year, as thermal constraints are believed to restrict calving (Bearzi et al. 1997; Möller et al. 2002; Díaz López 2012).

Abundance and demographic parameters

According to photo-identification analysis (Chapter 3), 190 adult bottlenose dolphins (of which 57 were documented as females and 40 were documented as males) were identified in the Ría de Arousa during the study period (2014-2016). The abundance of adult bottlenose dolphins, obtained from the Pollock robust design model, ranged from 56 (95% CI 55-66) to 144 (95% CI 133-166). Similar abundance estimates, in terms of the number of individuals present, of north-east Atlantic bottlenose dolphin populations living in rich coastal environments, such as the

Moray Firth, Scotland (Wilson et al. 1999), the Shannon Estuary, Ireland (Berrow et al. 2012), and Setúbal bay, Portugal (Martinho et al. 2015) have been obtained in other studies through other mark-recapture methods than the robust design model.

Results obtained in Chapter 3 indicate that seasonality is a prominent feature affecting bottlenose dolphin movement and demographic dynamics. There was a temporary influx of bottlenose dolphins during the transition periods from autumn to winter. Such seasonal fluctuations in abundance has been observed in other bottlenose dolphin populations (Smith et al. 2013; Sprogis et al. 2016b). Although there may be different factors playing a key role in bottlenose dolphin distribution, the observed changes in abundance and emigration rates most likely reflect seasonal fluctuations in the abundance of prey species. The winter season, with the highest abundance and lowest emigration rates of bottlenose dolphins, is in fact characterised by a peak in numbers of demersal fish species inside the Ría de Arousa (Chesney & Iglesias 1979).

Although several studies reported high by-catch mortality rate for bottlenose dolphins in Galician waters (López et al. 2003; Goetz et al. 2014), the estimated apparent survival rate was high and constant, suggesting no mortality and no permanent emigration of individuals during the duration of the study (two years) (Chapter 3). These results are common for long-lived species with slow growth rates and low fecundity, and have been reported in other bottlenose dolphin populations (Nicholson et al. 2012; Sprogis et al. 2016b).

Site fidelity

Bottlenose dolphins exhibited different levels of site fidelity for the Ría de Arousa (Chapter 3). Overall, 134 bottlenose dolphins (71% of the total catalogue) were identified in more than a single season of research and were considered resident individuals. Of these dolphins, 22 (4 females and 18 males) exhibited a high site fidelity, as they were observed in all research seasons. Long-term site fidelity is common in coastal bottlenose dolphins (Wells et al. 1987; Maze & Würsig 1999; Connor et al. 2000; Möller et al. 2002; Díaz López 2019). Conversely, 49 identified individuals (26% of the total catalogue) were considered transients, as they were only seen during a single month of research. Difference in site fidelity between individuals is also regularly reported for coastal bottlenose dolphins (Möller et al. 2002; Díaz López 2012).

Different factors could explain the observed differences in site fidelity, such as availability of food resources, different tolerances to human disturbance, or different individual prey preferences. The last is supported by a study about the diet of bottlenose dolphins in the region that indicated differences in diet between males and females (Santos et al. 2007). Additionally, the age and sex of each individual, as well as its ecological and social preferences, could explain the differences in the residence patterns observed (Bearzi et al. 1997). In contrast with other areas where females showed strong site fidelity by staying in sheltered waters for protection from predation (Nicholson et al. 2012; Smith et al. 2013), the absence of natural predators in the present study area may not constrain females to a small home range. Moreover, area defence by individuals or social groups could also help explain the observed differences in site fidelity and temporal occurrence rates observed (Díaz López 2012). The effects of human activities on bottlenose dolphins could differ between individuals because of individual variability in site fidelity. From a conservation perspective, individual bottlenose dolphins exhibiting long-term site fidelity may face a higher risk of injury or death due to the potential interaction with human activities (i.e. boat strikes, entanglement, water pollution), which could affect their survival.

Group dynamics and composition

The group size of bottlenose dolphins inside the Ría de Arousa ranged from 1 to 64 individuals (mean $10.65 \pm SE 0.34$ dolphins), which is quite high compared with other coastal bottlenose dolphin populations (e.g. mean $8.5 \pm SE 1.0$ in the Shannon estuary, Ireland: Berrow et al. 2012; mean $6.8 \pm SE 0.2$ in Kvarneric bay, Croatia: Bearzi et al. 1997; mean $4.8 \pm SE 0.2$ in Sarasota, USA: Irvine et al. 1981; mean $4.4 \pm SE 0.1$ in Golfo Aranci, Italy: Díaz López 2019) (**Figure 8.2**). Most of the groups observed during the study period were mixed-sex groups (84%), so sexes were not as segregated as in other studied populations (Connor et al. 2000; Bouveroux et al. 2010). Dependent calves (both immature and new-born dolphins) were present in 55% of the observed groups and new-born dolphins were present in 11% of the observed groups.

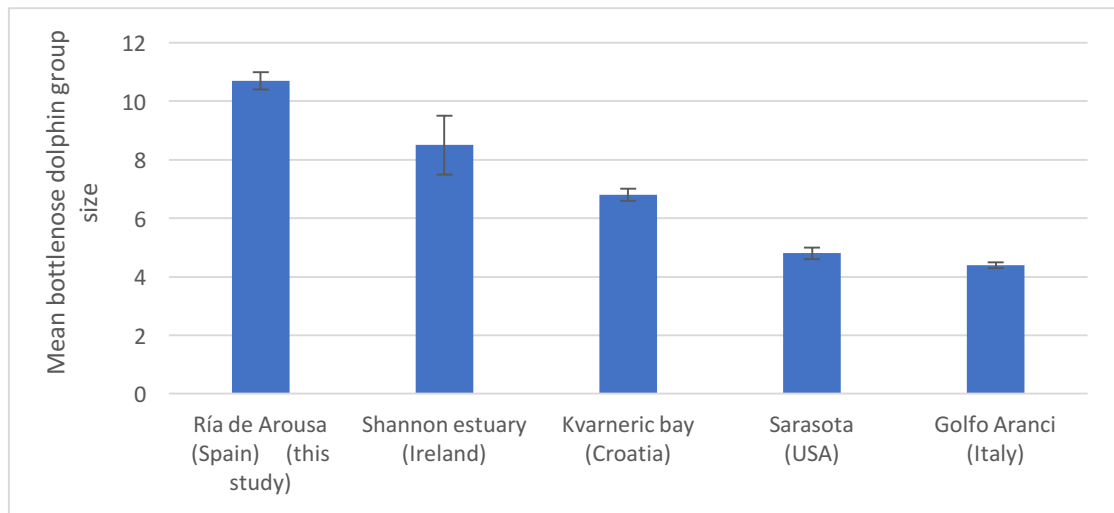


Figure 8.2. Mean bottlenose dolphin group size in various locations around the world.

Bars represent the standard error. Source: Irvine et al. 1981; Bearzi et al. 1997; Berrow et al. 2012; Díaz López 2019.

Cetaceans commonly form groups to increase access to resources and mating opportunity, and reduce predation risk (Alexander 1974; Díaz López et al. 2018b). An increase in group size with an increase in the number of calves in the group was observed. Similar patterns have been found for other coastal bottlenose dolphins (e.g. Wells et al. 1987; Bearzi et al. 1997; Möller et al. 2002; Hubard et al. 2004). Increased dolphin group size when calves are present has been related to enhanced calf assistance, increased protection from predators, and reduced maternal investment (Norris & Dohl 1980).

The findings of Chapter 4 indicated that environmental conditions (chlorophyll-a and dissolved oxygen) influence the spatio-temporal aggregation patterns of bottlenose dolphins. Fluctuations in primary production (chlorophyll-a concentration) could be responsible for short-term changes in bottlenose dolphin prey availability. The low chlorophyll-a concentration, associated with large groups of bottlenose dolphins, could be interpreted as a period of phytoplankton decay, mediated by zooplankton grazing, and therefore a high abundance of plankton-feeding fish species (Díaz López & Methion 2019). Dissolved oxygen is also an important factor affecting the distribution and abundance of both demersal and pelagic fish communities (Howell & Simpson 1994), with fish diversity and abundance increasing in areas of high oxygen levels (Mas-Riera et al. 1990; Howell & Simpson 1994). Therefore, the large groups of dolphins observed in higher concentration of dissolved oxygen might be related to a higher availability of prey for bottlenose dolphins.

Foraging behaviour

The results from Chapter 6 revealed that foraging behaviour was related to both environmental (sea surface temperature and time of day) and anthropogenic (shellfish farm areas) factors. Variability in bottlenose dolphin behaviour is likely a result of the interactions of these drivers with prey availability and physiological needs of the dolphins. The observed influence of the sea surface temperature and time of day on foraging behaviour may in fact be related to temporal changes in abundance of pelagic and demersal fish species. Indeed, pelagic and demersal fish species, which are the most important prey species of bottlenose dolphins in the region (Santos et al. 2007), show clear temporal changes (seasonal and circadian) in abundance and distribution inside of the Ría de Arousa (Chesney & Iglesias 1979; Tenore et al. 1995). As a result, during seasons characterized by low sea surface temperature, dolphins might tend to increase the time spent foraging because of their higher energy requirements (Shane 1990; Bräger 1993; Díaz López 2012).

The results of Chapter 6 further highlight the importance of shellfish farm areas as potential foraging grounds for this species. As reviewed earlier, shellfish farms lead to a variation in food resource distribution and abundance in the form of modified habitat that is favourable for bottlenose dolphin foraging activity (high diversity and abundance of fish species and physical space for the dolphins to move in between the rafts). The rafts provide a physical structure acting as fish aggregating devices, thus increasing the abundance of fish species within shellfish farm areas relative to adjacent areas (Tenore & Gonzalez 1976; Chesney & Iglesias 1979; Romero et al. 1982). Consequently, the pelagic and demersal fish species concentrated in the aquaculture areas, feeding directly on the shellfish-line associated community or using the structures as resting sites (Iglesias 1981; Freire & González-Gurriarán 1995), provide bottlenose dolphins with an important source of food. By reducing the time spent searching for prey, bottlenose dolphins reduce the energy required to feed and possibly increase the quantity and quality of the food consumed (Díaz López 2006a).

Chapter 7 findings indicate that bottlenose dolphins exhibited individual variation in foraging behaviour. While some dolphins were foraging frequently within shellfish farms, other dolphins were not. In Galicia, competition for food resources may motivate individual bottlenose dolphins to adopt different foraging strategies, and thus induce the observed differences in

foraging behaviour. Certain individual bottlenose dolphins frequently used the shellfish farm areas as foraging grounds, using specific foraging strategies to catch prey in between the floating rafts. These individuals therefore profit from a reliable and easily located (i.e. lower energetic and time expenditure when foraging) food source, which may increase their energy intake (Díaz López 2012; Chapter 6: Methion & Díaz López 2019a). A frequent interaction with shellfish aquaculture may have led these individuals to have an intimate knowledge of the characteristics of these human-altered areas and be able to efficiently obtain the food resources concentrated within these structures. Behavioural variation may reduce competition between group members and facilitate a stable society, playing an important role in the evolution of the social system (Barta 2016). Such variation has been previously documented in other parts of the world for bottlenose dolphins (e.g. Sardinia, Italy: Díaz López & Shirai 2008; Florida, USA: Nowacek 2002; Torres & Read 2009; Shark Bay, Australia: Mann & Sargeant 2003, Sargeant et al. 2007, Sargeant & Mann 2009; Brazil: Simões-Lopes et al. 1998). Bottlenose dolphins are considered generalists with regards to prey, but these findings demonstrate how individuals within a same population have some degree of specialisation as a consequence of human activities.

Social organisation

Results of Chapter 7 indicate that bottlenose dolphins exhibited fluid associations, interacting frequently with one another, which is characteristic of a fission-fusion social system (Connor et al. 2000). Although the dolphins associated with many individuals, they were showing preferred associations. Yet, social structure analysis indicated that there was no sub-structure into different communities. Further analysis revealed that sex, spatial use, and foraging preferences shaped their social organisation. In particular, bottlenose dolphins that frequently foraged within shellfish farms exhibited weaker associations when compared to others. Furthermore, the results demonstrated that bottlenose dolphins preferred to affiliate with other individuals with similar foraging strategies (i.e. homophily). Homophily based on foraging strategies has been previously shown in other bottlenose dolphin populations (e.g. sponge foraging in Australia: Mann et al. 2012; foraging in interaction with fishermen in Brazil: Daura-Jorge et al. 2012; Machado et al. 2019; “Feeding associates” interacting with finfish farm in Italy: Díaz López & Shirai 2008) (**Figure 8.3**). By associating with individuals of similar foraging preferences, bottlenose dolphins may facilitate the cooperation and the transmission of information (i.e.

learning) within foraging groups rather than between foraging groups. Efficient foraging requires knowledge of prey locations and foraging strategies, which may be learned by interacting with conspecifics (Sargeant et al. 2007; Díaz López 2009; Mann et al. 2012). The stronger associations observed in individuals foraging less frequently within the shellfish farm areas further suggest that they rely on cooperation, communication, and social learning (Wey et al. 2008), as they may face a patchy and irregular distribution of prey. Social learning is commonly used among mammals to acquire information about the environment and is a suggested process behind the development of individual foraging variation (Daura-Jorge et al. 2012; Mann et al. 2012). Given the observational learning skills of bottlenose dolphins (Kuczaj & Yeater 2006), the foraging strategies for capturing prey may be perpetuated by transmission of information between individuals (Rendell & Whitehead 2001). Learning through observation may help to maintain behavioural strategies by facilitating the transmission of behaviour from one bottlenose dolphin to another (Kuczaj & Yeater 2006). In bottlenose dolphins, there is ample opportunity for social learning since mothers care for their offspring for several years (Mann & Smuts 1998), and since they exhibit social systems characterized by fission-fusion dynamics, allowing both vertical and horizontal transmission of behaviour. The presence of females with calves during the study period supports the fact that foraging strategies could be passed down from mother to offspring (vertical transmission). Bottlenose dolphins may also learn these foraging strategies from individuals within a generation (horizontal transmission). The flow of information could, therefore, be increased between individuals exhibiting similar foraging behaviour. This learning homophily could promote, through time, a segregation of the population into behaviourally distinct groups (Centola et al. 2007).

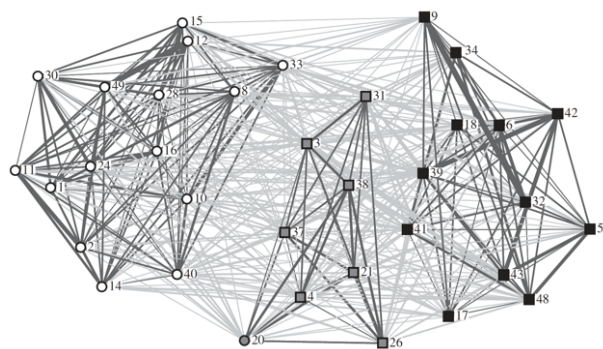


Figure 8.3. Social network of dolphins from Laguna (Brazil) defined by their foraging tactic (source: Daura-Jorge et al. 2012).

8.3 Influence of shellfish aquaculture on bottlenose dolphin ecology and behaviour

One of the objectives of this thesis was to study the influence of shellfish aquaculture on bottlenose dolphin ecology and behaviour. The findings of this thesis revealed that:

- **Shellfish aquaculture influences bottlenose dolphin distribution.**

The presence of bottlenose dolphins increases around shellfish farms. While shellfish farms occupy just around 17% of the total area of the Ría de Arousa, results demonstrated that the farms appear to represent a preferred area of distribution for bottlenose dolphins. By altering the distribution and availability of prey species, the shellfish aquaculture industry indirectly alters the distribution of bottlenose dolphins. This finding contrasts previous studies where the occurrence and distribution of cetacean species decreased in association with shellfish aquaculture which is thought to exclude cetacean species from the area (Markowitz et al. 2004; Watson-Capps & Mann 2005; Ribeiro et al. 2007; Visser 2007; Pearson et al. 2012). These differences suggest that the interactions between cetaceans and shellfish aquaculture might be influenced by the culture method and the cetacean species involved. It is therefore fundamental to study the impacts on a case-by-case basis in more detail. The type of bivalve culture technique used in Galician waters, characterized by floating rafts (described in Chapter 2), differs from the long-line systems found in the previous studies on interactions between cetaceans and shellfish aquaculture.

