



HAL
open science

On the macroecology and global distribution of the ecosystem engineer : *Sabellaria alveolata* in a changing world

Amelia Curd

► **To cite this version:**

Amelia Curd. On the macroecology and global distribution of the ecosystem engineer : *Sabellaria alveolata* in a changing world. Ecology, environment. Université de Bretagne occidentale - Brest, 2020. English. NNT: 2020BRES0034 . tel-03738043

HAL Id: tel-03738043

<https://theses.hal.science/tel-03738043>

Submitted on 25 Jul 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

THESE DE DOCTORAT DE

L'UNIVERSITE
DE BRETAGNE OCCIDENTALE

ECOLE DOCTORALE N° 598
Sciences de la Mer et du littoral
Spécialité : « *Ecologie marine* »

Par

Amelia CURD

**On the Macroecology and Global Distribution of the
Ecosystem Engineer; *Sabellaria alveolata* in a Changing World.**

Thèse présentée et soutenue à Plouzané, le 7 juillet 2020
Unité de recherche : Laboratoire d'écologie benthique côtière (IFREMER-DYNECO-LEBCO)

Rapporteurs avant soutenance:

Stephen J HAWKINS Professor of Natural Sciences
University of Southampton

David WETHEY Professor of Biological Sciences
University of South Carolina

Composition du Jury :

Stephen J HAWKINS Professor of Natural Sciences
University of Southampton

David WETHEY Professor of Biological Sciences
University of South Carolina

Sarah A WOODIN Professor Emeritus
University of South Carolina

Président du jury

Frédéric JEAN Professeur des universités
Université de Bretagne Occidentale

Directeur de thèse

Stanislas DUBOIS Cadre de recherche
IFREMER

Co-directeur de thèse

Louise B FIRTH Lecturer in Marine Ecology
University of Plymouth

“Expliquer, comprendre, pénétrer quelque chose au moins du mystère du monde, soulever au moins un coin du voile d’Isis, il n’est pas, dans le domaine des choses de l’esprit, de joie plus solide et de plus enivrant bonheur que d’avoir pu, fût-ce une seule fois, dans le plus humble domaine et sur le plus infime détail, y parvenir. ”

Theodore Monod – Méharées (1937)

“When we go down to the low-tide line, we enter a world that is as old as the earth itself – the primeval meeting place of the elements of earth and water, a place of compromise and conflict and eternal change. For us as living creatures it has special meaning as an area in or near which some entity that could be distinguished as Life first drifted in shallow waters – reproducing, evolving, yielding that endlessly varied stream of living things that has surged through time and space to occupy the earth.”

Rachel Carson – preface to ‘the Edge of the Sea’ (1955)

“Once you go worm, that’s what you’ll yearn!”

Men in Black II (2002)

REMERCIEMENTS

Mes premiers grands et sincères remerciements vont à mes encadrants de thèse, Stanislas Dubois et Louise Firth. Je n'aurais pu espérer mieux, vous formez un duo formidable et très complémentaire avec lequel j'ai eu un grand plaisir à travailler. Stan, merci pour ta rigueur, et merci d'avoir su me diriger tout en me laissant suffisamment de liberté pour que je puisse m'épanouir dans ce travail. Louise, merci pour tes relectures détaillées, ta force rédactionnelle et ton attitude positive. Au-delà de vos qualités scientifiques, j'apprécie également vos qualités humaines et vous remercie pour tous ces bons moments passés sur l'éstran (en Bretagne, en Angleterre, au Pays de Galle) en conférence (au Portugal et à Hong-Kong) ou en « retraite scientifique » (Le Pouldu). J'espère pouvoir collaborer avec vous dans de futurs projets de recherche au cours des nombreuses années à venir.

Je remercie mes responsables à l'Ifremer, Jérôme Paillet, responsable du département ODE en 2016, Cédric Bacher, responsable de l'unité DYNECO, et Philippe Cugier, responsable du LEBCO, qui ont tous donné leur feu vert pour que je consacre la plus grande partie des quatre dernières années à ma thèse.

J'adresse mes profonds remerciements aux membres du jury de ce doctorat, qui ont accepté de lire le manuscrit durant cette 'période sans précédent'. En particulier, je remercie les rapporteurs Steve Hawkins et David Wethey d'avoir accepté de juger ce travail, ainsi que les examinateurs, Sally Woodin et Fred Jean. Je remercie tout particulièrement les membres de mon comité de suivi individuel, Eric Thiébaud et Nicolas Desroy, pour leur disponibilité et précieux conseils.

Je remercie l'équipe REEHAB pour le terrain, les envois internationaux d'échantillons de carbo-glace, leurs inputs toujours précieux lors de réunions de projets. Merci à Laura Bush et Andy Davies d'avoir effectué du travail de terrain de nuit, à la frontale, en février dans le nord du Royaume-Uni, et pour une superbe réunion de « récifitude » à Bangor. Merci à Claudia Meneghesso, Rui Seabra et Fernando Lima d'avoir affronté la houle portugaise et partagé leurs ingénus T° loggers... j'ajouterais une pensée spéciale pour cette rencontre et ce travail de terrain improbable sur la péninsule de Dingle en octobre 2018, sans la moindre concertation!

Je remercie de tout cœur mes amis et collègues du LEBCO. La recherche est de plus en plus collaborative et cette thèse en est l'exemple ; pratiquement tout le laboratoire a été impliqué dans le projet REEHAB de prêt ou de loin ! Je commence par le « cercle 1 REEHAB » : Céline Cordier, Aurélien Boyé et Mickaël Vasquez. Sans vous, cette thèse serait allée bien moins loin. Pour sa rigueur,

pour l'énorme travail de saisie de feuilles de terrain, de calibration de FlowCAM et d'inventaire de données historiques, sans oublier son humour et sa douceur, je ne remercierai jamais assez Céline. Pour sa bonne humeur et ses prouesses en écologie numérique, je remercie Aurélien, et pour son humour irrévérencieux, sa disponibilité et ses exploits en modélisation statistique je remercie du fond du cœur Mick.