- **Shellfish aquaculture influences bottlenose dolphin foraging ground selection.**

Shellfish farms are important foraging ground areas for bottlenose dolphins. Dolphins were predicted to be more likely found foraging inside shellfish farm areas than outside (57% vs. 43%). The pelagic and demersal fish species concentrated in the aquaculture areas, feeding directly on the shellfish-line associated community or using the structures as resting sites (Freire & González-Gurriarán 1995; Iglesias 1981), therefore provide bottlenose dolphins with an important source of food. As discussed above, these findings differ from previous studies,

probably because of the differing the culture method used (i.e. floating raft vs. long-lines) and cetacean species studied.

- **Shellfish aquaculture alters bottlenose dolphin behavioural patterns.**

While bottlenose dolphins seem to increase their foraging behaviour while being in proximity of shellfish rafts, they seem to avoid these areas when travelling and resting. This is probably due to the three dimensional structure of the rafts, which may hinder bottlenose dolphins from successfully travelling and resting in the area (Ribeiro et al. 2007). Shellfish farms therefore modify bottlenose dolphin behavioural patterns, which can have repercussions on the animals' overall fitness (Constantine et al. 2004). This is consistent with the findings of other studies in which dolphins avoid shellfish farms while resting and travelling (Karczmarski 2000; Ribeiro 2007).

- **Shellfish aquaculture induces individual variation in foraging behaviour.**

By fragmenting the habitat and creating zones of higher fish abundance, certain bottlenose dolphins frequently use the shellfish farm areas as foraging grounds, using specific foraging strategies to catch prey in between the floating rafts. These individuals therefore profit from a reliable and easily located (i.e. lower energetic and time expenditure when foraging) food source, which may increase their energy intake (Díaz López 2012). This is the first study reporting individual behavioural variation induced by shellfish aquaculture in cetaceans.

- **Shellfish aquaculture induces changes in bottlenose dolphin social organisation.**

Bottlenose dolphins that frequently foraged within shellfish farms exhibited weaker associations when compared to others. The reliable, easily located, and large food source present within the shellfish farm areas may have made it less necessary for dolphins to cooperate with a large number of conspecifics. The presence of concentrated food resources within shellfish farms could increase the level of intraspecific competition between individuals (Díaz López 2019). Furthermore, this study's findings highlighted that bottlenose dolphins preferred to affiliate with other individuals with similar foraging strategies. Bottlenose dolphins that frequently forage between shellfish farms were therefore more closely connected with

each other rather than with individuals that do not forage regularly within the farms. This is the first study reporting that shellfish aquaculture induces social organisation changes in cetaceans.

This study therefore provides substantial information on the influence of shellfish aquaculture on coastal cetaceans. Further investigation demonstrated that there is no limitation for different age or sex class for bottlenose dolphins foraging within shellfish farm areas. Likewise, group size did not vary spatially between groups observed inside and outside the shellfish farm areas.

8.4 Implication for the conservation of bottlenose dolphins

Overall, the findings of this thesis improve the scientific basis for decision-making on the conservation and management of bottlenose dolphins living under the pressure of the shellfish aquaculture industry in coastal waters. The data presented in this thesis establish a scientific foundation on which a good management framework can be built. The findings of this thesis are of fundamental importance because they have the potential to facilitate the work of relevant authorities toward the implementation of national and international protection laws for bottlenose dolphins.

8.4.1 Recommendations for the conservation of bottlenose dolphins

As mentioned in Chapter 1, bottlenose dolphins are listed under the Annexes II and IV of the EU Habitats Directive. The Habitats Directive establishes the obligation to maintain or restore a favourable conservation status of habitats and species of interest, such as bottlenose dolphins, in the European Community. This may entail ensuring the availability of sufficient wild prey and of natural habitat, and managing anthropogenic activities effectively. For this purpose, the designation of special areas of conservation (SACs) is required in order to preserve core areas and critical habitats (i.e. breeding and feeding grounds), along with the development of periodic population assessments performed at least every 6 years. However, information about this is still limited to specific geographical regions. Pierce et al. (2010) pointed out the need for greater knowledge of the condition of bottlenose dolphin populations in Galician waters, which would allow for a more complete review of their conservation status in Europe.

The results of this thesis demonstrate that bottlenose dolphins: (a) exhibit a high degree of residency in the Ría de Arousa (Chapter 3), (b) use the area year-round (Chapters 3, 4, and 5), (c) use the area as a nursery area (Chapter 3) and, (d) use the area as a feeding ground (Chapter 6). Bottlenose dolphins and their habitat should therefore be protected, as required by the Habitat Directive of the European Union.

There is currently one SAC covering around 11.5% (28 km² out of 240km²) of the Ría de Arousa and the bottlenose dolphin is included as a feature (<http://natura2000.eea.europa.eu>, accessed on 10 August 2019) (**Figure 8.4**). The site was proposed as a site of community importance (SCI) in 1997, confirmed as SCI in 2003, and designated as SAC in 2014 (Decreto 37/2014; Dirección Xeral de Conservación da Natureza Consellería de Medio Ambiente e Ordenación do Territorio Xunta de Galicia, www.xunta.gal accessed on 10 August 2019). Therefore, a periodic population assessment should have been performed every 6 years. Yet, the SAC has been implemented in March 2014 and no abundance estimate has been given for bottlenose dolphins in the area. The results given in this thesis therefore provide the first robust abundance estimate for bottlenose dolphins in the area. Management authorities could now use this information to update their monitoring program.

As highlighted by the findings in this thesis, bottlenose dolphins forage in different parts of the Ría de Arousa. In protecting a specific population, the optimal protected area would cover that population's year-round distribution (Whitehead et al. 2000) and foraging habitat. The SAC boundaries in the Moray Firth (Scotland) were considered insufficient due to the large range of the resident dolphin population (Wilson et al. 2004). The important lessons from other previously established protected areas should be considered. The current SAC present in parts of the Ría de Arousa should, therefore, be expanded and should be specifically designated for the conservation of bottlenose dolphins. A first expansion could concern the areas where bottlenose dolphin foraging budget is more than 80% (based on Chapter 6; **Figure 8.4 a,b**). A second expansion could concern the areas where bottlenose dolphin foraging budget is more than 40% (based on Chapter 6; **Figure 8.4 a,c**). Ideally, the SAC should be expanded to the whole Ría de Arousa (**Figure 8.4 d**). A long-term management and monitoring plan, contributing to the conservation of bottlenose dolphins and of their habitat should also be developed. Conservation measures that are intended to protect bottlenose dolphins may also be beneficial to other cetaceans in these waters, including the harbour porpoise (Díaz López & Methion 2018a: annex 2), which is also listed under the Annexes II and IV of the Habitat Directive.

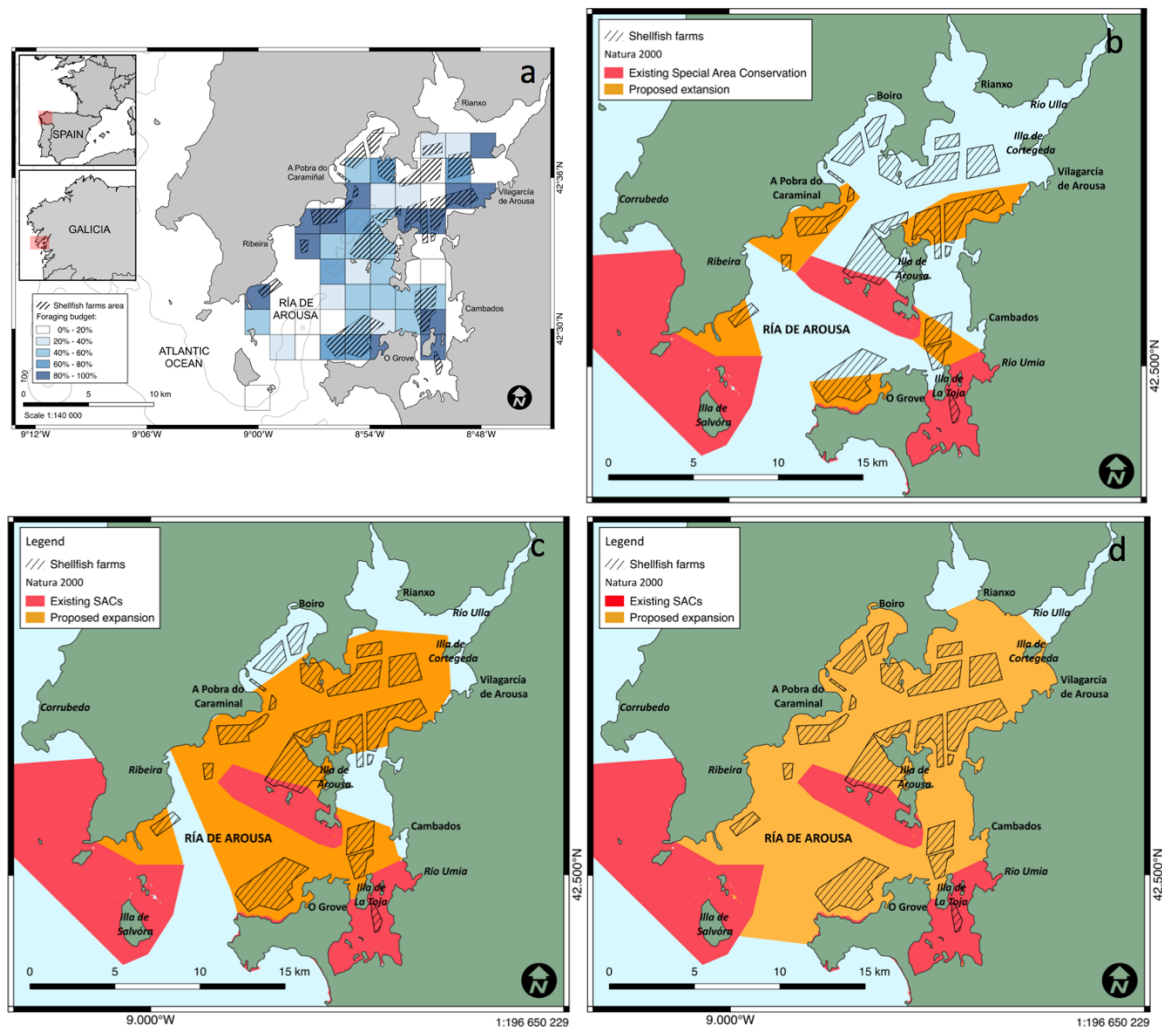


Figure 8.4. Existing SACs and proposed expansions in the Ría de Arousa.

a. Map representing the foraging budget of bottlenose dolphins in the Ría de Arousa (Chapter 6). b. Proposed SAC expansion based on the areas where bottlenose dolphin foraging budget is more than 80%. c. Proposed SAC expansion based on the areas where bottlenose dolphin foraging budget is more than 40%. d. Proposed SAC expansion covering the full Ría de Arousa.

8.4.2 Recommendations for the shellfish farming industry

Management of the effects of shellfish aquaculture activities on marine mammals is currently a pressing issue. This study provides new insights into the influence of shellfish aquaculture on bottlenose dolphin ecology and behaviour, and hence supports the design of policies aimed at implementing ecosystem management principles.

Findings of this study highlight that bottlenose dolphins regularly forage around shellfish farms. Previous studies have shown that interaction between dolphins and marine aquaculture can cause damage to both the aquaculture industry (i.e. damage to gear, depredation of farmed fish) and to dolphins (i.e. fatal entanglement, habitat loss and degradation, introduction of diseases) (Díaz López 2012; Würsig & Gailey 2002). While dolphins around finfish farm areas can feed on both wild and farmed fish, often causing damage to the equipment and the stock (Díaz López 2006a), dolphins in shellfish farm areas only feed on wild prey, thus not affecting the aquaculture product and the equipment (local shellfish producer, personal communication). Besides, the presence of bottlenose dolphins around shellfish farms could keep away species of fish (e.g. sea bream) that could potential damage the aquaculture product (Díaz López & Methion 2018b). Therefore, attempts to dissuade bottlenose dolphins, through the use of predator nets or acoustic harassment devices, are not necessary in shellfish aquaculture.

Shellfish aquaculture can pose direct threats to coastal cetaceans in a number of ways: (a) increased mortality as a result of fatal collisions with vessels working in the area (Ribeiro et al. 2007) or entanglement with ropes; (b) habitat loss (Watson-Capps & Mann 2005); (c) increased levels of noise pollution due to the high number of vessels in the area; and (d) water pollution due to the use of antifouling paint biocides containing toxic compounds (i.e. lead, arsenic, mercury, copper, cuprous oxide, organotin compounds such as tributyltin), associated with the maintenance of the floating rafts and working vessels (Terlizzi et al. 2001). Some authors have claimed that the accumulation of biocides may cause cetacean mortality by suppressing their immune system (Kannan et al. 1996). Therefore, cetaceans frequently foraging within shellfish farms may face higher risk of injury or death (i.e. boat strikes, entanglement, water pollution) which could alter population social dynamics and overall fitness. From a conservation perspective, aquaculture management should consider the presence of cetaceans foraging in shellfish farm areas and minimize the associated risks that this industry may pose to these coastal cetaceans. Management actions for the shellfish industry threats listed in this study should be implemented following the European Union legal obligations under the Habitats Directive to protect bottlenose dolphins, a species listed under Annexes II and IV. Below is a list of management recommendations to reduce the risks associated with shellfish farming for coastal cetaceans:

- **Establish a speed limit for vessels operating inside shellfish farm areas.**

A speed < 10 kn is suggested to reduce the threat of death and serious injury to coastal cetaceans that result from collisions with ships (following the Marine Mammal Protection Act, www.fws.gov, accessed on 10 August 2019). This measure would leave more time for cetaceans to take evasive action and could also decrease the amount of underwater noise.

- **Regulate the use of antifouling paints containing biocides used for the floating rafts and for the working boats.**

This measure could minimize the potential impacts of this industry on cetacean health, and ultimately, survival.

- **Conduct environmental impact assessments.**

The implementation of shellfish farms in areas of particular ecological importance for any cetacean species should be regulated. Before implementing shellfish farms, aquaculture management should assess the potential presence of coastal cetaceans, collect baseline data about their ecology, study the potential impacts on cetaceans, and take in consideration the results of this thesis in order to implement a management plan. After the introduction of shellfish farms, a permanent monitoring plan, targeting the conservation of local cetacean species, should be implemented to assess the effectiveness of the management plan by determining if the conservation objectives are met in the long-term.

8.5 Limitations and suggestions for future studies

This thesis contributes to the understanding of bottlenose dolphin ecology and behaviour and offers several perspectives to enhance future research on bottlenose dolphins.

Since the distribution of dolphins is not spatially or temporally uniform (i.e. patchy distribution of prey resources), field research relies on extensive and consistent data collection effort and appropriate time and area coverage. The area monitored during the study was mainly limited to the Ría de Arousa. However, coastal bottlenose dolphins move between Galician rías and groups of pelagic bottlenose dolphins transit off the Galician coast (Díaz López & Methion 2018a: annex 2; Díaz López et al. 2018b: annex 1). Further observational and photo-identification studies, monitoring a larger area, are therefore needed to define the movements patterns of coastal bottlenose dolphins along the Galician coast and the occurrence of pelagic bottlenose dolphins in offshore waters. Such studies would also allow to obtain valuable data for further demographic and abundance estimates of bottlenose dolphins in Galician waters. In addition, satellite tagging of individuals would complement the photo-identification data and give further insight into bottlenose dolphin range and movements. This information would help clarify the ranging patterns of bottlenose dolphins in Galician waters and would facilitate the understanding of the distribution of this species in North East Atlantic waters.

Given that bottlenose dolphins have long life spans and low reproductive rates (Leatherwood & Reeves 2012), extensive periods of monitoring are required to obtain trends in abundance and demographic parameters, and to identify changes in distribution and habitat use in order to detect potential threats (Hammond et al. 2013). Further dedicated photo-identification effort, over a longer time span, is therefore required in order to evaluate any trend in the abundance and habitat use of this population.

Several physiographic (e.g. depth, bottom slope, bottom aspect), oceanographic (e.g. water temperature, water salinity, dissolved oxygen), anthropogenic (e.g. shellfish farms), and biological variables (e.g. chlorophyll-a concentration) have been employed in this study to comprehend bottlenose dolphin habitat preference, grouping patterns, and foraging behaviour. However, bottlenose dolphin distribution and behaviour is likely driven by multiple

factors that act synergistically, and some of these factors might not have been taken into account in this study. Because bottlenose dolphins are mostly sensitive to prey abundance (Ballance 2018), the use of more proximal variables, such as prey distribution, would allow for a better understanding of bottlenose dolphin ecology. Nevertheless, field data on prey distributions are not available at a fine scale in the region. Besides, while this study identified local and ephemeral mechanisms that influence bottlenose dolphin ecology and behaviour at fine temporal and spatial scales, further studies with larger temporal and spatial scales would allow a better understanding of dolphin distribution patterns associated with broader environmental changes. Research at different spatial and temporal scales may provide further insight into causal factors of bottlenose dolphin abundance, distribution, and habitat use in the region.

Studying the behaviour of cetaceans is particularly challenging because they are difficult to observe (they spend a lot of time under water) and they often surface rapidly making their behaviour easy to miss (Heithaus & Dill 2009). In recent years, technological advances have supplemented behavioural data collection for cetaceans (e.g. time depth recorder; Falcone et al. 2017). These methods are expensive, and not always feasible for studying large numbers of individuals, but they provide accurate data not obtainable from observational studies. Further studies could therefore use time depth recorders to obtain valuable insights into the diving behaviour of bottlenose dolphins.

Additionally, future research that compares reproductive success of individual bottlenose dolphins would help reveal individual-level effects of human disturbance, should they exist. Further information about the reproductive state of females would also help the understanding of bottlenose dolphin association patterns.

Genetic data have been widely used to identify population structure by detecting divergence of allele frequencies between populations (Louis et al. 2014). Several studies explored the genetic relationships between Galician bottlenose dolphins and dolphins from neighbouring areas, but all samples were from stranded individuals (Fernández et al. 2011b; Louis et al. 2014; Nykänen et al. 2019). Tissue samples from biopsies of free-ranging dolphins could be collected for bottlenose dolphins encountered both in coastal and in pelagic waters. Genetic studies

would therefore provide further information on population structure and would allow to have a comprehensive understanding of the genetic link between the coastal and the pelagic ecotypes. Genetic analysis would also help to understand the association patterns between photo-identified individuals, as bottlenose dolphin social organisation may also be driven by kinship (Parsons et al. 2003; Wiszniewski et al. 2010).

Biopsies of free-ranging dolphins could also allow for studying bottlenose dolphin feeding ecology (e.g. within and between sexes and ecotypes). Fatty acids can be used to determine the type of prey consumed by individuals with precision. Two studies previously used this technique for studying bottlenose dolphin foraging ecology in Galician waters, but few samples from stranded individuals were analysed, thus not allowing a confirmed potential difference in habitat use (Fernández et al. 2011a; Méndez-Fernández et al. 2013). Therefore, further studies would give important insights into the potential foraging variation between individuals.

Furthermore, biopsies could allow studies of individual differences in concentration of pollutants. Bottlenose dolphins have a high bioaccumulation potential, which can have immune-toxic and endocrine disruptive effects and may impact their reproductive success (Aguilar & Borrell 2005). High levels of persistent organic pollutants have been found in juvenile bottlenose dolphins stranded along the Iberian Peninsula (Méndez-Fernández et al. 2014a). A study investigating whether individuals regularly feeding within shellfish farms exhibit higher levels of organic pollutants than other conspecifics would be interesting. Since coastal bottlenose dolphins are more exposed to anthropogenic influences than their pelagic counterparts, comparing the concentration of organic pollutants between free-ranging individuals of both ecotypes, would be critical.

Finally, as Galicia is one of the most important fishing regions of Europe, further studies should focus on the interaction between bottlenose dolphins and coastal fisheries, as well as the impact of marine traffic on bottlenose dolphin behaviour.

8.6 Conclusions

The findings of this thesis provide important baseline information on the ecology and behaviour of a marine top predator living in a coastal area under shellfish aquaculture industry pressure. Specifically, this thesis offers valuable insights into the abundance, demographic parameters, distribution, habitat use, grouping patterns, foraging behaviour, and social organisation of bottlenose dolphins in Galician waters. Additionally, the results further the understanding of the influence of human-induced changes in the marine environment on bottlenose dolphin habitat use, foraging behaviour, and social systems. Overall, this study enhances available knowledge of the variation in ecology and behaviour found among bottlenose dolphin populations, and acts as a model for future studies. This thesis also contributes to the growing body of literature addressing environmental consequences of suspended shellfish aquaculture, particularly their effects on coastal cetaceans, which have rarely been evaluated. The findings of this thesis improve the scientific basis for decision-making on the conservation and management of bottlenose dolphins living under the pressure of shellfish aquaculture in coastal waters. Furthermore, these results provide baseline information for future comparisons with other bottlenose dolphins' populations living in areas subject to intense human activities (i.e. aquaculture, fisheries, and marine traffic).

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Annexes

Annex 1. Infanticide attacks and associated epimeletic behaviour in bottlenose dolphins.

Díaz López B, López A, Methion S, Coveló P. 2018. Infanticide attacks and associated epimeletic behaviour in free-ranging common bottlenose dolphins (*Tursiops truncatus*). Journal of the Marine Biological Association of the United Kingdom 98(5):1159-1167.

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Infanticide attacks and associated epimeletic behaviour in free-ranging common bottlenose dolphins (*Tursiops truncatus*)

Bruno Díaz López^{1,2}, Alfredo López^{1,3}, Séverine Methion^{2,4}, Pablo Coveló¹

¹Coordinadora para o Estudo dos Mamíferos Mariños (CEMMA), P.O. Box 15. 36380, Gondomar, Pontevedra, Spain

²Bottlenose Dolphin Research Institute (BDRI), Av. Beiramar 192, 36980, O Grove, Pontevedra, Spain

³Departamento de Biología & CESAM, Campus de Santiago, Universidade de Aveiro, 3810-193 Aveiro, Portugal

⁴Université Bordeaux, UMR CNRS 5805 EPOC, Allée Geoffroy St Hilaire, 33615 Pessac Cedex, France

Abstract

Infanticide is considered a conspicuous expression of sexual conflict amongst mammals, including bottlenose dolphins. Although reported previously in this species, confirmed cases of infanticide and associated epimeletic behaviour are very rare and their socio-behavioural context remains poorly understood. Here, we provide evidence of epimeletic and infanticide behaviours in free-ranging bottlenose dolphins in Galicia, NW Spain. After describing the observed events, we include a complete description of the post-mortem examinations (where the carcasses were recovered) in order to confirm the cause of death. With evidences of blunt trauma in two of the presented cases, we confirm that the calves were intentionally killed by adult individuals. The aggressive interaction between adult individuals and the neonates together with the observed ante-mortem injuries bore a strong resemblance to the behaviours and traumatic injuries described in other cases of violent dolphin interactions in other parts of the world. The circumstances under which these infanticides occurred at our site fit the conditions proposed under the sexual selection hypothesis. The difficulties for researchers to observe this type of behaviour in the field and to find carcasses in good enough condition to determine the cause of death, emphasizes the importance of this type of study.

Introduction

The primary reasons for group formation in mammals are suggested to be environmental variables such as protection and prey resources (Alexander 1974). Female grouping patterns tend to be more directly related to these parameters, while male social strategies are more related to mate access (Trivers 1972; Connor et al. 2000).

Infanticide by males, or the killing of dependent offspring by males, is considered one of the most conspicuous expressions of sexual conflict between males and females in mammalian societies (Hrdy 1979; Palombit 2015). It is regularly observed in primates, equids, rodents, carnivores and cetaceans (van Schaik 2000). These are species in which lactation is longer than gestation and females experience lactational amenorrhea, so postpartum mating does not occur (van Schaik 2000). Males, therefore, benefit from killing a female's offspring if they are not the sire, if they can mate with the female when she returns to oestrous, and if they have a chance of siring her next offspring (i.e. the sexual selection hypothesis; Hrdy 1979). This would suggest, therefore, that adult males who have not invested time and energy toward rearing the offspring may carry out infanticide and gain the chance to mate with the newly receptive female whose infant has been killed.

Bottlenose dolphins have relatively long inter-birth periods during which time young are dependent on the mother (Mann & Smuts 1998). If a female loses her offspring prematurely, she soon becomes sexually receptive, reducing time between births (Hrdy 1979). The first description of infanticide by common bottlenose dolphins (*Tursiops truncatus*, Montagu 1821), and by any cetacean species, was done by Patterson et al. (1998) from post-mortem examinations of stranded specimens in the Moray Firth (Scotland). Direct observations of this behaviour at sea are rare, which makes it difficult to understand the context or the cause of such infanticide. To date, only three cases of observed or suspected infanticide have been witnessed in long-term studies of common bottle-nose dolphins. The most detailed and compelling description of calf-directed aggression by males in the field was recorded by Robinson (2014) during a long-term study on *T. truncatus* at Moray Firth, in Scotland, where several adult males directed an attack towards an adult female and her male infant; after intense fighting, the infant was severely injured. Two other additional cases of suspected

Annex 1. Infanticide attacks and associated epimeletic behaviour in bottlenose dolphins.

infanticide attacks have also been reported for *T. truncatus* by Kaplan et al. (2009) off the coast of Florida and Perrtree et al. (2016) in Georgia (USA). All these observations were considered an attempt of infanticide based on the nature of the attacks; nonetheless the calf did not die suddenly after the attacks. In all these cases the causes of the death of the calves were not supported by post-mortem examinations because it was not possible to recover the carcasses.

Although reported previously in this species, cases of infanticide and associated epimeletic behaviour are very rare and their socio-behavioural context remains poorly understood (Reggente et al. 2016). Epimeletic behaviour, care or attention giving, can be associated with an infanticide episode. This assistance is generally conducted by a healthy adult dolphin (presumably the mother) swimming with a dead or incapacitated calf, helping it to stay floating at the surface, or maintaining it away from an apparent source of danger (Cockcroft & Sauer 1990; Connor & Smolker 1990; Harzen & dos Santos 1992; Fertl & Schiro 1994; Félix, 1994; Ritter 2007; Moura et al. 2009). This type of behaviour may be considered generally adaptive for the survival of possibly genetically related individuals within specific groups (Cockcroft & Sauer 1990), particularly for dolphins that appear to be dependent on group structure for survival (Norris & Dhol 1980).

Here, we provide evidence of infanticide and associated epimeletic behaviours in free-ranging bottlenose dolphins along the NW coast of Spain. After describing the observed events, we include a complete description of the post-mortem examinations (where the carcasses were recovered) in order to confirm the cause of the death. Furthermore, we discuss the potential factors that may help explain the observed behaviours and the implications for understanding dolphin socioecology.

Methods

Data for this study were collected as part of a longitudinal study of common bottlenose dolphins inhabiting the Galician coast, Spain (**Figure 1**). Galicia is a region situated in the north-west of the Iberian Peninsula with 1195 km of coastline, where there are a series of ancient drowned tectonic valleys that were taken over by the sea (also referred to as 'rías') (Evans & Prego 2003).

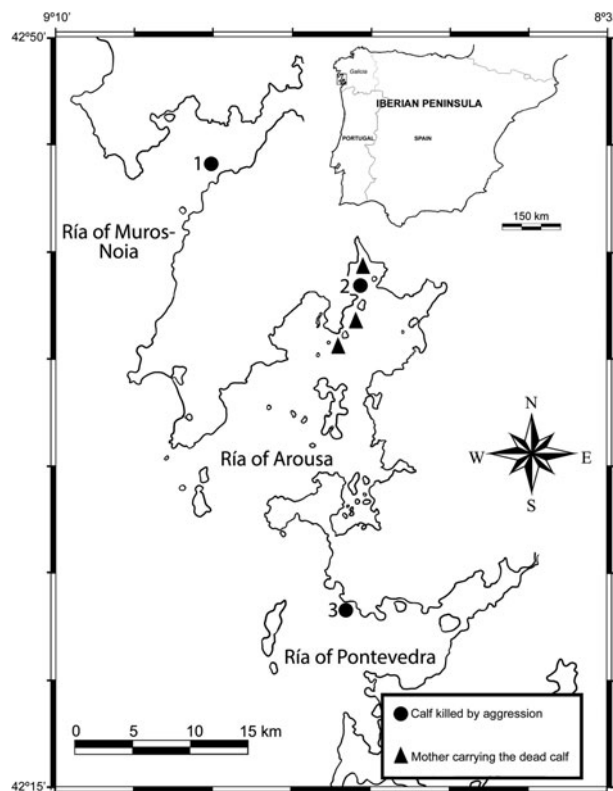


Figure 1. Geographic locations of the three reported cases of calf-directed aggression carried out by adult common bottlenose dolphins (represented by circles) and cases of observed epimeletic behaviour (one reported and two anecdotal cases represented by triangles), in Galicia (NW Spain).

Systematic recording of stranded cetaceans along the Galician shoreline commenced in 1990 with the establishment of the NGO Coordinadora para o Estudio dos Mamíferos Mariños (CEMMA), a group which records strandings, conducts boat and land-based surveys, carries out necropsies and provides samples for biological studies (López 2003; Santos et al. 2007; Pierce et al. 2010; Fernández et al. 2011; Louis et al. 2014). Since 2014, as a result of the cooperation between the CEMMA and the Bottlenose Dolphin Research Institute (BDRI), regular year-round

Annex 1. Infanticide attacks and associated epimeletic behaviour in bottlenose dolphins.

boat surveys were conducted as part of a multi-year mark– recapture study along Galician waters, improving the photo-identification work carried out by the CEMMA (Fernández et al. 1996; Vázquez et al. 2006; López et al. 2011). Individuals were identified by photo-identification based on the distinctive characteristics of their dorsal fins and surrounding area as unique natural markers (Würsig & Jefferson 1990). Sex was determined primarily by observations and photographs of the genital region. Digital photographs and videos were taken using DSLR cameras equipped with telephoto zoom lenses.

This study reports three cases, provided by the Galician Marine Mammal Stranding Network (coordinated by the CEMMA), of free-ranging bottlenose dolphin reactions to dead calves and the results of the necropsy examinations. The described field observations are presented chronologically, as observed, filmed and photographed from two motor vessels (cases 1 and 3) and the BDRI research vessel (case 2). Onboard the BDRI research vessel, six observers monitored the bottlenose dolphins, either with the naked eye or with binoculars, in order to collect behavioural data and to record changes in group composition. During these observations, continuous data (Altmann 1974) were collected on the behaviour and occurrence of affiliative and agonistic interactions between the participants, including the identities of actors and recipients and the time of onset and termination for each bout.

In two of the three observed cases (cases 2 and 3), the carcass of the calf was recovered immediately after the field observations, and necropsied within 24 h according to a standard protocol defined by the European Cetacean Society (Kuiken 1996). Photographs of the necropsy were taken. Dead calves were measured, weighed, sexed and classified following Smithsonian Condition Codes (Geraci & Lounsbury, 2005). The carcasses received a complete standard necropsy with systematic examination of all organ systems. Necropsies were attended by experienced personnel of the CEMMA.

Results

– Case 1. Ría of Muros, 14 July 2014.

Field observations

Opportunistic observers in a motor boat reported to the CEMMA the observation of one group of bottlenose dolphins in the Ría of Muros (42844.29'N 009800.22'W; UTM 29T, x 499,700, y 4,731,740, **Figure 1**). The observation supported by photographs began at 17:00 h UTC and lasted around 30 min. At 17:00 h a group of bottlenose dolphins were seen moving hurriedly close to the shore. An adult bottlenose dolphin accompanied by a neonate in echelon position (**Figure 2a**) were observed, together with at least six other bottlenose dolphin adults circling around. For the next 20 min, the adults were seen harassing the adult-neonate pair in an apparently coordinated manner, with some perpetrators sandwiching the pair while others rammed and separated the neonate from the accompanying adult (presumably the mother) and occasionally tossed the neonate out of the water (**Figure 2b**). Subsequently, surface activity increased with tail slaps, after which an adult resurfaced with the calf lying motionless on its head. During the next minutes it was possible to observe the accompanying adult (presumably the mother) lifting the corpse above the surface.