Je remercie Jean-Do Gaffet pour son aide avec les méga-quadrats, le tri de plus de 80 carottes de récifs, et les centaines de kilomètres au volant du Traffic. Merci à Erwan Le Gall d'avoir fabriqué en un rien de temps dans son atelier un sous-échantillonneur d'hermelles. Pour leur solidarité entre thésards, je remercie Auriane Jones, Thibault Androuin et Bastien Taormina. Merci à Antoine Carlier, Xavier Caisey, Céline et Mick d'avoir subi les longues journées, les repas en décalé, et les risques d'engelures, ou de coups de soleil selon la saison, que constituent les campagnes de terrain sur l'estran par grands coeff. Je veux remercier Touria Bajjouk pour tout son soutien moral et calorique (vive le sellou!), Aline Blanchet pour son partage d'expérience d'une thèse en formation continue. Pour ses conseils très justes sur un large éventail de sujets, et pour ses talents de comédiens mis au profit des films de thèse du labo, je remercie Martin Marzloff. Pour son enthousiasme, ses idées, et pour un road-trip mémorable d'élucidation de la phylogénie des hermelles irlandaises, je remercie Flavia Nunes.

Pour leur accueil, je remercie tous les collègues du LPI – ce fut une chance de pouvoir connaître un deuxième laboratoire sur le centre Bretagne. Je remercie Valérian Leroy et Lizenn Delisle pour les heures passées « en manip' » ainsi que Claudie Quéré pour son travail d'orfèvre avec le GC. Pour sa pédagogie, sa technique de rédaction, et pour m'avoir aidée à vivre plus sereinement la thèse en publiant un article à mi-parcours, je remercie Fabrice Pernet. Merci à Charlotte Corporeau pour sa fougue et son envie de prendre part au projet REEHAB. Je remercie Arnaud Huvet pour l'accès à cette superbe machine qu'est le Flowcam, et Elodie Fleury pour le naturel avec lequel elle mène son équipe. Je souhaite que l'écologie et la physiologie des invertébrés marins aient un bel avenir ensemble !

De très nombreuses personnes ont participé au travail de terrain du projet REEHAB dans lequel cette thèse s'insère, parfois dans des conditions thermiques extrêmes. Je remercie Annabelle Aish pour son partage de connaissances de gestion des milieux marins, et d'avoir trouvé le temps de faire un tour des estrans du grand Ouest pour 'operation worms', ainsi que de nombreux d'étudiants : Maïwenn Lescop, Camille Poitrimol, Gaëtan Hazevis, Gautier Sourimant, Alice Bello, Morgane Seroux. Pour avoir ouvert les portes de la perception du langage R et pour des moments de déconnexion bienvenus, je remercie Claire Bissery. Merci aussi à Fanny Kerninon et Morgane Dessert pour nos déjeuners entre étudiantes 'pas si matures que ça quand-même' de l'EDSML.

Je remercie à nouveau Maiwenn ainsi qu'Anne-Louise Blier pour leur travail de laboratoire irréprochable pour préparer les analyses biochimiques. Merci à Gaëtan et Gautier pour leurs mesures de traits de vie de centaines d'hermelles et pour la qualité de leurs rapports de stage.

Mes premiers pas dans le monde de la recherche française ont foulé le sol du CRESCO à Dinard, où j'ai eu la chance de nouer des contacts qui perdurent à ce jour. Je remercie Patrick Le Mao d'avoir partagé ses connaissances sur les hermelles du golfe normand-breton, pour son savoir naturaliste, et pour avoir décrypté (avec Nico Desroy), l'écriture de médecin d'Edouard Fischer-Piette dans ses carnets de terrain. Pour sa disponibilité et son partage de sa très grande culture scientifique malgré tous les projets qu'il mène de front, je remercie tout particulièrement Jérôme Fournier.

Je remercie Francis Kerckhof pour des discussions animées sur les *Sabellaria* de la Belgische Kust, et pour avoir déniché des spécimens et références historiques précieuses. Je remercie à nouveau David et Sally pour avoir débusqué au muséum national d'histoire naturelle les carnets de terrain d'Edouard Fischer Piette, et pour avoir partagé de nombreux documents historiques scannés manuellement au Woods Hole Public Library. L'un des temps forts de cette thèse est la rencontre d'Yves Gruet, que je remercie ainsi que Marie-Annick pour de riches et agréables discussions, sur l'estran ou autour d'un tomographe.

Le travail de rédaction s'est effectué en grande partie en condition de télétravail, en raison de l'épidémie mondiale de covid-19. A lui aussi j'adresse mes remerciements : rien de tel qu'une pandémie pour relativiser, pour faire perdre la notion du temps et surtout, pour donner l'envie de travailler en écologie, d'étudier le monde vivant dans son contexte.

Fernando, je te remercie de m'avoir soutenue dans ce projet professionnel sachant bien mieux que moi l'envergure que cela prendrait dans nos vies. Enfin, je souhaite exprimer ici toute ma gratitude à mes parents, pour leur soutien sans faille.

À Francesca.

PUBLICATIONS PRESENTED IN THIS THESIS

1. **Curd, A.**, Pernet, F., Corporeau, C., Delisle, L., Firth, L.B., Nunes, F.L.D., Dubois, S.F., 2019. Connecting organic to mineral: How the physiological state of an ecosystem-engineer is linked to its habitat structure. *Ecological Indicators* 98, 49–60. <https://doi.org/10.1016/j.ecolind.2018.10.044>
2. **Curd, A.**, Boyé, A., Cordier, C., Pernet, F., Firth, L.B., Bush, L., Davies, A.J., Lima, F.P., Meneghesso, C., Quéré, C., Seabra, R., Vasquez, M., Dubois, S.F. An egg-centric perspective into the reproductive trait variability of a foundation species. *Prepared for Ecology*.
3. **Curd, A.**, Vasquez, M., Boyé, A., Bricheno, L.M., Bush, L., Burrows, M.T., Cordier, C., Davies, A.J., Firth, L.B., Green, M., Lima, F.P., Marzloff, M., Meneghesso, C., Seabra R., Dubois, S.F. To the edges and beyond: projecting the biogeographic distribution of an intertidal reef-builder under climate change. *Prepared for Nature Climate Change*.

Contributions to the individual chapters:

	Chapter I	Chapter II	Chapter III
Design & Methods	SFD, FP, CC, FLDN	SFD, LBF	AC , MV, AB, LBF, MM, SFD
Data Collection	SFD, FP, CC, FLDN	AC , CC, LBF, LB, AJD, FPL, CM, RS, SFD*	AC , MV, AB, CC [†]
Data Analyses	FP, AC	AB, AC , FP	MV, AC , AB
Manuscript Preparation	AC , FP, LBF, SFD	AC , AB, LBF, SFD	AC , MV, AB, LBF, MM, SFD

* plus students and colleagues/volunteers.

† plus all contributors to dataset presented below.