The adult individuals present in the observed group were not identified from previous encounters by the authors. Opportunistic observers confirmed the death of the neonate by the observation of the body floating motionless at the surface of the water. Unfortunately, it was not possible to retrieve the body of the dead calf but the cause of death was likely to be related to the aggressive interactions.

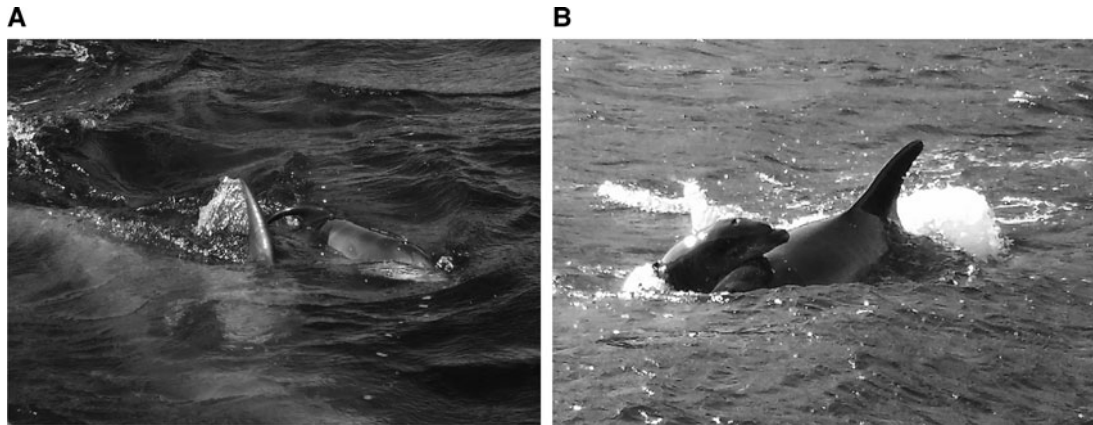


Figure 2. Photographs authenticating the attempted infanticide of the newborn bottlenose dolphin calf observed on 14 July 2014 in the Ría of Muros (NW Spain). (a) Image of an adult bottlenose dolphin accompanied by a neonate in echelon position. The foetal folds and furled dorsal fin are still evident. (b) Image of the calf being abducted by one adult that rises partially out of the water and slaps the neonate with its front upper body and rostrum. Photographs: Miguel Prado.

– Case 2. Ría de Arousa, 11 September 2016.

Field observations

At 11:30 UTC on 11 September 2016, the Galician stranding network was notified of a dead newborn bottlenose dolphin floating in the Bay of Rianxo at 42836.98°N 008849.91°W (UTM 29T, x 520,300, y 4,694,349), 9.4 m depth, and 0.4 nautical miles from the coast (**Figure 1**). Upon the arrival of the BDRI's research vessel at 13:00 h, local fishermen related having observed other bottlenose dolphins swimming around the carcass. According to the local fishermen, the dolphins were continuously pushing the carcass away from their boat and towards the surface with their rostrum and other parts of their bodies.

The behavioural activities of the group of dolphins were monitored continuously from the arrival of the researchers, between 13:09 and 15:25 h (UTC). The research vessel remained in the same position (at a distance of around 100 m from the dolphins) to minimize the effect of the observers' presence on the dolphins' behaviour. The following events are presented chronologically, as observed, filmed and photographed from the research vessel.

Annex 1. Infanticide attacks and associated epimeletic behaviour in bottlenose dolphins.

13:09 UTC – A group of bottlenose dolphins was observed swimming between mussel rafts in close formation at 400 m from the shore in the inner part of the Ría of Arousa. The presence of a dead newborn was confirmed together with two adult bottlenose dolphins swimming around the carcass. Both adults were identified by direct observation of their dorsal fins (one male known as ID#A9 and one female known as ID#C7). The female (ID#C7) was keeping the dead calf afloat, while the male (ID#A9) circled around them in an anticlockwise direction.

13:20 UTC – All at once, the two adult individuals became notably more active. Suddenly the large adult male dolphin (ID#A9) rapidly emerged pushing the body of the newborn calf underwater.

13:26 UTC – The male (ID#A9) began circling energetically with continuous tail stock dives with abrupt changes in direction. The mother then positioned herself between the calf and male (ID#A9) as he circled around them.

13:28 UTC – The mother held the dead calf on her rostrum while swimming (**Figure 3a**). A second male dolphin (ID#C9) was spotted swimming 80 m away from the other individuals.

13:40 UTC – The male (ID#A9) launched himself directly into the mother-calf pair, driving his body between the two animals and forcing them apart. Thereafter, the same male breached and charged towards the body of the infant, holding the calf beneath the water from above.

13:46 UTC – The male aggressor (ID#A9) rammed the calf with his peduncle with enough impact that the carcass was tossed into the air 2 – 3 m high and flipped on its side.

13:51 UTC – The mother was observed doing sequences of regular dives followed by tail stock dives as she circled around the male (ID#A9) and the dead newborn (**Figure 3b**).

14:03 UTC – Followed by the male (ID#A9), the mother (ID#C7) surfaced with her dead calf lying across her back. Afterwards, the mother (ID#C7) lifted the corpse above the surface during several seconds (**Figure 3c**).

14:09 UTC – The female (ID#C7) was seen repeatedly trying to come in between the body of the calf and the adult male (ID#A9).

14:19 UTC – The male (ID#A9) continued his aggressions, charging towards the calf hard from one side, and with such velocity that the newborn was launched clear out of the water.

14:21 UTC – The female carried the carcass on its rostrum and repeatedly blocked the male (ID#A9) from reaching the dead neonate.

Annex 1. Infanticide attacks and associated epimeletic behaviour in bottlenose dolphins.

14:28 UTC – The dead calf was pushed away from the immediate area by the male aggressor (ID#A9). Then, the mother, after a sequence of tail stock dives, got closer to the carcass and the adult (ID#A9) that was pushing it. During these social bouts, both adult dolphins exhibited rapid movements including sudden changes in direction and compact circling behaviour with repeated tail stock dives.

14:40 UTC – Over the course of several minutes the female's response, with rapid movements and tail stock dives, became gradually less vigorous. The female always remained close to the body of the calf, but was never seen in physical contact with the male aggressor (ID#A9).

14:49 UTC – After a tail stock dive and subsequent long dive period, the female – male (ID#A9) pair was observed heading south-west leaving the carcass of the newborn calf 200 m away. This pair of dolphins was swimming on a consistent course, spaced within a few body lengths of each other, and with rhythmic surfacings followed by shallow dives.

14:56 UTC – The second male dolphin appeared thereafter (known as ID#C9) and started to regroup around the female dolphin. At this point the male (ID#A9) was observed swimming on a consistent course (south) with regular dives and short ventilations.

15:02 UTC – The male (ID#A9) stayed 100 m away from the other two individuals (ID#C7 and ID#C9) swimming slowly (less than 1 knot), with shallow dives and floating. This dolphin did not engage in any other activities during this apparently resting behaviour.

15:10 UTC – The second male (ID#C9) and the female (ID#C7) were seen exhibiting long dives and changes in direction with repeated tail stock and flukes up dives. The carcass of the calf was adrift by the swell 600 m away from the position of the adult dolphins.

15:25 UTC – All three dolphins (ID#A9, ID#C7 and ID#C9) were observed swimming on a consistent course (south), spaced within a few body lengths of each other and with synchrony ventilations followed by shallow dives. The carcass of the calf was adrift by the swell 900 m away from the position of the adult dolphins.

15:30 UTM – The research vessel moved towards the position of the dead calf to recover the carcass (**Figure 3d**).

All three adult individuals present during the encounter (ID#C7, ID#C9 and ID#A9) were well-known due to a long-term study of the *T. truncatus* population in this location by the authors, including data on the sex, reproductive history and associations of the animals reported since 2014. The known female detailed in the present report (ID#C7) was seen eight times in the area

Annex 1. Infanticide attacks and associated epimeletic behaviour in bottlenose dolphins.

since first recorded by the authors in May 2014. Between May and September 2014 the female was observed four times in company of a 2 – 3-year-old calf, so we can assume that she was not a first-time mother. Mother–newborn pair was sighted for the first time during the reported encounter on 11 September 2016. The two adult males detailed in the present report (ID#A9 and ID#C9), were re-sighted 14 times and 7 times in the study area, respectively. Both the female (ID#C7) and the male (ID#C9) were seen three times together since 2014. The adult male (ID#A9) was never seen previously with the female (ID#C7). During the period of most likely conception of the infant (between August and October 2015) a total of 58 encounters with bottlenose dolphins were done in the Ría of Arousa (N=27 days at sea). While the female (ID#C7) was not seen during any of these encounters, both males were observed in the area during this period (ID#A9 was seen on 5 different days and ID#C9 was seen on 2 different days). Following the reported field observations on 22 September 2016 and during photo-identification surveys in the Ría of Arousa, the female (ID#C7) and the male (ID#C9) were seen swimming in association as part of a group of bottlenose dolphins in which the male (ID#A9) was not present. This male (ID#A9) was sighted in two different groups of dolphins (23 September and 27 October) where the second male (ID#C9) and the female (ID#C7) were not present.

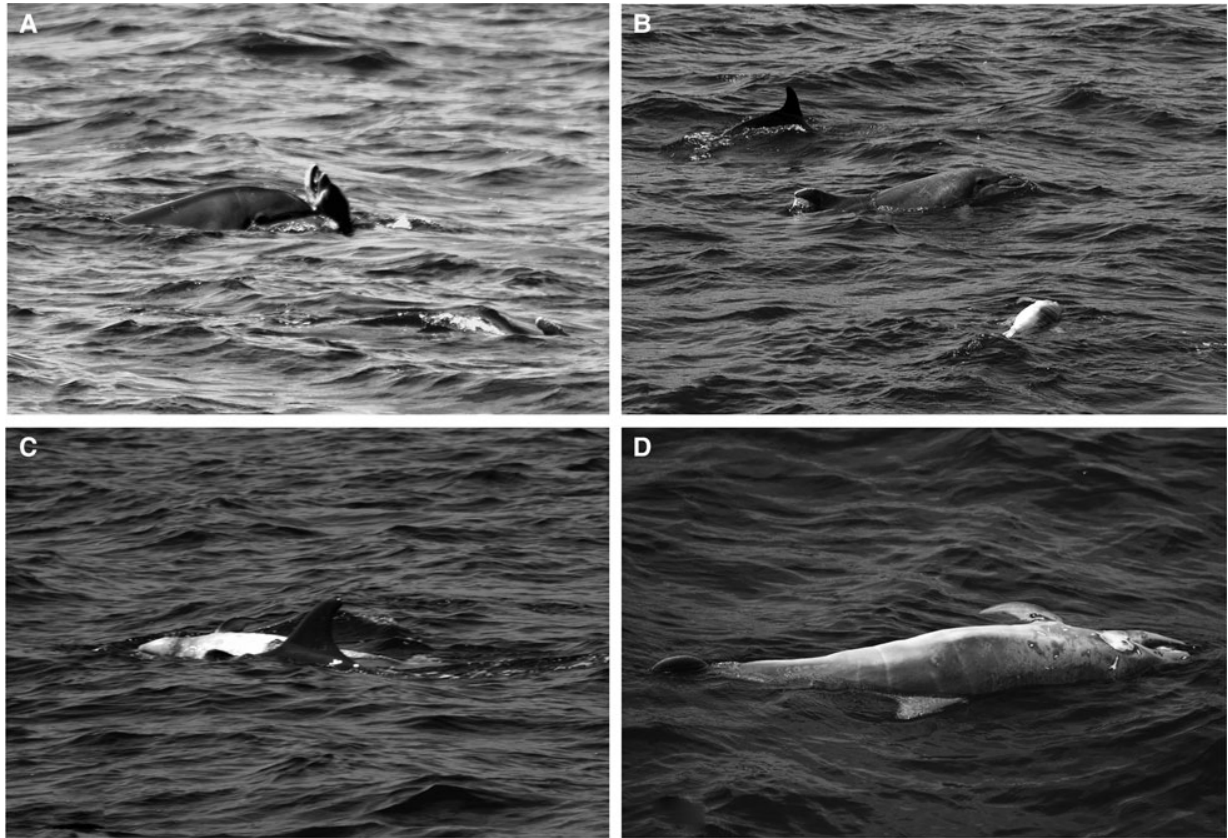


Figure 3. Photographs of the epimeletic and infanticide behaviour observed in the Ría of Arousa (NW Spain) on 11 September 2016. (a) The female carried the carcass on its rostrum and repeatedly blocked the male (ID#A9) from reaching the dead neonate. (b) The mother doing sequences of regular dives followed by tail stock dives as she circled around the male (ID#A9) and the newborn. The foetal folds are still evident. (c) The mother (ID#C7) surfaced with her calf lying motionless across her back; she lifted the corpse above the surface. (d) The carcass of the calf before its recovery hours after the first sighting of the group.

Summary of necropsy data

The bottlenose dolphin neonate was a male weighing 32 kg and measuring 150.5 cm from the tip of the rostrum to the tail notch. From its length, evident foetal folds, marginal papillae, rostral hairs, un-erupted teeth, and furred flukes and dorsal fin, it was estimated to be within its first days of life and therefore would still be dependent (Mead & Potter 1990). The animal was assessed to be in good body condition, and the preservation of the carcass was determined to be between codes 2 and 3 (Geraci & Lounsbury 2005).

The regularly spaced, parallel lacerations observed on the skin of this neonate were characteristic of rake marks produced when an adult bottlenose dolphin slides its teeth across

Annex 1. Infanticide attacks and associated epimeletic behaviour in bottlenose dolphins.

a cutaneous surface. These lesions, mainly involving the epidermis, were organized in parallel groups of 2 – 4 regularly spaced lacerations on both sides of the thorax with inter-tooth distances between 11 and 13 mm.

The individual exhibited multiple, internal, ante-mortem injuries including bruising around the head and thorax, rib fractures with associated haemorrhage, large bruise on its lower jaw (**Figure 4a**), atlanto-occipital dislocation (**Figure 4b**), and the thoracic vertebrae (T-6) fractured and luxated with a concomitant severed spinal cord (**Figure 4b**). Rib fractures occurred only on the left side of the thorax in a linear pattern involving 1st and 2nd adjacent ribs in correspondence with the position of the scapula. Other findings included occipital haematoma, abdominal haemorrhage, liver lacerations and contusions and multiple soft tissue contusions. Soft tissue contusions and bruises were bilateral, separate and discrete.

Gross necropsy findings indicated severe blunt-force trauma was the cause of death which is consistent with the aggressive behaviours seen during our field observation. The pattern of bilateral, multiple fractures and discrete soft tissue injuries, suggests repeated trauma and trauma inflicted from multiple directions.

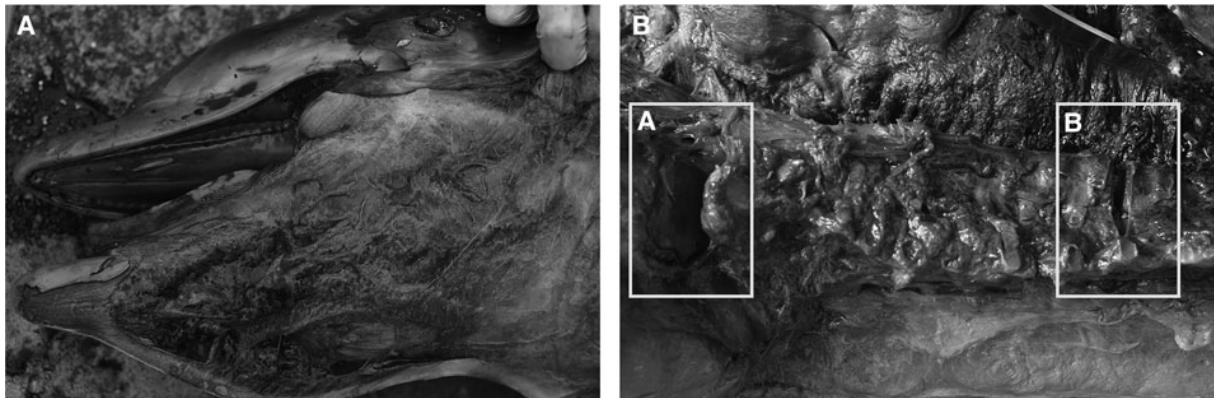


Figure 4. Post-mortem photographs of the wounds inflicted on the neonate male common bottlenose dolphin recovered in Ría of Arousa (NW Spain) where the cause of death was diagnosed to be blunt-force trauma. (a) Large bruise on the neonate calf's lower jaw. (b) Atlanto-occipital dislocation (box A), and the thoracic vertebrae (T-6) fractured and luxated with a concomitant severed spinal cord (box B).

– Case 3. Ría de Pontevedra, 12 September 2016.

Field observations

On 12 September 2016, in Raxó, Poio (42824.07'N 008845.20'W; UTM 29T, x 520,300, y 4,694,349), local fishermen observed a dead bottlenose dolphin calf. Moments before the carcass was recovered, people related having observed other bottlenose dolphins swimming in the vicinity and around the carcass. When one of the observers was confident that the calf was dead, the body was recovered for further examination of the carcass in the laboratory. When they carried the body to the shore the other dolphins went very close to the coastline and became notably more active with continuous tail stock dives and full leaps with abrupt changes in direction. It was not possible to identify the adult individuals present during the encounter.

Summary of necropsy data

The bottlenose dolphin neonate was a female weighing 28 kg and measuring 128 cm from the tip of the rostrum to the tail notch. The animal was assessed to be in moderate decomposition, and the preservation of the carcass was determined to be code 3 (Geraci & Lounsbury 2005). The calf had external evidence of injury with a large wound across the lower jaw region (**Figure 5a**). From its length, evident foetal folds, un-erupted teeth, and furled flukes and dorsal fin, it was estimated to be within its first days of life and therefore would still be dependent (Mead & Potter 1990).

The skull presented several fractures and the lower jaw and inner ears were absent. Multiple superficial cutaneous lacerations were present on the left flank, belly and flukes of the animal (**Figure 5b**). These lesions (rake marks), mainly involving the epidermis, were organized in parallel groups of 3 – 8 regularly spaced lacerations with inter-tooth distances between 12 and 13 mm.

The individual exhibited multiple, internal, ante-mortem injuries including bruising around the head and thorax, disarticulated ribs on both sides of the thorax in a linear pattern involving adjacent ribs, large bruise around the thoracic vertebrae (T-5) fractured and luxated. Other

Annex 1. Infanticide attacks and associated epimeletic behaviour in bottlenose dolphins.

findings included multiple soft tissue contusions and bruises bilateral, separate and discrete. Gross necropsy findings indicated severe blunt-force trauma was the cause of death.

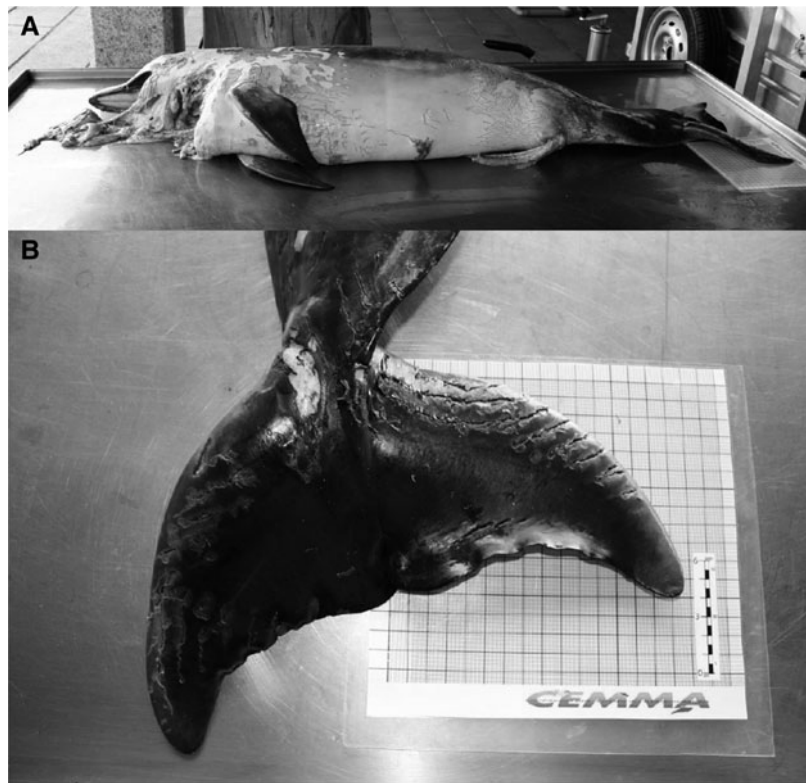


Figure 5. Post-mortem photographs of the wounds inflicted on the neonate female common bottlenose dolphin recovered in Ría of Pontevedra (NW Spain) where the cause of death was diagnosed to be blunt-force trauma. (a) Body of the calf with an external evidence of injury with a large wound across the lower jaw region. (b) Numerous rake marks are present on the fluke region (grid 1 × 1 cm).

Discussion

Because observing and interpreting social interactions among wild dolphins is difficult, it is likely that the best opportunity for recognizing epimeletic and infanticide behaviours lies in documenting field observations and, whenever is possible, the associated post-mortem findings.

Here we provide for the first time evidence for infanticide and associated epimeletic behaviour along the NW coast of Spain. Epimeletic behaviour in bottlenose dolphins has been recognized for some time (Caldwell & Caldwell 1966), however this type of behaviour is rarely observed in the field during sightings or strandings research (Reggente et al. 2016). While there are

Annex 1. Infanticide attacks and associated epimeletic behaviour in bottlenose dolphins.

previous accounts of epimeletic behaviour in bottlenose dolphins in relation to the death of a calf (e.g. Cockcroft & Sauer 1990; Connor & Smolker 1990; Harzen & dos Santos 1992; Fertl & Schiro 1994), these studies did not confirm the causes of the death of the neonate.

In two cases presented in this study (cases 2 and 3), the reports involved calves that were dead when the observations were made and in both cases the cause of the death was confirmed by further post-mortem examinations. In both cases, we conclude that purposeful violent dolphin interaction was the cause of the death of the bottlenose dolphin neonates. With evidence of blunt trauma in both of these cases, the hypothesis that emerged from field observations during the first case (that the calf was intentionally killed by adult individuals) is supported.

The aggressive interaction that we observed between adult bottlenose dolphins and the neonate during the first and second cases bears a strong resemblance to the behaviours seen in the intra- and inter-specific interactions in other parts of the world (Ross & Wilson 1996; Cotter et al. 2012; Robinson 2014; Perrtree et al. 2016). Moreover, in the last two cases, the traumatic lesions observed in addition to the rake marks on the body of the calves were consistent with lesions reported by Ross & Wilson (1996), Jepson & Baker (1998), Dunn et al. (2002), Barnett et al. (2009), Cotter et al. (2012) and Robinson (2014), in attacked bottlenose dolphin calves and harbour porpoises (*Phocoena phocoena*, Linnaeus 1758).

These observations provide a new and plausible explanation for earlier reports of interspecific interactions in Galician waters, NW Spain. A comparison of the post-mortem findings in the observed cases with traumatic injuries described in one stranded harbour porpoise (López & Rodríguez 1995) and one striped dolphin (*Stenella coeruleoalba*, Meyen 1833) (Alonso et al. 2000) in Galicia, revealed remarkable similarities. Therefore, the cases presented here provide the evidence that attacks of adult bottlenose dolphins may also lead to the stranding and death of other small cetaceans in Galician waters (NW Spain).

The regularly spaced, parallel lacerations observed on the skin of the neonates were characteristic of rake marks produced when an adult bottlenose dolphin slides its teeth across a cutaneous surface with inter-tooth distances between 10.97 and 12.32 mm (Ross & Wilson 1996). The presence of these marks on the body of the examined neonates can be related with

Annex 1. Infanticide attacks and associated epimeletic behaviour in bottlenose dolphins.

purposeful violent dolphin interaction and/or the epimeletic behaviour of the mother. The presence of rake marks as a result of the epimeletic behaviour of the mother is supported by: (i) neonate carcasses had tooth marks on the thorax and (ii) during field observations the mother had tried to keep the body of the neonate afloat with her rostrum. Di Benedetto et al. (2001) attributed conspecific tooth marks on the body of *Pontoporia blainvillei* (Gervais & d'Orbigny 1844) specimens accidentally caught on the northern Rio de Janeiro coast to rescue attempts by one or more members of the group. In addition, the calves or young dolphins that have been the subject of care-giving behaviour have exhibited fresh parallel scratches on their bodies from the adults' teeth (Félix 1994; Cremer et al. 2006; Moura et al. 2009). The damage to the head of case 3 (mandible detached) might be related to the moderate degree of autolysis and water pressure, as the dead calf was carried by the mother/group, rather than being a 'wound' inflicted pre-mortem. Two more anecdotal observations of adult bottlenose dolphins insistently trying to keep the body of a neonate carcass afloat were also reported to the CEMMA in Galician waters.

In the Galician population, infanticidal events may be orchestrated by one male (as the aggressive attacks seen in case 2) or by several cooperating individuals at once (as seen in case 1). Nonetheless, all reported events essentially involve the same prolonged chasing, compact circling behaviour, repeated ramming, tossing out of the water, and pushing the body of the targeted neonates. Robinson (2014) and Perrtree et al. (2016) reported similar coercive strategies associated with infanticide behaviours used by common bottlenose dolphins towards newborn calves in Moray Firth (Scotland) and in Georgia (USA) respectively. The circumstances under which infanticide occurred at our site fit the conditions proposed under the sexual selection hypothesis (e.g. Hrdy 1979). First, the observed newborns were still nursing and potentially vulnerable to infanticide by males (Mann & Smuts, 1998). Moreover, during the two month period following the second case, one of the males involved in the aggression was observed in close association with the mother, reinforcing the hypothesis that an infanticidal male may gain the chance to mate with the newly receptive female whose infant has been killed (Hrdy 1979).

This study adds new information on infanticide and associate epimeletic behaviour for *T. truncatus*. Documented events of such cases are scarce and their socio-behavioural context

Annex 1. Infanticide attacks and associated epimeletic behaviour in bottlenose dolphins.

remains poorly understood (Reggente et al. 2016). The difficulties for researchers to observe this type of behaviour in the field and to find carcasses in good enough condition to determine the cause of death, emphasizes the importance of this type of study.

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Annex 2. Habitat use and relative density in harbour porpoises.

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Does interspecific competition drive patterns of habitat use and relative density in harbour porpoises?

Bruno Díaz López¹, Séverine Methion^{1,2}

¹Bottlenose Dolphin Research Institute (BDRI), Av. Beiramar 192, 36980, O Grove, Pontevedra, Spain

²Université Bordeaux, UMR CNRS 5805 EPOC, Allée Geoffroy St Hilaire, 33615 Pessac Cedex, France

Abstract

Determining the drivers that are responsible for the fine-scale distribution of cetacean species is fundamental to understand better how they respond to changes in their environment. We utilized information theoretic approach to carry out a comprehensive investigation of the key environmental and anthropogenic correlates of habitat use and relative density of harbour porpoises. In all, 273 daily boat surveys over a period of 38 months, between April 2014 and November 2017, were spent in the field monitoring 9417 km along the coastal and shelf waters of Northwest Spain. Throughout this period, there were 70 encounters with harbour porpoises and 712 encounters with common bottlenose dolphins. The observed unequal use of available habitat indicates that harbour porpoises present a fine-scale pattern of habitat selection along the study area, which is likely related to the variation in oceanographic variables and human disturbance mainly caused by marine traffic and fisheries. While differences in habitat use between harbour porpoises and bottlenose dolphins were observed, interspecific competition with bottlenose dolphins (as competitive exclusion hypotheses) did not appear to play an important role in the distribution and relative density of harbour porpoises. These findings highlight the importance of considering both environmental and anthropogenic variables in ecological studies, in addition to highlighting the importance of using a multi-species ecology approach in research and conservation management planning.

Introduction

Habitat choice is the outcome of decisions that balance the trade-off between resource availability and predation risk (Lima & Dill 1990). Understanding the habitat use and determining the factors that are responsible for the distribution of marine predators, such as the harbour porpoise (*Phocoena phocoena*, Linnaeus 1758), are fundamental to understand better how these potentially vulnerable species respond to changes in their environment. The harbour porpoise is a highly mobile cetacean species found throughout the waters of the Northern Hemisphere (Gaskin et al. 1974).

While some surveys have recorded this species in offshore waters (MacLeod et al. 2003; Bjørge & Øien 1995), the harbour porpoise is generally distributed in highly productive coastal areas with upwelling and high tidal flow (Hammond et al. 2002; Skov & Thomsen 2008; Marubini et al. 2009), at depths up to 200 metres (Otani et al. 1998; Booth et al. 2013).

With the expansion of human activities in coastal and shelf waters, there has been general concern over the status of harbour porpoises in European waters and the establishment of Special Areas of Conservation (SACs) has been suggested as a method to protect this cetacean species (Embling et al. 2010; Hammond et al. 2013). The designation of these SACs for harbour porpoises, as required under the EU 'Habitats Directive' (Directive 92/43/EEC), is especially challenging, because harbour porpoises are small, highly mobile, spend limited time at the surface, and change behaviour in response to boats (Westgate et al. 1995; Otani et al. 1998).

Fluctuations in the use of habitat of harbour porpoises have been the subject of several studies in different parts of its range, almost exclusively from analysis of the relationship with oceanographic features that could determine food availability and abundance (e.g. Johnston et al. 2005; Marubini et al. 2009; Edrén et al. 2010; Embling et al. 2010; Booth et al. 2013). Few studies have included anthropogenic explanatory variables (such as the presence of fishing nets, fishing vessels, and marine traffic) in the habitat models for harbour porpoises, although the species is known to be sensitive to anthropogenic noise (Johnston 2002; Dähne et al. 2013; Thompson et al. 2013). Moreover, all these previous studies were only based on a single species approach that ignores potential effects of sympatric competitors on harbour porpoises' habitat

use. It is likely that harbour porpoises select habitats that have high food availability (Johnston et al. 2005; Sveegaard et al. 2011). Likewise, other cetacean species with similar food preferences and commercial fisheries will be present in these rich habitats (Ross & Wilson 1996; Jepson & Baker 1998; Díaz López & Methion 2017), in which harbour porpoises may have to trade off food and the safety when selecting a habitat to occupy (see Lima & Dill 1990 for a review of behavioural choices made under risk). Little or no attention has been given to the effects caused by the presence of sympatric cetacean species on the fine-scale distribution and numbers of harbour porpoises.

Recent studies suggest that harbour porpoises from the Northwestern coast of the Iberian Peninsula (Spain and Portugal) and Mauritania could well represent a distinct ecotype from those from the NE Atlantic continental shelf waters (*P. phocoena meridionalis*) (Fontaine et al. 2014). This area has been identified as a zone of high density of harbour porpoises (López et al. 2004; Pierce et al. 2010; Fernández et al. 2013), and it has been suggested to be suitable for the creation of possible Special Areas of Conservation (SACs) under the EU Habitats Directive. Harbour porpoises and common bottlenose dolphins (*Tursiops truncatus*, Montagu 1821) are distributed along the coastal and shelf waters of Galicia (Northwest Spain) with different geographical patterns of relative abundance (López et al. 2004; Pierce et al. 2010; Díaz López & Methion 2017). The diets of these two species follow a similar pattern in these waters (Santos & Pierce 2003; Santos et al. 2007; Méndez-Fernández et al. 2012), which is consistent with all two marine top predators exploiting the same locally abundant resources. Complementary approaches based on the analysis of foraging niche segregations (Méndez-Fernández et al. 2012; Fernández et al. 2013) proposed that trophic competition occurs between harbour porpoises and common bottle-nose dolphins in Galician waters as also suggested in other adjacent areas of the Northeast Atlantic (Spitz et al. 2006). Aggressive, non-predatory interactions between these two sympatric species have been often documented in different regions including the Northwestern coast of Spain (López & Rodríguez 1995; Ross & Wilson 1996; Jepson & Baker 1998). However, the reasons for bottlenose dolphins' attacks, some of which were fatal on harbour porpoises, are often unclear and the ultimate causes may be complex (Ross & Wilson 1996; Díaz López et al. 2017).

In this paper, we present a comprehensive investigation of the key environmental and anthropogenic correlates of habitat use and relative density of harbour porpoises along the Northwestern coast of Spain. As such, investigating these fluctuations in their coastal habitat utilization and relative density is essential for a better understanding of the ecology and for the conservation of this potentially vulnerable small cetacean species. Moreover, a competitive exclusion hypothesis was tested including, as part of the environmental correlates, the presence of bottlenose dolphins in the model framework. Indeed, we examined temporal and spatial link-ages between the presence and relative abundance of harbour porpoises and the presence of bottlenose dolphins in the area.