DATASET PRESENTED IN THIS THESIS

Curd, A., Cordier, C., Firth, L.B., Bush, L., Gruet, Y., Le Mao, P., Blaze, J.A., Board, C., Bordeyne, F., Burrows, M.T., Cunningham, P.N., Davies, A.J., Desroy N., Edwards H., Harris D.R., Hawkins, S.J., Kerckhof, F., Lima, F.P., McGrath, D., Meneghesso, C., Mieszkowska, N., Nunn, J.D., Nunes, F.L.D., O' Connor, N.E., O' Riordan, R.M., Power, A.M., Seabra, R., Simkanin, C., Dubois, S.F., 2020. A broad-scale long-term dataset of *Sabellaria alveolata* distribution and abundance curated through the REEHAB (REEF HABitat) Project. SEANOE. <https://doi.org/10.17882/72164>

ORAL COMMUNICATIONS

1. **Curd A.**, Dubois S.D., Firth L.B., Davies A.J. and Lima F. Assessment of the Distribution and Ecological Status of *Sabellaria alveolata* reefs in Europe: the REEHAB project. The Plymouth Marine Science and Education Foundation Conference, 9 February 2017, Plymouth, United-Kingdom.
2. **Curd A.**, Firth L.B., Dubois S.D., Davies A.J. and Lima F. Assessment of the shifts in perception and changing distribution of *Sabellaria alveolata* reefs in Europe: the REEHAB project. Oceans Past VI Project, 16-18 May 2017, Sesimbra, Portugal.
3. **Curd A.**, Cordier C., Firth L.B., Bush L., Davies A.J., Lima F., Meneghesso C., Seabra R. and Dubois S.D. Large-scale patterns in the reproductive characteristics of the honeycomb worm *Sabellaria alveolata*, 12th International Temperate Reefs Symposium, 6-11 January 2019, Hong-Kong.
4. **Curd A.**, Vasquez M., Boyé A., Bricheno L.M., Bush L., Cordier C., Davies A.J., Firth L.B., Green M., Lima F., Marzloff M., Meneghesso C., Seabra R and Dubois S.D. Modélisation statistique de la distribution spatiale des récifs intertidaux d'hermelles en Atlantique. Conférence merIGéo, 3ème édition, 17-19 March 2020, Bordeaux, France. *Postponed until November 2020.*

CONTENTS

REMERCIEMENTS	IIII
PUBLICATIONS PRESENTED IN THIS MANUSCRIPT	VII
ORAL COMMUNICATIONS	VII
CONTENTS	VIII
LIST OF TABLES	X
LIST OF FIGURES	XII
LIST OF APPENDICES	XIV
INTRODUCTION	1
HOW LIFE IS DISTRIBUTED	1
THE NICHE: HOW DIFFERENT ASPECTS ARE EXPLORED THROUGH DIFFERENT DISCIPLINES	10
MODEL ORGANISM AND SYSTEM	19
THESIS OUTLINE.....	30
CHAPTER I	33
ARTICLE I - CONNECTING ORGANIC TO MINERAL: HOW THE PHYSIOLOGICAL STATE OF AN ECOSYSTEM-ENGINEER IS LINKED TO ITS HABITAT STRUCTURE	34
1. INTRODUCTION	35
2. MATERIALS AND METHODS.....	42
3. RESULTS.....	50
4. DISCUSSION	55
5. CONCLUSION	62
CHAPTER II	63
ARTICLE II - AN EGG-CENTRIC PERSPECTIVE INTO THE REPRODUCTIVE TRAIT VARIABILITY OF A FOUNDATION SPECIES	64
1. INTRODUCTION	65
2. MATERIALS AND METHODS.....	69
3. RESULTS.....	77
4. DISCUSSION	85
CHAPTER III	91
SECTION III-A	92
A BROAD-SCALE LONG-TERM DATASET OF <i>SABELLARIA ALVEOLATA</i> DISTRIBUTION AND ABUNDANCE CURATED THROUGH THE REEHAB (REEF HABITAT) PROJECT	92
1. INTRODUCTION	93
2. DATA SOURCES	98
3. ABUNDANCE	99
4. TIME SERIES.....	101
5. HISTORICAL ECOLOGY.....	103
6. CONCLUSION	106

SECTION III-B	107
ARTICLE III – TO THE EDGES AND BEYOND: PROJECTING THE BIOGEOGRAPHIC DISTRIBUTION OF AN INTERTIDAL REEF-BUILDER UNDER CLIMATE CHANGE	107
1. INTRODUCTION	108
2. MATERIALS AND METHODS	111
3. RESULTS	120
4. DISCUSSION	128
5. CONCLUSION	136
SECTION III-C	138
SPATIAL SCALE EFFECTS ON SPECIES DISTRIBUTION MODELLING: THE CASE OF THE HONEYCOMB WORM	138
1. INTRODUCTION	138
2. MATERIALS AND METHODS	140
3. RESULTS	142
4. DISCUSSION	146
CONCLUSIONS AND FUTURE WORK	148
KEY CONCLUSIONS: RETURNING TO ORIGINAL QUESTIONS	149
RESEARCH FOR POLICY	153
FUTURE PERSPECTIVES.....	157
MORE MECHANISM.....	157
HYBRID MODELS	159
TOWARDS FUNCTIONAL BIOGEOGRAPHY	160
LOOKING BACKWARDS TO LOOK FORWARDS.....	164
CONCLUDING REMARKS	165
REFERENCES	167
APPENDICES	204

LIST OF TABLES

TABLE 1. THE THREE GENERAL MECHANISMS THROUGH WHICH ORGANISM PHYSIOLOGICAL PERFORMANCE IS INFLUENCED BY ENVIRONMENTAL CONDITIONS..	4
TABLE 2. SUMMARY OVERVIEW OF HYPOTHESES TESTED, DATA TYPES AND ANALYTICAL METHODS APPLIED TO <i>SABELLARIA ALVEOLATA</i> IN THE THREE CHAPTERS.	31
TABLE 3. SUMMARY OF THE SAMPLING DESIGN.	44
TABLE 4. SUMMARY OF THE MIXED ANALYSES OF COVARIANCE (ANCOVA) MODEL USED FOR COMPARING FEMALES. DF = DEGREES OF FREEDOM.....	50
TABLE 5. REEHAB DATASET METADATA	95
TABLE 6. NUMBER OF OCCURRENCES PER COUNTRY AND SACFOR SCALE CATEGORY PRESENT IN REEHAB DATASET.	100
TABLE 7. NUMBER OF OCCURRENCE RECORDS PER TIME PERIOD, RANKED BY COUNTRY.	102
TABLE 8. LIST OF FINAL PREDICTORS INCLUDED IN MODELS AFTER COLLINEARITY CHECKS.	116
TABLE 9. MEAN ACCURACY METRICS (\pm STANDARD DEVIATION) OF MODELS OBTAINED FOR EACH APPROACH, POST-FILTERING MODEL RUNS WITH A TRUE SKILL STATISTIC (TSS) >0.61	118
TABLE 10. PROJECTED DISTANCES SHIFTED, CONVERTED TO DECADAL RATES OF HABITAT SHIFT AND TOTAL DIFFERENCE IN DISTANCE BETWEEN THE PRESENT-DAY ENSEMBLE MODEL OUTPUT AND FUTURE RCP SCENARIOS AND TIME PERIODS.	127
TABLE 11. FINAL PREDICTORS USED IN MODELS AFTER COLLINEARITY CHECKS FOR THE TWO GRAIN SIZES AND EXTENTS.	140
TABLE 12. MEAN ACCURACY METRICS (\pm STANDARD DEVIATION) OF MODELS OBTAINED FOR EACH APPROACH, POST-FILTERING MODEL RUNS WITH A TRUE SKILL STATISTIC (TSS) >0.61 : GENERALIZED ADDITIVE MODEL (GAM), RANDOM FOREST (RF).....	141
TABLE 13. FIELD LOCATIONS AND SAMPLING DATES.	206
TABLE 14. METEOROLOGICAL VARIABLE SOURCES, UNITS AND HORIZONTAL RESOLUTION.....	207
TABLE 15. KEY REPRODUCTIVE, METEOROLOGICAL AND BIOCHEMICAL VARIABLES AND THEIR RELATIONSHIP WITH LINEAR AND QUADRATIC LATITUDE.	211
TABLE 16. DATABASES VIA WHICH 22 OF THE 109 SOURCES WERE ACCESSED.	214
TABLE 17. LIST OF ALL THE SOURCES OF <i>SABELLARIA ALVEOLATA</i> RECORDS COLLATED ACROSS THE NORTHEAST ATLANTIC..	214
TABLE 18. ENVIRONMENTAL PREDICTORS USED FOR MODELLING THE DISTRIBUTION OF <i>SABELLARIA ALVEOLATA</i>	222
TABLE 19. DESCRIPTION OF MODELLING METHODS USED IN THE STUDY.....	226
TABLE 20. CORRESPONDENCE BETWEEN TRUE ABSENCES AND PROBABILITY OF PRESENCE FOR THE VALIDATION DATASET FOR THE ~ 3 KM SPATIAL RESOLUTION MODEL.	228
TABLE 21. CORRESPONDENCE BETWEEN TRUE ABSENCES AND PROBABILITY OF PRESENCE FOR THE VALIDATION DATASET FOR THE 10-12KM SPATIAL RESOLUTION MODEL.	228

LIST OF FIGURES

FIGURE 1. THE ‘BAM DIAGRAM’, SHOWING A SIMPLIFIED FRAMEWORK FOR UNDERSTANDING WHERE SPECIES WILL AND WILL NOT BE DISTRIBUTED.....	3
FIGURE 2. THEORETICAL DIAGRAM SUMMARISING THE DIFFERENT TYPES OF RESPONSES EXPLAINED BY THE MACROECOLOGICAL THEORY ON THE ARRANGEMENT OF LIFE (METAL) FROM THE SPECIES LEVEL TO THE COMMUNITY AND ECOSYSTEM LEVELS..	5
FIGURE 3. EXAMPLE OF THE RELATIONSHIP BETWEEN RESPONSE AND EFFECT TRAITS.	13
FIGURE 4. DIAGRAM OF THE FOUR BASIC TYPES OF ZONATION.	16
FIGURE 5. TRENDS IN THE NUMBER OF MARINE (TURQUOISE LINE) AND TERRESTRIAL (YELLOW LINE) PUBLICATIONS.....	17
FIGURE 6. A OCCURRENCE LOCALITIES FOR THE SCLERACTINIAN CORAL <i>ACROPORA PALMATA</i> ; B THREE-DIMENSIONAL MODEL OF THE ECOLOGICAL NICHE OF <i>A. PALMATA</i> , C GEOGRAPHIC PROJECTION OF <i>A. PALMATA</i> ’S NICHE MODEL AND CORRESPONDING SUITABILITY VALUES.	18
FIGURE 7. A: A <i>SABELLARIA ALVEOLATA</i> INDIVIDUAL. B: A CLOSE-UP OF <i>S. ALVEOLATA</i> ’S TENTACULAR FILAMENTS. C: A CLOSE-UP OF THE BIOCONSTRUCTION, SHOWING THE AGGREGATION OF INDIVIDUAL TUBES. D: ZOOMING OUT FROM THE BIOCONSTRUCTION, THE HIGH DENSITY OF INDIVIDUALS AND PRESENCE OF EPIBIONTS (RHODOPHYTES AND TROCHIDAE) CAN BE SEEN. E: REEF PLATFORMS IN THE MONT-SAINT-MICHEL BAY SHOWING A HEIGHT OF ~1.6M. F: VERY WELL-DEVELOPED HUMMOCKS AND PLATFORMS IN THE MONT-SAINT-MICHEL BAY.	20
FIGURE 8. PHOTO PANEL ILLUSTRATING THE DIVERSITY OF <i>S. ALVEOLATA</i> BIOGENIC STRUCTURES ACROSS ATLANTIC EUROPE.....	21
FIGURE 9. AN ILLUSTRATION FROM CHENU (1842) OF <i>SABELLARIA SPP.</i> BIOGENIC REEFS.	24
FIGURE 10. LEFT SIDE-VIEW OF <i>SABELLARIA ALVEOLATA</i> ANTERIOR REGION.....	25
FIGURE 11. DIAGRAM SUMMARISING KEY <i>S. ALVEOLATA</i> RESEARCH PAPERS AND TOPICS.	27
FIGURE 12. CONCEPTUAL DIAGRAM OF A) THE DIFFERENT BIOCONSTRUCTION TYPES OF <i>S. ALVEOLATA</i> . PROGRADATION AND RETROGRADATION, AS DEFINED IN B), ARE REPRESENTED BY FULL VERSUS HATCHED ARROWS RESPECTIVELY.	38
FIGURE 13. MAP OF THE STUDY SITE WITH THE TWELVE SAMPLING POINTS. V=VENEER, HR= RETRGRADING HUMMOCK, HPHS=PROGRADING HUMMOCK HIGH SHORE, HPLS=PROGRADING HUMMOCK LOW SHORE.	43
FIGURE 14. ORGANIC MACROMOLECULES AS A FUNCTION OF BIOCONSTRUCTION TYPE, BIOCONSTRUCTION PHASE AND SHORE LEVEL (A-C, N=59), WORM MASS (D-F, N=59) AND SEX (G-I N=8 (5 FEMALE, 3 MALE)).....	51
FIGURE 15. POLAR LIPIDS AS A FUNCTION OF BIOCONSTRUCTION TYPE, BIOCONSTRUCTION PHASE AND SHORE LEVEL (A-D, N=59), WORM MASS (E-H, N=59) AND SEX (I-L, N=8 (5 FEMALE, 3 MALE))..	52
FIGURE 16. NEUTRAL LIPIDS AS A FUNCTION OF BIOCONSTRUCTION TYPE, BIOCONSTRUCTION PHASE AND SHORE LEVEL (A-F, N=59), WORM MASS (G-K, N=59) AND SEX (M-R, N=8 (5 FEMALE, 3 MALE)).....	53