Methods

Study area

The shelf waters off Galician coastline (Northwest Spain) correspond to the northern zone of the Canary Upwelling System, one of the four major upwelling regions in the world (Santos et al. 2011). The complex shoreline and topography along this coastline is penetrated by a series of flooded tectonic valleys (named rías), which support very high primary production (Prego et al. 1999).

The study area extends approximately 450 km², inshore and offshore the largest and most productive of the Galician rías, the Ría of Arousa (**Figure 1**). Along this area, upwelling practically reaches the coastline, penetrating the Ría of Arousa (Prego et al. 1999). The entire system is subjected to a strong tide regime, with a tidal range of 1.1 and 3.5 m during neap and spring tides, respectively (Alvarez et al. 2005). These waters are subject to significant use by humans including professional fisheries, shellfish aquaculture industry, and important marine traffic (Vieites et al. 2004; Díaz López & Methion 2017).

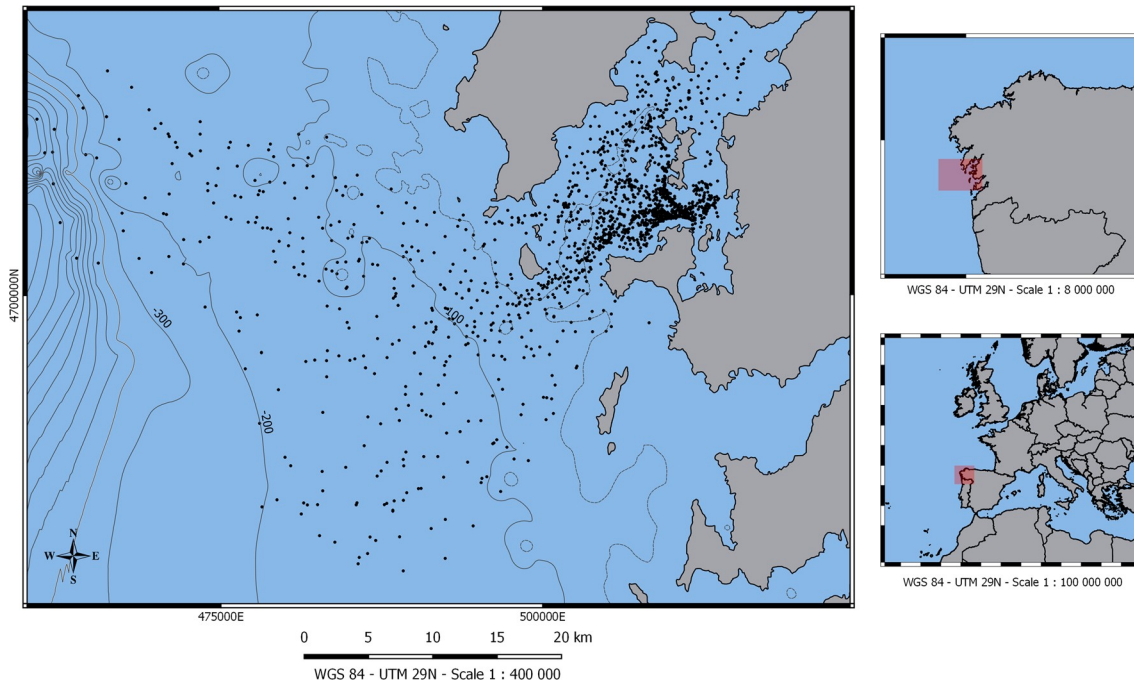


Figure 1. Map of the study area surveyed along the Northwestern coast of Spain, including 20 min sampling points searching for cetaceans (on effort) represented by circles.

Data collection

Data for this study were collected as part of a longitudinal study carried out by the Bottlenose Dolphin Research Institute BDRI (<http://www.thebdri.com>) about the ecology of cetacean species inhabiting the Galician waters. Boat-based surveys on-board a 12 m research vessel were conducted between April 2014 and November 2017. In all, 38 months were spent in the field. Surveys were done when the sea conditions were up to 3 on the Douglas sea force scale (approximately equivalent to the Beaufort wind force scale) and visibility was not reduced by rain or fog. Because of bad weather conditions during December, we were unable to complete surveys in this month.

The study area was monitored during daylight hours at a constant speed, between 6 and 8 kn, with at least three experienced observers, stationed on the flying bridge (4 m above sea level), scanning 360° of the sea surface in search of cetacean species (with the naked eye and/or 10 × 50 binoculars). Systematic surveys were attempted to equally cover certain fixed track lines designed to cover all the study area on each month, although the geographic distribution of effort could vary according to weather conditions and time constraints. On each survey, the time, position, vessel speed, the presence of cetaceans (within a 1000 m radius of the boat's

position), and environmental and anthropogenic data were recorded as an instantaneous point sample every 20 min (Díaz López & Methion 2017). These 20 min sets were used to summarize field conditions and distribution of the survey effort since the beginning until the end of each survey irrespective of cetacean' presence. The spatial resolution of this 20 min interval was approximately 2 nm (given a 6–8 kn speed). The presence–absence (visual detection–no detection) of cetaceans was recorded instantaneously during all of the 20 min sampling points.

Upon sighting a group of cetaceans, searching effort (on-effort time) ceased and the vessel slowly manoeuvred towards the group (off effort time) to minimise disturbance during the approach. A group of harbour porpoises was defined as one or more individuals observed within a 100 m radius. Size of the aggregations and composition were estimated before and after the harbour porpoises had been approached based on the total count of individuals observed at one time in the area. Because the research vessel often stayed with the animals, we could observe animals at close ranges (< 100 m) and for long durations (> 15 min). After the end of an encounter, the searching effort continued along the previously planned route.

Exploratory variables were chosen according to data availability and relevance to the environmental and anthropogenic conditions that could potentially affect harbour porpoises' use of habitat (Skov & Thomsen 2008; Marubini et al. 2009; Edrén et al. 2010; Embling et al. 2010; Isojunno et al. 2012; Booth et al. 2013; Dähne et al. 2013; Dyndo et al. 2015). The environmental and anthropogenic variables listed below were initially considered to have potential ecological significance, and were available for each 20 min sample recorded during the study.

- Environmental variables: date, time (UTC), position (UTM longitude and UTM latitude, WGS 84 UTM Zone 29N), depth (m), bottom slope gradient (the maximum rate of change in depth in a given grid cell and expressed as percent slope), bottom slope aspect (the compass orientation of the slope, ranging from – 180° to + 180° with respect to true north), tide level (m), tide cycle (rising with the flooding tide and falling with the ebbing tide), sea-surface temperature (SST in °C), sea-surface salinity (SSS in parts per thousand), chlorophyll-a (Chl-a in mg/m³), wind speed (m/s) and direction (°), Douglas sea force scale, sea level pressure in tenths

of hectopascals (hPa), and presence/absence of bottlenose dolphins within a 1000 m radius from the boat's position.

- Anthropogenic variables: distance to the coast (m), number and type of vessels (professional fishing vessels and motor boats) within a 2 nm visual range.

The date, time, position, depth, vessel speed (kt), and SST were obtained by a GPS-Plotter Map Sounder associated with an 83–200 kHz echo-sounder transducer. The echo-sounder signal contained audible energy up to at least 200 kHz for the porpoises and dolphin species monitored, which encompassed most of their hearing range (Díaz López 2011; Dyndo et al. 2015). SSS was measured with an optical refractometer on a scale of 0–100 ppt. The wind speed and direction were measured when the vessel was stationary during 1 min at the end of each 20 min set, by a cup anemometer and compass situated 4 m above the sea level. Tide level (m) and tidal cycle (presence/absence of food tide) were obtained for the harbour of Vilagarcia de Arousa, sited inside of the Ría of Arousa, from the Galician weather service (<http://www.meteogalicia.gal>). Bottom slope gradient and slope aspect were computed from the bottom depth obtained from a bathymetric chart data set, with a 500 m × 500 m resolution, digitized from two 1:50000 scale nautical charts from the Instituto Hidrográfico de la Marina (Spain). This data set was converted to a raster format and then interpolated using QGIS software (<http://www.qgis.org>) terrain analysis tools. All distances to coast were minimum distances in metres from the GPS position of each 20 min point sample to the perimeter of the feature, taking into account the coastal profile and calculated via spatial analyst tools using QGIS software. Chlorophyll-a data were obtained as daily rasters, with a spatial resolution 1 km × 1 km, for the position of each 20 min set from the COPERNICUS Marine Environment Monitoring Service website (<http://marine.copernicus.eu>).

Data analysis and modelling framework

Overall 3114 samples were collected instantaneously every 20 min of which 1677 were on effort (searching for cetaceans). A total of 70 harbour porpoise encounters (20 min presence points) were available for modelling. An absence data set was generated by selecting at random 500 samples on effort (35% of the total 20 min absence points), where harbour porpoises had

not been sighted in the area covered by surveys. By down-sampling the on-effort data, the lack of independence arising from consecutive samplings was limited, avoiding the influence of variations in the observation effort, and limiting pseudo-replication problems.

Following Burnham and Anderson (2002), only predictors with strong biological relevance (based on a priori investigation of the literature: Skov & Thomsen 2008; Marubini et al. 2009; Edrén et al. 2010; Embling et al. 2010; Isojunno et al. 2012; Booth et al. 2013; Dähne et al. 2013; Dyndo et al. 2015) were included from the outset, to prevent over-parameterization. Thus, based on the available data and past experience with factors that appear to affect cetaceans' distribution and abundance, 17 predictor variables were selected, including 12 environmental and 5 anthropogenic variables. Coordinates were not included as covariates, because they were correlated with sea-surface temperature, sea-surface salinity, human activities, and water depth, which were included instead due to their biological interpretability (Forney 2000).

Data exploration protocols described by Zuur et al. (2010) were used to identify outliers, data variability, and relationships between covariates and response variable. Modelling was initiated using a basic GLM to assess collinearity of covariates (Zuur 2012). Explanatory variables were tested for multicollinearity by examining the variance inflation factor (VIF); when $VIF > 5$, we discarded the variable from the analysis (Dormann et al. 2013); following this procedure, we excluded distance to the coast, aspect, Douglas sea force state, and wind direction from the analyses.

A generalized additive modelling (GAM) framework was used to investigate variables affecting the two response variables selected in this study: the presence and number of harbour porpoises. One of the advantages of the use of GAMs is that they allow for flexible relationships between the predictor and response variables (Hastie & Tibshirani 1990). We modelled the presence-absence of harbour porpoises as a binomial GAM with a logistic link function, and for numbers of harbour porpoises seen (given presence), a Poisson distribution was assumed. GAMs require a method for representing the smooth functions and deciding how smooth they should be. The smooth functions were represented by cubic regression splines (Wood 2006). For all continuous explanatory variables, smoothers were constrained to a maximum k value of 5 (i.e. a maximum of 4 df), thus limiting relationships to plausible simple forms and avoiding overfitting. The GAMs' results and diagnostic information about the fitting procedure were

implemented from the package `mgcv` (Wood 2006) in v. 1.8.1. of the statistics and graphics tool R (R Development Core Team 2011). Model assumptions were checked by visual inspection of the residuals and regression fits were examined using plots of residuals against fitted values. The Durbin–Watson test [from the package “`lmtest`” (Zeileis & Hothorn 2002)] and auto-correlation functions (ACF) were used to check for serial correlation, both in our raw data and in the residuals from the models. The optimum final model (hereafter referred to as global model) was selected based on the lowest Unbiased Risk Estimator (UBRE), which can be viewed as an approximation to an Akaike’s Information Criterion (AIC) for many GAMs (Hastie & Tibshirani 1990), and there were no clear patterns in the residuals.

Due to the large number of possible combinations of covariates, model simplification and selection were performed using a multi-model inference approach based on the methods and recommendations of Burnham and Anderson (2002) and Grueber et al. (2011). The information theoretic approach, and specifically model averaging, can lead to robust predictions without the need to identify a unique solution “best model”, but rather to account for uncertainty in model selection by making inferences from an ensemble of possible solutions (Burnham & Anderson 2002). We used the R package ‘`MuMIn`’ (Barton 2011) to produce a candidate model set consisting of all simplified versions of the global model and compared them based on their AIC corrected for small sample sizes (AICc) (Grueber et al. 2011). To ensure that the most parsimonious models were maintained within the best supported model set, the models with $\Delta\text{AICc} < 2$ to identify the relative importance of each model term in predicting the response variable and to estimate the effect sizes of the predictors (Burnham and Anderson 2002). Ecological conclusions were then drawn from the direct comparison of this set of competing models that provided substantial support. Models were ranked from the best to the worst using the difference in AICc between the particular model and the first-ranked model (Δ_i) ($\Delta_i = \text{AICc}(i) - \text{AICc}(\text{min})$) and the Akaike weights (w_i) were calculated to give the relative support for a given model compared with the others (Grueber et al. 2011). Moreover, the relative importance of a predictor variable (RVI) was calculated as the sum of the Akaike weights over all of the models in which the predictor appears (Burnham & Anderson 2002). Partial predictions with 95% confidence intervals were plotted for each covariate included within the best supported model set.

Results

Survey effort and presence of harbour porpoises

The field effort entailed over four consecutive years of field-work from April 2014 to November 2017. In all, 273 daily boat surveys over a period of 38 months were spent in the field covering 9417 km. A total of 1015 h were spent in satisfactory conditions (up to 3 on the Douglas sea force scale and absence of rain or fog). During this time, 3114 instantaneous sets were recorded every 20 min, of which 1677 were on effort (searching for cetaceans). Throughout this period, there were 712 encounters with common bottlenose dolphins (average sighting distance = 475 ± 52 m) and 70 encounters with harbour porpoises (average sighting distance = 190 ± 26 m) (Figure 2).

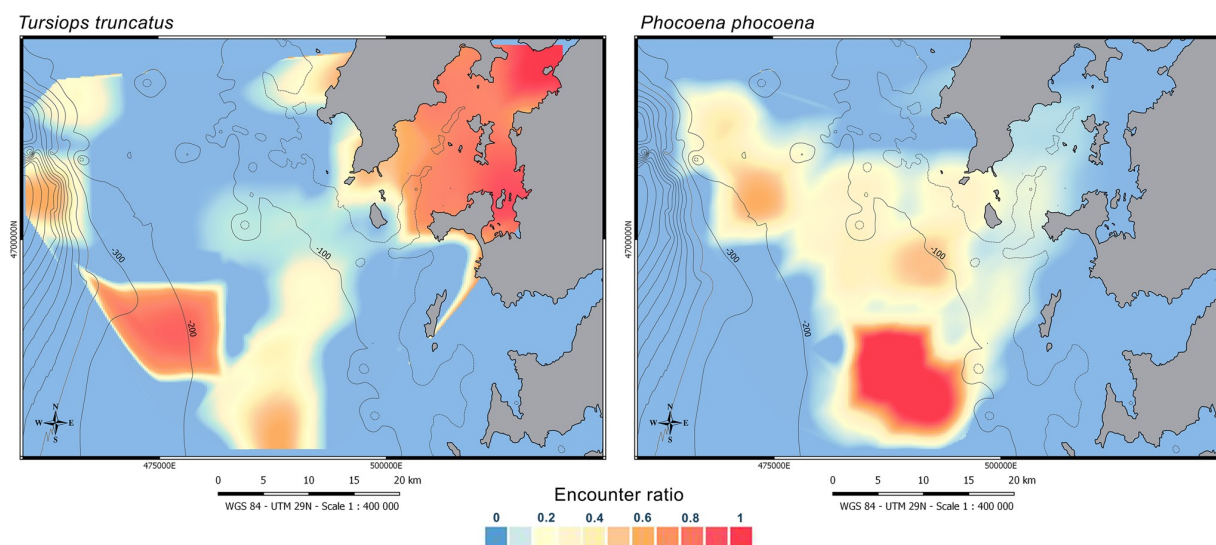


Figure 2. Spatial distribution of bottlenose dolphins (*Tursiops truncatus*) and harbour porpoises (*Phocoena phocoena*) represented by the encounter ratio (number of on-effort samples with the presence of one species in each 2 nm × 2 nm cell of a grid divided by the total number of on-effort samples collected in each cell).