FIGURE 17. ENZYME LEVELS AS A FUNCTION OF BIOCONSTRUCTION TYPE, BIOCONSTRUCTION PHASE AND SHORE LEVEL (A-C, N=59), WORM MASS (D-F, N=59) AND SEX (G-I, N=8 (5 FEMALE, 3 MALE))..	55
FIGURE 18. SAMPLING SITES AND BARPLOTS OF KEY REPRODUCTIVE AND BIOCHEMICAL <i>S. ALVEOLATA</i> TRAITS VS. LATITUDE MEASURED OVER SUMMER AND WINTER.	71
FIGURE 19. GRAPHICAL RESULTS OF THE CO-INERTIA ANALYSIS OF THE REPRODUCTIVE AND BIOCHEMICAL VARIABLES FOR WINTER 2018.	78
FIGURE 20. RDA VARIANCE PARTITIONING OF EGG SIZE AND RELATIVE FECUNDITY DURING WINTER AMONG METEOROLOGICAL, BIOCHEMICAL AND LATITUDE PREDICTOR GROUPS.	80
FIGURE 21. (FOLLOWING PAGE) REDUNDANCY ANALYSIS (RDA) OF SELECTED CENTRED AND STANDARDIZED REPRODUCTIVE TRAITS (DISPLAYED AS RED VECTORS IN THE RIGHT-HAND PANEL B; SCALING 2) CONSTRAINED BY SELECTED STANDARDIZED METEOROLOGICAL VARIABLES (DISPLAYED AS BLACK VECTORS PANEL B; SCALING 2). THE LEFT-HAND PANEL A SHOWS THE CENTROID SCORES FOR EACH SAMPLING SITE AND SEASON, LINKED TO EACH INDIVIDUAL (SCALING 1).	80
FIGURE 22. (FOLLOWING PAGE) REGRESSION COEFFICIENT PLOTS FOR THE BEST LINEAR REGRESSION MODELS, AS DETERMINED BY AIC COMPARISONS, FOR TOTAL EGG DIAMETER AND RELATIVE FECUNDITY IN SUMMER 2017 AND WINTER 2018.	83
FIGURE 23. DONUT PLOT ILLUSTRATING THE RELATIVE CONTRIBUTION OF DIFFERENT TYPES OF SOURCES TO THE 21,571 RECORDS COLLECTED, DIVIDED AMONGST 331 DIFFERENT SOURCES.	99
FIGURE 24. <i>SABELLARIA ALVEOLATA</i> RECORDS IN REEHAB DATASET PROJECTED ONTO A 50KM GRID. THE INSET MAP IN THE TOP-RIGHT CORNER IS A VIEW OF THE GEOREFERENCED RECORDS HELD IN GBIF (ACCESSED ON 28-05-2020).	101
FIGURE 25. THE OLDEST EUROPEAN RECORD IN THE DATASET - <i>SABELLA ALVEOLATA</i> LINNAEUS, 1767 (SUPERSEDED ORIGINAL COMBINATION). FROM DE GERVILLE, 1825.	103
FIGURE 26. AN ENGRAVING FROM THE MUSÉE D’HISTOIRE DE MARSEILLE DEPICTING THE BAITS MARKET THAT WAS HELD ON THE ‘QUAI AUX HUILES’ IN THE OLD PORT IN MARSEILLE EVERY SATURDAY EVENING.	104
FIGURE 27. EXTRACT FROM GOURRET (1894) WITH DRAWINGS AND QUANTIFICATION OF THE QUANTITY OF ‘HERMELLES’ EXTRACTED.	105
FIGURE 28. VARIABLE IMPORTANCE SCORES FOR THE MODEL, FOR THE TWO MODELLING APPROACHES USED (GAM - GENERALIZED ADDITIVE MODELS AND RF - RANDOM FORESTS) RANKED ACCORDING TO THE IMPROVEMENT IN AUC (AREA UNDER THE RECEIVER OPERATING CHARACTERISTIC CURVE) RESULTING FROM THE INCLUSION OF THE VARIABLE IN THE MODELS	120
FIGURE 29. VARIABLE RESPONSE CURVES FOR THE WEIGHTED MEAN ENSEMBLE MODELS. VARIABLES ARE ARRANGED IN ORDER OF IMPORTANCE (SEE FIG. 28).	121
FIGURE 30. WEIGHTED MEAN ENSEMBLE PREDICTIONS FOR HABITAT SUITABILITY ACROSS OUR STUDY AREA.	123
FIGURE 31. (PREVIOUS PAGE). PREDICTED SHIFTS IN HABITAT SUITABILITY, OBTAINED FROM OVERLAYING THE BINARY PRESENCE-ABSENCE PREDICTIONS OF THE WEIGHTED MEAN ENSEMBLE MODEL FOR THE PRESENT PERIOD WITH PREDICTED BINARY DISTRIBUTIONS IN THE 2040S AND 2090S UNDER RCP 4.5 AND 8.5.	126

FIGURE 32. VARIABLE IMPORTANCE SCORES FOR THE TWO DIFFERENT GRAINS AND EXTENTS, FOR THE TWO MODELLING APPROACHES USED (GENERALIZED ADDITIVE MODELS, GAM, AND RANDOM FORESTS, RF) RANKED ACCORDING TO THE IMPROVEMENT IN AUC (AREA UNDER THE RECEIVER OPERATING CHARACTERISTIC CURVE) RESULTING FROM THEIR INCLUSION IN THE MODELS.....	143
FIGURE 33. VARIABLE RESPONSE CURVES FOR THE WEIGHTED MEAN ENSEMBLE MODELS AT ~3KM AND 10-12KM GRAIN SIZE, RANKED IN ORDER OF IMPORTANCE OF THE ~3KM GRAIN SIZE AND 24° LATITUDE EXTENT MODEL (FIG. 32).....	145
FIGURE 34. WEIGHTED MEAN ENSEMBLE PREDICTIONS FOR THE A) 10-12KM GRAIN LARGER EXTENT B) ~3KM GRAIN SMALLER EXTENT AND C) THE DIFFERENCE IN PREDICTED HABITAT SUITABILITY BETWEEN THE TWO.....	146
FIGURE 35. AN INTEGRATED SCIENCE OF FUNCTIONAL BIOGEOGRAPHY WILL DRAW FROM MULTIPLE SOURCES AND APPROACHES.....	156
FIGURE 36. FUNCTIONAL BIOGEOGRAPHY: AN EMERGENT FIELD AT THE CROSSROADS OF SEVERAL SCIENCE FIELDS.	162
FIGURE 37. PRINCIPAL COMPONENT ANALYSIS (PCA) BIPLLOT OF 52 FEMALE <i>SABELLARIA ALVEOLATA</i> INDIVIDUALS AND 26 BIOCHEMICAL VARIABLES.	205
FIGURE 38. CORRELATIONS BETWEEN THE <i>IN-SITU</i> TEMPERATURE LOGGERS AND THE METEOROLOGICAL MODELS OVER THE 30-DAY PERIOD PRIOR TO SAMPLING, FOR ALL REEHAB PROJECT SAMPLING DATES (2016-2018 SUMMER AND WINTER, WINTER 2019)..	208
FIGURE 39. BOXPLOTS OF VARIANCE COMPONENT ANALYSES ACROSS TWO NESTED SCALES ON 1000 RESAMPLING OF 5 INDIVIDUALS PER SITE FOR A) SUMMER TOTAL EGG DIAMETER B) WINTER TOTAL EGG DIAMETER C) SUMMER RELATIVE FECUNDITY AND D) WINTER RELATIVE FECUNDITY.....	209
FIGURE 40. SCREENSHOT OF THE 2274 GEOREFERENCED RECORDS FOR ' <i>SABELLARIA ALVEOLATA</i> ' HELD IN THE GLOBAL BIODIVERSITY INFORMATION FACILITY (GBIF - ACCESSED 12-03-2020).	212
FIGURE 41. MAPS ILLUSTRATING THE DISTRIBUTION AND DENSITY OF THE 19354 COLLATED <i>SABELLARIA ALVEOLATA</i> RECORDS ALONG THE NORTH-EAST ATLANTIC COAST	213
FIGURE 42. INTERNATIONAL PANEL ON CLIMATE CHANGE (IPCC) REPRESENTATIVE CONCENTRATION PATHWAYS (RCP).....	225
FIGURE 43. BINARY MAPS OF PRESENT-DAY PRESENCE ABSENCE FOR BOTH MODEL SCALES.....	227
FIGURE 44. MAPS ILLUSTRATING THE LOCATION OF ABSENCE RECORDS, COLOUR-CODED ACCORDING TO THE HABITAT SUITABILITY INDEX THRESHOLD OF 0.8.....	229

LIST OF APPENDICES

APPENDIX 1 CHAPTER I SUPPLEMENTARY MATERIAL	205
APPENDIX 2 CHAPTER II SUPPLEMENTARY MATERIAL	206
APPENDIX 3 GBIF AND PRESENT STUDY OCCURRENCE RECORDS	212
APPENDIX 4 SUMMARY OF THE OBSERVATION RECORDS USED FOR THIS STUDY.	214
APPENDIX 5 PREDICTOR VARIABLES	222
APPENDIX 6 IPCC MODELS RCP SCENARIOS	225
APPENDIX 7 MODELLING METHODS USED.....	226
APPENDIX 8 BINARY MAPS OF PRESENT-DAY PRESENCE/ABSENCE	227
APPENDIX 9 MODEL EVALUATION THROUGH INDEPENDENT TRUE ABSENCE RECORDS ...	228

INTRODUCTION

How life is distributed

Why do species live where they live? What determines their abundance in a given area? What role do species play in the functioning of entire ecosystems? All of these questions can be rolled into one: what defines a species ecological position in the world? The answer lies within a core ecological concept: the niche, which can be defined as the combination of environmental factors, together with the effects a species exerts on them (Peterson et al., 2011).

After presenting how the environment, and biological responses to the environment, shape species' distributions, the second part of this introduction will detail niche theory and the different uses of niche thinking that are explored in the following chapters. The third part of this introduction will present the model species and study system used to explore the niche concept: the intertidal reef-forming honeycomb worm *Sabellaria alveolata* (Linnaeus, 1767) in Atlantic Europe and North Africa, before finally presenting the thesis outline and objectives.

1. The geographic distribution of species

Each species has a unique geographic range, which is shaped by the biotic and abiotic conditions it needs for its survival. Species' ranges can be conceived of as a consequence of three factors: (i) the presence of environmental (abiotic) conditions under which the species can establish, survive and reproduce; (ii) the biotic environment determined by the presence of species interactions such as competition or predation in which species can persist, and (iii) the area that is accessible to species via its movement or dispersal capabilities. These restrictions have been captured in the so-called BAM (Biotic-Abiotic-Movement) diagram (

Figure 1, modified from Soberón and Peterson, 2005), which provides a simplified framework for understanding where species will or will not be distributed.