A total number of 338 harbour porpoises were seen on 35 different days at sea (13% of total number of daily surveys). This species was encountered in coastal and shelf waters throughout the study area and in all seasons of the year.

Harbour porpoises' group size and composition were examined for 70 independent groups monitored during 1109 min. Each group was frequently observed during an average of $15.8 \pm$

2 min. Group size ranged from 1 to 25 individuals (mean 4.8 ± 0.5). The most commonly observed were pairs of individuals (20% of the groups) followed by solitary individuals (19%) and aggregations of five harbour porpoises (16%). Most encountered groups (89%) contained less than 9 animals. Group composition showed that 95% of the observed harbour porpoises were considered adults; thus, the remaining 5% were categorized as dependent calves. Calves were present in 17% of the observed groups. Group size was not related with the presence of dependent calves in the group (Spearman ρ 0.17, $p > 0.05$). Likewise, the number of adult individuals in the group was not significantly higher in the presence of dependent calves (mean with calves 5.25 ± 0.9 vs. mean without calves 4.14 ± 0.4) (Mann–Whitney, $p > 0.05$).

Environmental and anthropogenic factors affecting harbour porpoises' presence

The global model explained around 45.3% of the variation in the data ($R^2 = 0.4$, UBRE = -0.528 , AICc = 270.4). We produced a candidate model set consisting of all 1024 simplified versions of the global model and compared them based on their AICc. The three models with $\Delta\text{AICc} < 2$ were used to produce model-averaged parameter estimates (**Table 1**).

Table 1. Most likely models explaining the variation in the presence of harbour porpoises in relation with environmental and anthropogenic variables.

Model	<i>df</i>	<i>logLik</i>	AICc	Δ_i	w_i
MB/D/FB/SST/W	13.68	- 117.0	262.1	0.00	0.53
MB/D/FB/SST/W/SSS	14.18	- 117.3	263.7	1.60	0.24
MB/D/FB/SST/W/TC	14.69	- 116.8	263.8	0.70	0.23

Only three most candidate models ($\Delta_i \leq 2$) of the 1024 are presented. *df* degrees of freedom, Δ_i difference in AIC between the particular model and the first-ranked model, w_i Akaike weight showing the relative support of a given model compared to the others, D depth, W wind speed, SST sea-surface temperature, SSS sea-surface salinity, TC tidal cycle, MB number of motor boats, FB number of fishing boats.

Variables, including depth, number of motor boats, water temperature, wind speed (as a measure of the sea state), and number of fishing vessels, were all retained in each model within the candidate model set having a relative variable importance (RVI) of 1 in the final average model (**Table 2**). Sea-surface salinity and tidal cycle had a relative variable importance (RVI) of 0.24 and 0.23 in the final averaged model, respectively. Time of the day, slope, and presence of bottlenose dolphins were not present in the top model set, indicating that these covariates

were not important predictors of the presence of harbour porpoises. Harbour porpoise occurrence was predicted to be more likely at greater depths, moderate water temperatures, moderate number of fishing boats, in the absence of wind, and tended to decrease with a higher number of motor boats (**Figure 3, Table 3**).

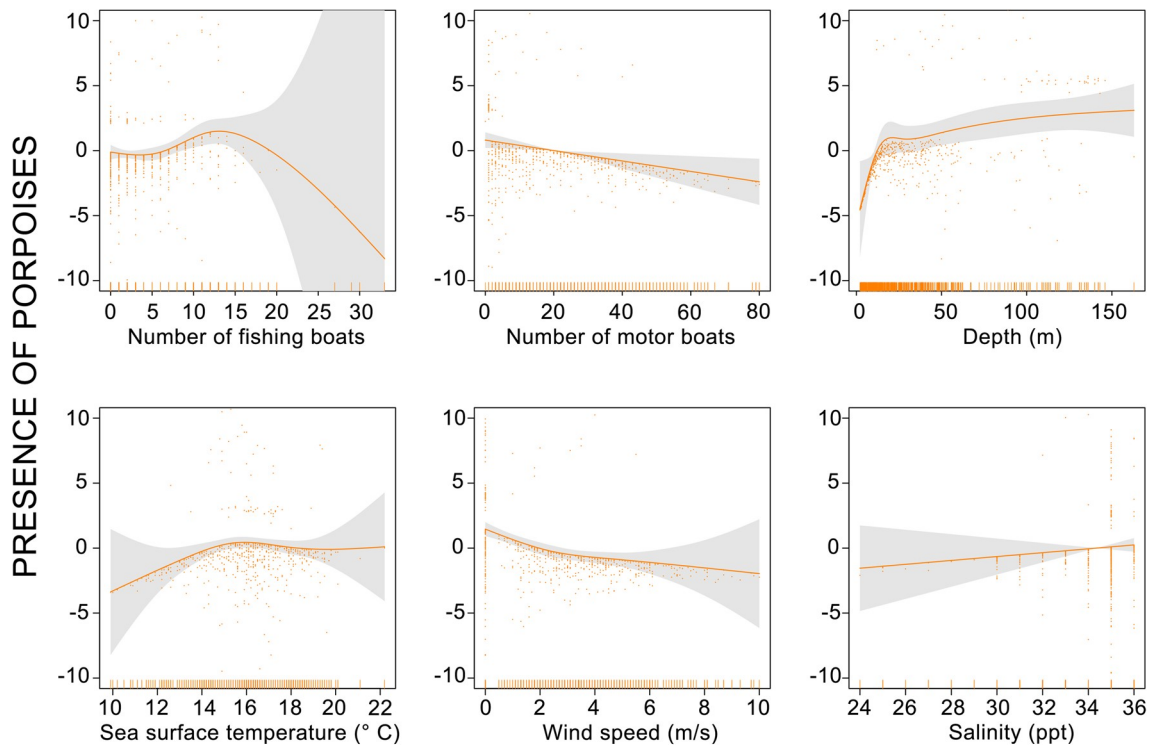


Figure 3. Averaged predictions of harbour porpoise presence for each covariate present in the confidence set of models and their 95% confidence limits when all other variables are fixed to their mean value.

Table 2. Model-averaged coefficients, adjusted standard error (SE), z value, and relative variable importance (RVI) estimated by a generalized additive model to determine the effects of depth (D), wind speed (W), sea-surface temperature (SST) and salinity (SSS), tidal cycle (TC), number of motor boats (MB), and number of fishing boats (FB) on harbour porpoises' presence (n = 570). Superscript numbers represent the smooth terms of the spline with 4 degrees of freedom.

	Estimate	Adj. Std Error	z value	P	RVI
Intercept	-4.41	0.89	4.93	<0.001	
MB	-0.27	0.10	2.74	0.006	1
D ¹	2.50	1.27	1.28	0.050	1
D ²	1.17	0.64	1.84	0.066	
D ³	3.49	1.30	2.68	0.007	
D ⁴	3.31	1.06	3.12	0.001	
W ¹	-0.87	0.26	3.33	<0.001	1
W ²	-1.19	0.29	4.16	<0.001	
W ³	-1.49	0.61	2.45	0.014	
W ⁴	-2.12	2.11	1.00	0.316	
FB ¹	0.22	0.54	0.40	0.689	1
FB ²	1.95	0.83	2.36	0.018	
FB ³	-1.75	3.76	0.47	0.640	
FB ⁴	-100	129	0.78	0.435	
SST ^a	2.25	1.61	1.39	0.164	1
SSS	0.06	0.13	0.54	0.592	0.24
TC (Flood)	0.27	0.36	0.74	0.457	0.23

Table 3. Examples of the predicted effect of each variable included in the model-averaged model on the presence and numbers of harbour porpoises, with the other predictors held at their mean.

Predictor		Estimated presence of harbour porpoises	Estimated number of harbour porpoises
D	50 metres	4.8 ± 2.1 %	4.0 ± 0.7
	100 metres	14.3 ± 6.6 %	7.5 ± 1.9
SST	12 Celsius	0.5 ± 0.4 %	1.9 ± 0.6
	16 Celsius	3.8 ± 1.8 %	3.2 ± 0.8
W	0 m/s	17.2 ± 6.2 %	2.1 ± 0.7
	5 m/s	1.8 ± 1.1 %	2.2 ± 0.8
MB	0	5.8 ± 2.8 %	2.6 ± 0.6
	10	4.0 ± 1.9 %	3.2 ± 0.8
FB	0	3.2 ± 1.6 %	3.6 ± 0.9
	10	7.0 ± 3.8 %	2.8 ± 0.8
SSS	30 ppt	2.2 ± 1.8 %	1.2 ± 0.8
	35 ppt	4.2 ± 2.0 %	3.3 ± 0.8
T	8:00 h	<i>Na</i>	4.4 ± 1.1
	16:00 h	<i>Na</i>	2.5 ± 0.7
Tc	Ebb	3.5 ± 1.9 %	2.3 ± 0.6
	Flood	4.5 ± 2.3 %	3.3 ± 0.8

D depth, W wind speed, SST sea-surface temperature, SSS sea-surface salinity, TC tidal cycle, T time, MB number of motor boats, FB number of fishing boats, Na predictor not included in the model-averaged model.

Effects of environmental and anthropogenic factors on the number of harbour porpoises seen

The global model explained around 48.1% of the variation in the data ($R^2 = 0.21$, UBRE = 1.06, AICc = 381.1). Out of 1024 simplified versions of the global model, 4 models with $\Delta AICc < 2$ were used to generate model-averaged parameter estimates (**Table 4**). Covariates including depth, time of the day, number of motor boats, tidal cycle, and water temperature were retained in each model within the candidate model set having a relative importance (RVI) of 1 in the final average model (**Table 5**). The salinity and wind speed had an RVI of 0.60. The number of fishing boats and wind speed, however, was only retained in one of the top models with a RI of 0.16. The presence of bottlenose dolphins and slope was not present in the top model set, indicating that these covariates were not important predictor of the number of harbour porpoises seen.

The number of harbour porpoises was predicted to change with environmental variables (depth, wind speed, water temperature, and salinity), number of motor and fishing boats, and time of the day (**Figure 4, Table 3**).

Table 4. Most likely models explaining the variation in numbers of harbour porpoises in relation to environmental and anthropogenic variables. D = depth, W = wind speed, SST = sea surface temperature, SSS = sea surface salinity, Tc = tidal cycle, MB = number of motor boats, FB = number of fishing boats, and T = time of the day.

Model	df	logLik	AICc	Δ_i	wi
D/MB/SSS/T/SST/Tc	13.05	-168.6	369.74	0.00	0.44
D/MB/T/SST/Tc	12.48	-170.0	370.97	1.23	0.24
D/MB/T/SST/Tc/W	15.03	-166.4	371.7	1.96	0.16
D/MB/SSS/T/SST/FB/Tc	14.86	-166.7	371.7	1.99	0.16

Only four most candidate models ($\Delta_i \leq 2$) of the 1024 are presented. df degrees of freedom, Δ_i difference in AIC between the particular model and the first-ranked model, wi Akaike weight showing the relative support of a given model compared to the others.

Table 5. Model averaged coefficients, adjusted standard error (SE), z value and relative variable importance (RVI) estimated by a generalized additive model to determine the effects of depth (as spline), wind speed, sea surface temperature and salinity, tidal cycle, time of the day (as a spline), number of motor boats, number of fishing boats (as a spline), and presence of bottlenose dolphins on the relative density of harbour porpoises (n = 570).

	Estimate	Adj. Std Error	Z value	P	RVI
Intercept	1.22	0.12	10.5	<0.001	
D ¹	0.21	0.25	0.84	0.398	1
D ²	-0.63	0.19	3.37	<0.001	
D ³	0.62	0.23	2.70	0.007	
D ⁴	0.32	0.20	1.63	0.103	
T	-1.12	0.08	1.55	0.121	1
SST	0.16	0.06	2.45	0.014	1
MB ¹	0.24	0.18	1.33	0.184	1
MB ²	0.005	0.23	0.02	0.980	
MB ³	-1.15	0.35	3.31	<0.001	
MB ⁴	0.49	0.33	1.50	0.131	
TC (Flood)	0.33	0.13	2.43	0.015	1
SSS ¹	-0.21	0.25	0.83	0.406	0.60
SSS ²	-0.11	0.16	0.67	0.503	
SSS ³	0.57	0.62	0.91	0.361	
SSS ⁴	0.15	0.21	0.69	0.490	
W ¹	0.02	0.08	0.19	0.844	0.16
W ²	0.05	0.13	0.36	0.719	
W ³	0.05	0.14	0.36	0.719	
W ⁴	-0.17	0.46	0.37	0.708	
FB ¹	-0.01	0.04	0.33	0.739	0.16
FB ²	-0.02	0.06	0.36	0.719	
FB ³	-0.02	0.07	0.28	0.781	
FB ⁴	-0.002	0.12	0.02	0.984	

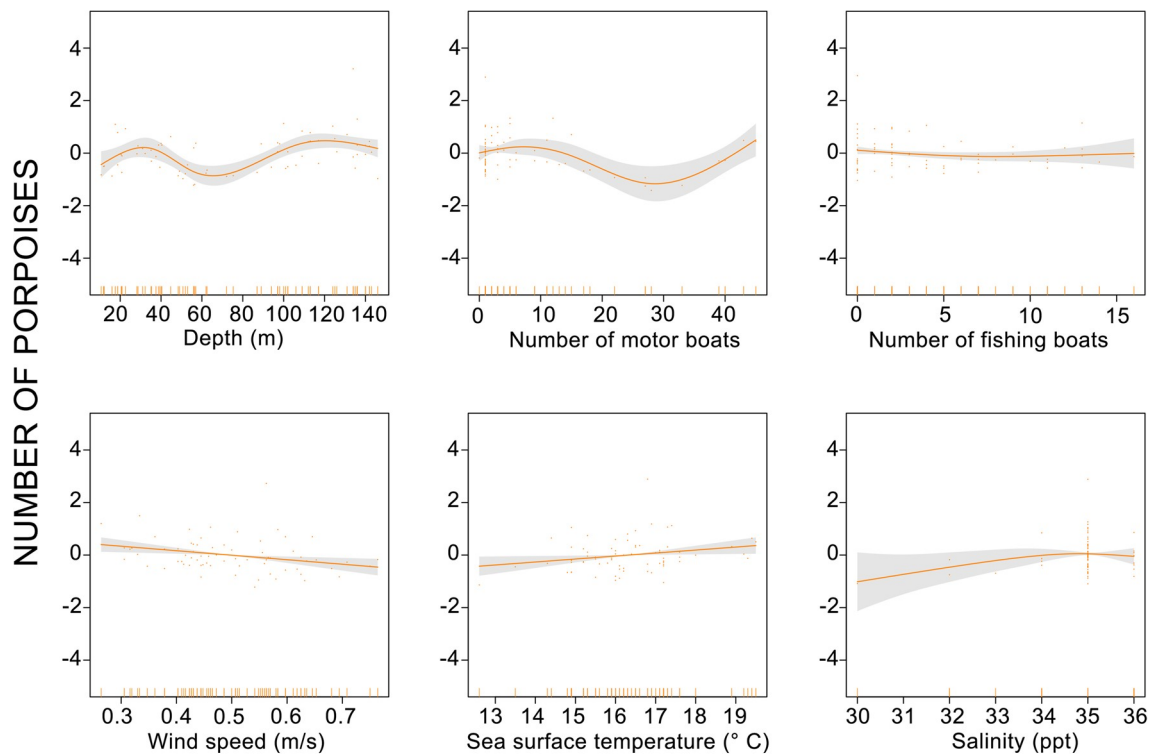


Figure 4. Averaged predictions of number of harbour porpoises (given presence) for each significant covariate in the confidence set of models and their 95% confidence limits when all other variables are fixed on their mean value.

Discussion

The multitude of different environmental and anthropogenic factors in near-shore and shelf waters has cumulative impacts on marine predators' distribution and density at different spatial and temporal scales (Tittensor et al. 2010; Ross et al. 2011). This represents an important challenge when trying to understand the ecology and protect coastal cetacean populations. In this context, our study provides new and relevant insights into the understanding of how both environmental and anthropogenic features impact on the presence and relative density of harbour porpoises along the Northwestern coast of Spain. This information is particularly important for the conservation of this species, because recent studies have identified strong barriers to gene flow that isolate almost completely the Iberian population (Fontaine et al. 2014). In addition to these data, we also tested for the first time a competitive exclusion hypothesis, including as part of the correlates the presence of a sympatric species, the bottlenose dolphin, in the model framework.