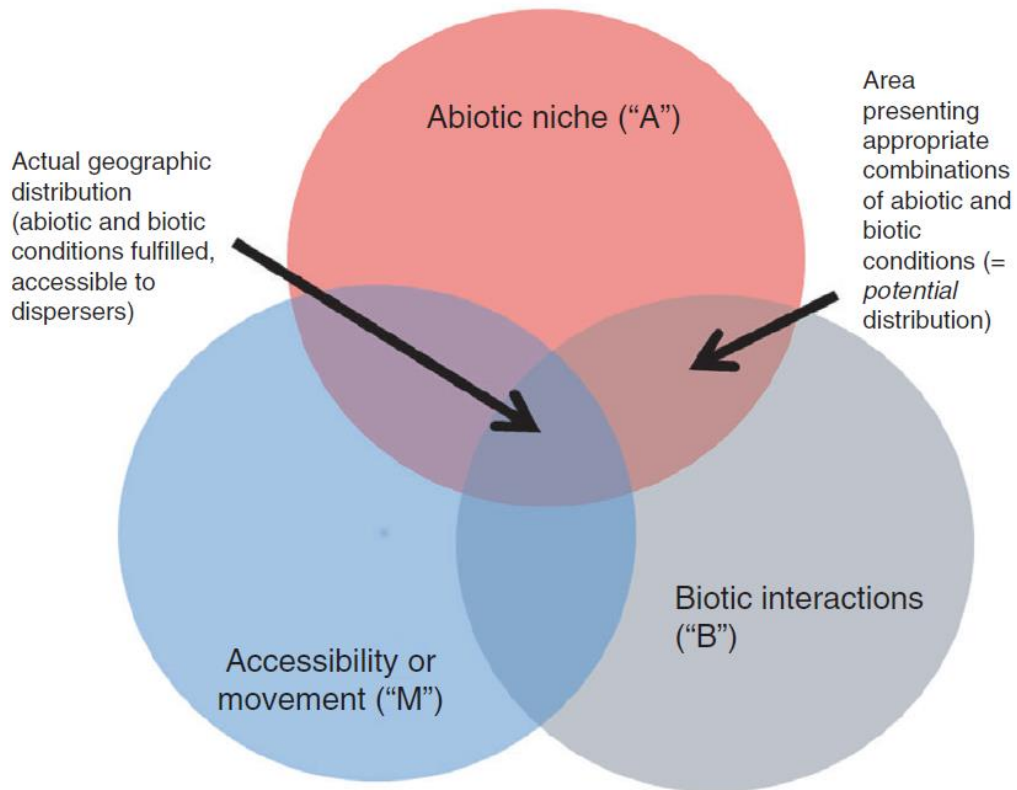


Figure 1. (Previous page) The ‘BAM diagram’, showing a simplified framework for understanding where species will and will not be distributed. Distributions of species are seen as responding to three sets of factors: the abiotic environment (A) and the biotic conditions (B), which roughly correspond to Hutchinson’s fundamental ecological niche (A) and the realised ecological niche ($A \cap B$, here termed the potential distribution). A further modification to distributional potential, however, is that of access (here ‘M’ for movement), which constrains species distribution quite dramatically. From Soberón and Peterson, 2005.

Species’ range limits are not however simply set by unsuitable or inaccessible abiotic and biotic conditions at their range margins. To appreciate how climatic variability affects species’ distributions, we need a clear idea of the processes that shape living systems, founded both in biogeography and macroecology. As multiple meanings exist for both terms, biogeography is defined here as the study of the distribution of species and ecosystems across space and time, and of the underlying biotic and abiotic factors, mechanisms and processes (Violle et al., 2014). Macroecology is the study of relationships between organisms and their environment at the aggregate level of aggregate ecological entities made up of large numbers of particles, that

involves characterising and explaining statistical patterns of abundance, distribution and diversity for the purposes of pursuing generality (Blackburn and Gaston, 2002; McGill, 2018).

2. Mechanisms affecting distribution

Over time, species can potentially adapt to changing environmental conditions and to different sets of co-occurring species (e.g. Davis, 2001). To explain large-scale biogeographic patterns, we also need to explain why species do not simply adapt to the ecological conditions at the margins of their geographic ranges and continue expanding their area of distribution (Wiens, 2011). Environmental conditions influence organismal physiology through three general mechanisms (Table 1). When environmental conditions cannot be overcome by physiological adjustments such as acclimatisation or phenotypic plasticity, it eventually leads to the local extirpation of a species (Beaugrand and Kirby 2018). Changes to population abundance resulting from the positive and negative effect of the local environment can later alter a species' spatial distribution. The sum of all local effects on population abundance, which eventually leads to local extirpation or appearance, can be perceived at a macroecological scale as a biogeographic shift.

Table 1. The three general mechanisms through which organism physiological performance is influenced by environmental conditions. Adapted from Helmuth et al. 2005.

Genetic Adaptation	Phenotypic Plasticity	Acclimatisation
<i>A change in allele frequencies in a population via natural selection</i>	<i>Variable expression of genetic or biochemical traits</i>	<i>A short-term compensatory modification of physiological function and tolerance</i>
<ul style="list-style-type: none"> • Slow (>1 generation) • Irreversible 	<ul style="list-style-type: none"> • Relatively brief (<1 generation) • Reversible or irreversible 	<ul style="list-style-type: none"> • Fast (seconds to days) • Reversible

➡ Environmental conditions exceed ability of some individuals to cope

➡ Small environmental changes

Species range unchanged, but alleles may vary

Species range unchanged

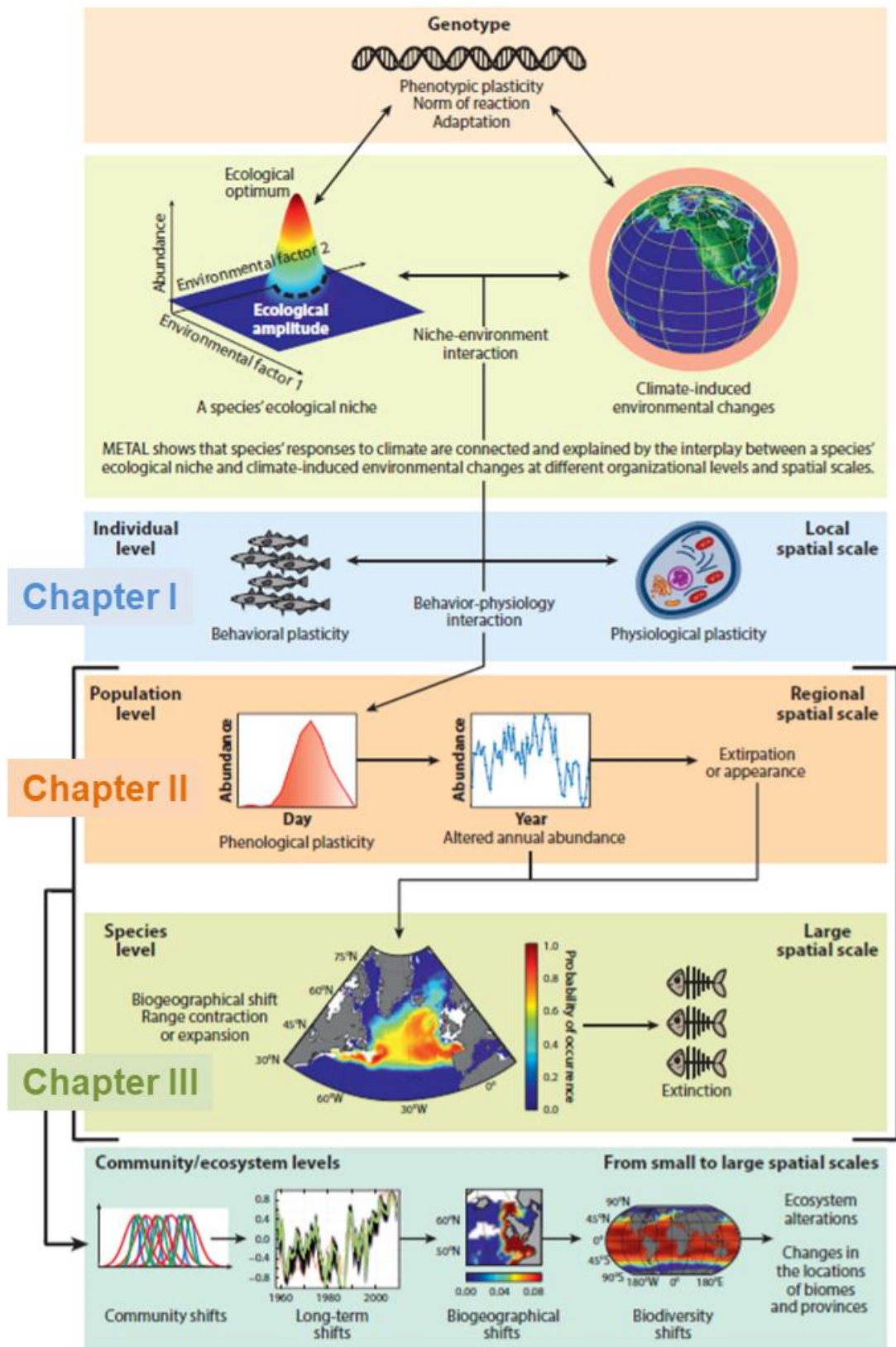
Note If environmental conditions are sufficiently severe, all organisms in the population will die or emigrate and the species range will shift.