Over the last years, model averaging, specifically information theoretic approaches based on Akaike's information criterion (IT–AIC approaches), have had a major influence on statistical practices in the field of ecology (Grueber et al. 2011; Nakagawa & Freckleton 2011). The importance of this study lies within the broad temporal range of data and the use of model averaging approach to evaluate fluctuations in occurrence and relative density of harbour porpoises. Multi-model inference is based on weighted support from several models (model averaging). Such procedure leads to more robust and stable results than those based on choosing one best single model (Richards et al. 2010).

Our findings reveal that both environmental and anthropogenic variables play an important role in the variation of presence and relative density of harbour porpoises. Specifically, depth, water temperature, and marine traffic were important predictors in the data, for both porpoise presence and relative abundance. All models in the confidence set included these three variables and the model-averaged parameter estimates highlighted how changes in both the presence and the number of harbour porpoises are affected by these oceanographic variables and marine traffic. The observed unequal use of available habitat indicates that harbour porpoises present a fine-scale pattern of habitat selection along the study area, which is mostly related to the variation in both environmental and anthropogenic variables. The relationship between depth and harbour porpoises' occurrence and relative density is consistent with the literature, and likely associated with the availability of food (Northridge et al. 1995; Skov & Thomsen 2008; Marubini et al. 2009; Embling et al. 2010; Isojunno et al. 2012). Likewise, the observed influence of the sea-surface temperature on the fluctuations in the presence and relative density of harbour porpoises may be related to changes in prey abundance. Owing to the regularity of upwelling events along the Northwestern coast of Spain, the study area exhibits enhanced primary production because of the presence of nutrient-rich water masses that upwell towards surface layers. Furthermore, the results of our analysis indicate that the tidal cycle could affect the presence and relative density of harbour porpoises in the area. Indeed, both the presence and relative porpoise density were expected to be higher during flood than ebb tide phases. Similar results were observed in studies about the fine-scale distribution of harbour porpoises using satellite telemetry (Johnston et al. 2005), reporting that tidal cycle facilitates the aggregation of harbour porpoises' preys. The upwelling events, together with strong tidal streams, islands wakes, and headland eddies, make the

Northwestern coast of Spain a suitable foraging habitat for harbour porpoises by aggregating and supporting high densities of their prey (Farina et al. 1997).

On the other hand, these rich waters are subject to significant use by humans including professional fisheries, aquaculture industry, and important marine traffic (Vieites et al. 2004; Díaz López & Methion 2017). Our results show what appears to be harbour porpoises' avoidance behaviour in response to marine traffic as both the occurrence and the relative density of harbour porpoises tended to decrease with a higher number of motor boats present. The effects of boat traffic on the presence of harbour porpoises have been poorly documented, and while there is a general agreement that harbour porpoises will evade individual motor vessels (Palka & Hammond 2001), to our knowledge, this is the first habitat modelling study that concludes that high boat traffic levels correlate with both low occurrence and low relative density of harbour porpoises. These results are consistent with behavioural responses to vessel noise observed in captive harbour porpoises (Dyndo et al. 2015), suggesting that vessel noise is a substantial source of disturbance for harbour porpoises in shallow water areas.

Furthermore, our results report that the visual detection from our research vessel might be impacted by the sea state conditions. Indeed, the estimated probability to detect harbour porpoises decreased as wind force increased. Harbour porpoises' density estimates were also documented as depending on sea state in other study areas (Palka 1996).

Interspecific competition with bottlenose dolphins does not appear to affect the distribution and relative density of harbour porpoises. Data from the top model sets for probability of encountering harbour porpoises and relative abundance of this species confirmed that the presence of a trophic competitor is not an important predictor of the distribution and number of harbour porpoises seen. These results differ from the conclusions reported in other studies carried out from land-based observation platforms that described a negative relationship between the presence of bottlenose dolphins and the presence of harbour porpoises along the Northwestern coast of Spain (Pierce et al. 2010). Behavioural observations during field work, including four sightings in which harbour porpoises were present at the same time and location than bottlenose dolphins, reinforce our modelling results. During these encounters, harbour porpoises have never been seen avoiding bottlenose dolphins and bottlenose dolphins did not

display aggressive behaviour towards the porpoises. These observations contrast with bottlenose dolphins' attacks towards harbour porpoises reported in British waters, where bottlenose dolphin aggressions cause a significant mortality of harbour porpoises in areas, where both species occur (Ross & Wilson 1996; Jepson & Baker 1998). Different reasons could help to explain the observed fine spatial separation between both sympatric species such as different prey preference in this particular area, or the different tolerance to human disturbance. The latter is supported by our results that indicate a harbour porpoise avoidance of motor boats, being less tolerant of the boat traffic than bottlenose dolphins that have been observed in areas characterized by higher levels of marine traffic (Díaz López 2017; Díaz López & Methion 2017).

These findings highlight the importance of considering the interactions between multiple variables in ecological studies on fine temporal and spatial scales, in addition to underlining the importance of using a multi-species ecology approach in research and conservation management planning (Head et al. 2012). Moreover, future studies on both harbour porpoises and common bottlenose dolphins in different areas could incorporate the methods framework of this study to define the role of multiple environmental and anthropogenic factors in the distribution of these potentially vulnerable odontocete species. From a conservation perspective, further studies are needed to understand whether the observed avoidance of marine traffic can impact the viability of the local harbour porpoise population.

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Annex 3. Supervision of Bachelor and Master students

I have supervised the bachelor/master thesis of the following students as part of my work at the BDRI, as an external supervisor:

1. Sara de Almeida Simões. 2019. Skin mark patterns in bottlenose dolphins from the Ría de Arousa (Galicia, Spain). Master of Science, Universidad de Aveiro, Portugal.
2. Emma Stuart. 2019. Respiratory patterns in free-roaming *Tursiops truncatus*. Bachelor of Science, University of West of Scotland, Scotland.
3. Coline Arque. 2019. Impact of aquaculture on the behaviour of bottlenose dolphins. Licence 3, Université de Pau et des Pays de l'Adour, France.
4. Magali De Poret. 2019. Communication of bottlenose dolphins by whistles (*Tursiops truncatus*). Licence 3, Université Paris Descartes, France.
5. Sarah van Dahl. 2019. Using GIS to identify suitable site for marine protected areas for bottlenose dolphins in Galician waters. Bachelor of Science, Universitat Rostock, Germany.
6. Lisa-Marie Phostein. 2019. The comparison of the distribution of bottlenose dolphins (*T. truncatus*) and harbour porpoises (*P. phocoena*) along the Galician coast. Master 1, Université de Bordeaux, France.
7. Alex Otto. 2019. Diet composition and age analysis of the Eurasian otter in the waters of the Ría de Arousa. Bachelor of Science, University of Nebraska-Lincoln, USA.
8. Nathan Perez. 2019. Le comportement du grand dauphin et l'influence du trafic maritime. Licence 2, Université d'Artois, France.
9. Louise Lefrère. 2019. Influence des activités anthropiques sur le comportement du grand dauphin (*Tursiops truncatus*). Licence 2, Université Paris Sud, France.
10. Maxence Dumortier. 2019. Comportement du grand dauphin dans la Ría d'Arousa (Espagne). Licence 2, Université Paris Sud, France.
11. Kimberley Cloirec. 2019. Étude du comportement du grand dauphin. Licence 2, Université d'Artois, France.
12. Laurène Manusset. 2019. Structure sociale d'une population résidente de grand dauphin dans la baie d'Arousa (Galice, Espagne). Master 2, Université de Tours, France.
13. Julia Ruiz. 2019. Les coulisses de la gestion environnementale : réponse à deux appels d'offre en faveur des grands cétacés du littoral galicien (Espagne). Master 2, Université Lumières Lyon 2, France.
14. Rozenn Jehanno. 2019. Le comportement du grand dauphin dans la baie d'Arousa (Espagne). Licence 3, Université catholique de l'ouest, France.
15. Sarah Levasseur. 2019. Study of the short-beaked common dolphin (*Delphinus delphis*) and harbour porpoises (*Phocoena phocoena*) distribution along the Galician coast. Licence 3, Université de Rouen, France.

16. Elizaveta Vesnina. 2019. The impact of mussel farming on the bottlenose dolphins. People's friendship University of Russia, Russia.
17. Morgane Ferrer. 2019. Comparaison de la distribution de deux oiseaux marins en Galice : puffins et cormorans. Licence 3, Université de Bordeaux, France.
18. Florine Aune. 2019. Distribution of bottlenose dolphins in the Ría de Arousa (NW Spain). IUT Aix Marseille, Aix Marseille Université, France.
19. Gailane Bonaglia. 2019. Analyse de la distribution du grand dauphin. Licence 3, Université de Bordeaux, France.
20. Yulian Dobrev. 2019. Évaluation de la distribution des grands dauphins *Tursiops truncatus* et des débris plastiques flottants dans la ría d'Arousa (Espagne) par l'usage de SIG. Master 1, Université de La Rochelle, France.
21. Jessica Ceglareck. 2018. Impact of noise pollution of whistle production of bottlenose dolphin. Bachelor of Science. University of Copenhagen, Denmark.
22. Valentina Rossi. 2018. Boat traffic and bottlenose dolphin behaviour. Bachelor of Science, Università degli studi di Udine, Italy.
23. Alex Govoni. 2018. Bottlenose dolphin distribution and shellfish aquaculture. Bachelor of Science, Università di Bologna, Italy.
24. Lora Almutairi. 2018. The effect of boat disturbance on bottlenose dolphin (*Tursiops truncatus*) behaviour in the Ría de Arousa. Master of Science, York University, UK.
25. Madeleine Nedelcu. 2018. The diet of *Lutra lutra* in Galician waters. Bachelor of Science, University of Vienna, Austria.
26. Lucie Reinwalt. 2018. Sound production in relation to activity, background noise and group size in the resident population of bottlenose dolphins of the Ría de Arousa, Spain. Master of Science, University College Dublin, Ireland.
27. Tamara Narganes. 2018. Using habitat model to identify suitable sites for marine protected areas for harbour porpoises (*Phocoena phocoena*) in Galician waters, NW Spain. Bachelor of Science, York University, UK.
28. Shannon Moore. 2018. Marine vessel traffic and bottlenose dolphin (*Tursiops truncatus*) behavior. Bachelor of Science, St. Olaf College, USA.
29. Estel Villanueva. 2018. Distribution del delfín mular (*Tursiops truncatus*) en la Ría de Arousa. Bachelor of Science, Universitat de Barcelona, Spain.
30. Laura Stock. 2018. Spatial analysis of dolphin populations and marine vessels using GIS in order to inform of the best areas for the creation of marine protected areas. Master of Science, Queen's University Belfast, UK.
31. Nastasia Belle. 2018. Caractéristique de la production de sons par une population de grand dauphin (*Tursiops truncatus*) dans la baie d'Arousa (NO Espagne). Licence, Université de La Rochelle, France.
32. Matthew Anderson. 2018. The effect of marine traffic on the behaviour of bottlenose dolphin. Bachelor of Science, University of Hull, UK.

33. Andy Quéllec. 2018. Recreational boat impact on *Tursiops truncatus* distribution in the Ría de Arousa. Licence, Université de La Rochelle, France.
34. Robin Garçon. 2018. Distribution du grand dauphin (*Tursiops truncatus*) dans la Ría d'Arousa (Espagne). Licence, Université Paris Sud, France.
35. Lucas Bouyge. 2018. Études des variables naturelles qui influencent la distribution du dauphin commun à bec court le long de la côte sud de la Galice, dans le nord ouest de l'Espagne. Master 2, University of Corse Pascal Paoli, France.
36. Oriane Peigner. 2018. Modélisation trophique : la place du grand dauphin au sein de l'écosystème de la Ría d'Arousa, Galice. Master 2, University of Corse Pascal Paoli, France.
37. Jeanne Bienvenu. 2018. Étude du comportement de plongée des grands dauphins (*Tursiops truncatus*) dans la Ría d'Arousa en Galice (Espagne) via l'analyse de modèles respiratoires. Licence 3, University de Nantes, France.
38. Capucine Szilas. 2018. Variation dans le comportement de plongée du grand dauphin (*Tursiops truncatus*) exposé au trafic maritime dans la Ría d'Arousa (Galice, Espagne). Master 1, University de Tours, France.
39. Sarah Bienassis. 2018. Distribution du grand dauphin (*Tursiops truncatus*) dans la Ría d'Arousa et relation avec la présence de plastique. Licence 3, Université de Nantes, France.
40. Manon Briendo. 2018. Étude du mode de distribution spatiale du grand dauphin et de l'impact humain dans les eaux galiciennes en vue de la création d'aires marines protégées. Master 1, University du Littoral Côte d'Opale, France.
41. Oihana Olhasque. 2018. Impact des filets et des nasses de pêches sur le comportement du grand dauphin (*Tursiops truncatus*) dans la baie d'Arousa (Galice, Espagne). Licence 3, Université de Pau et des Pays de l'Adour, France.
42. Sophia Ighiouer. 2018. Influence des variables environnementales sur la distribution du grand dauphin dans la Ría d'Arousa, au nord ouest de l'Espagne. Master 1, École Pratique des Hautes Études Paris, France.
43. Loïc Leseignoux. 2018. Impact of marine traffic on bottlenose dolphins' behaviour. Master 2, Université de La Rochelle, France.
44. Jessica Chen. 2017. Influence of group size and presence of calves on bottlenose dolphins' behaviour. Bachelor of Science, University of California Davis, USA.
45. Marie-Charlotte Lefèvre. 2017. Co-occurrence of bottlenose dolphins and marine birds in the Ría of Arousa, Spain. Licence 3, Université de Rouen, France.
46. Emma Persyn. 2017. Impact des filets de pêche sur la distribution du grand dauphin dans la Ría d'Arousa, Galice, Espagne. Master 1, Université de Poitiers, France.
47. Paul Batard. 2017. Influence du comportement, de la taille de groupe et de la présence de juvéniles sur la production vocale du grand dauphin. Master 1, Université d'Angers, France.

48. Maxime Lauvergeon. 2017. Influence de la taille du groupe et de la présence de petits sur le comportement du grand dauphin (*Tursiops truncatus*). Master 1, Université de Reims, France.
49. Kevin Biscaye. 2017. Distribution du marsouin commun au sud de la côte Galicienne (Espagne). Licence 3, Université de La Rochelle, France.
50. Damien Devilly. 2017. Distribution du dauphin commun (*Delphinus delphis*, Linnaeus - 1758) au large de la Ria d'Arousa (Nord-Ouest de l'Espagne). Licence 3, Université de La Rochelle, France.
51. Sophie Lopez Carmona. 2017. Impact des filets maillants sur la distribution du grand dauphin (*Tursiops truncatus*) dans la baie d'Arousa (NO Espagne). Licence 3, Université d'Avignon et des Pays du Vaucluse, France.
52. Arnaud Puig. 2017. Impact of seines fisheries on bottlenose dolphins' distribution. Master 1, Université de Perpignan, France.
53. Clémentine Séguigne. 2017. Intra population variability of social communication in bottlenose dolphin (*Tursiops truncatus*). Master 2, Muséum national d'histoire naturelle, Paris, France.
54. Aude Mazurie Desgarennés. 2016. Modélisation de l'habitat préférentiel du grand dauphin selon les facteurs environnementaux du milieu. Master 2, Université de Poitiers, France.
55. Kamel Benali. 2016. Distribution saisonnière du grand dauphin dans la baie d'Arousa (Galice, Espagne) en 2015. Master 1, Université de Perpignan via Domitia, France.
56. Julia Boucachard. 2016. Influence de la pêche au filet sur la distribution de la population de grands dauphins dans la baie d'Arousa (Galice, Espagne). Master 1, Université de Nantes, France.
57. Justine Ngosso Macky. 2016. Impact du trafic maritime sur la distribution du grand dauphin dans la baie d'Arousa, Galice, Espagne. Licence 3, Université Paris 11, France.
58. Sophie Forgeron. 2016. Caractéristiques et fréquence de production des sifflements d'une population de grand dauphin, dans la baie d'Arousa, Espagne. Master 1, Université de Poitiers, France.