In extreme cases, when range contraction is complete, extinction eventually occurs. Adaptation is a modification in the genotype that enables a species to functionally adapt to its environment, which ultimately modifies its ecological niche and can enable a species to avoid global extinction. Adaptation may be impossible if the magnitude and speed at which environmental conditions change is too great; whilst the species' range remains unchanged, in effect the shape of its ecological niche is altered, and so is therefore the interaction between the organism and its environment (Beaugrand and Kirby, 2018). Niche conservatism, which is simply the idea that species will retain similar ecological traits and environmental distribution over time (see Wiens et al., 2010 for a review), means that in effect species rarely change biomes (Crisp et al., 2009).

This summary of how changing environmental conditions alter biological arrangements in space and time at different organisational levels (e.g. species, community, ecosystem) has been formalised, for the marine environment, by the MacroEcological Theory on the Arrangement of Life (METAL) (Beaugrand, 2015). METAL propose a hierarchical sequence of responses of species to environmental changes that involve, in the following order: behaviour, physiology, annual abundance, biogeographical shifts, extinction and adaptation (Figure 2). The biological organisational levels and scales analysed in the following chapters are highlighted.

Figure 2. Theoretical diagram summarising the different types of responses explained by the macroecological theory on the arrangement of life (METAL) from the species level to the community and ecosystem levels. METAL connects and explains climate-induced behavioural, physiological, and phenological shifts, as well as changes in annual average abundance, local extirpation and appearance,

biogeographical shifts, range expansion and contraction, and extinction. Note that the norm of reaction is included in the ecological amplitude of the niche, whereas adaptation modifies the shape of the niche. How the different chapters of the thesis assess different aspects of the niche are described in more detail in the final part of the introduction. From Beaugrand and Kirby (2018).



3. Climate change in the marginal world

The shore has a dual nature, changing with the swing of the tides, belonging now to the land, now to the sea. On the ebb tide it knows the harsh extremes of the land world, being exposed to heat and cold, to wind, to rain and drying sun. On the flood tide it is a water world, returning briefly to the relative stability of the open sea.
(Carson, 1955, p.1).

Rachel Carson is best known for 'Silent Spring', but she was profoundly concerned about the environment as a whole, and her deepest passion was for the sea. The above quote are the opening sentences to her work 'The Edge of the Sea', which eloquently summarises how the intertidal zone exists at the margins of both the terrestrial and marine realms. The organisms in this ecosystem are subject to mutable environmental challenges posed by both aquatic and aerial climatic regimes (Helmuth et al., 2006).

The world is changing rapidly, because of the cascading and intertwined effects of human population growth, economic globalization, land-use change, and, looming over it all, climate change (Wiens et al., 2009). These changes are having profound effects on the living world that will only become more dramatic and dire as the pace of environmental change quickens. With 40% of the world's population living within 100km of the coast (Lane et al., 2015), the coastal zone is at centre-stage. Rising concentrations of heat-trapping gases have led to an energy imbalance in the Earth's climate system. The oceans, and in particular their surface waters, are the main repository of this energy imbalance (Cheng et al., 2019). Climate change may have different outcomes depending on the physiological tolerances and responses of the species or populations in question (Table 1). Species can respond by adapting or acclimatising to changing conditions in place (proximate responses, *sensu* Harley et al., 2006), through distribution shifts to follow changing environments (emergent responses, *sensu* Harley et al., 2006), or, if unable to do either, by becoming extinct (Wiens et al., 2009).

Niche concepts and theory are central in efforts to understand how future climate change will impact species and habitats. Ecological niches underpin range limits, and range limits underpin biogeographical patterns. Rocky coastlines have long been valuable arenas in which to test ecological theories concerning fundamental and realised niches because, across a small spatial scale between the high and low tide lines, abiotic factors vary dramatically (Ricketts et al. 1985). The fascination and relative accessibility of rocky intertidal habitats has led to them being among the most-intensively experimentally studied ecosystems globally (i.e. Connell, 1961; Paine, 1974 – see Hawkins et al., 2016 for an overview), providing experimental evidence for realised and fundamental niches. Connell's (1961) classic work on the barnacle (*Chthamalus stellatus*) in the intertidal zone in Scotland shows how the realised niche of this species is explained by a combination of biotic (predation and competition) and abiotic factors (desiccation). However, the pattern of distribution in question is a vertical distribution of a few metres on an island coastline, and it is not clear if these same factors would explain broad-scale biogeographic distributions.

The effects of temperature at the level of individual intertidal organisms are reasonably well understood, however we now know temperature is only one of a suite of potentially interacting climatic variables (ocean circulation, pH, UV radiation) that will drive future ecological change in intertidal systems (Harley et al., 2006). Range shifts across wide spatial scales are a key way in which marine species cope with climate change (Pinsky et al., 2020). Evidence for changes in the latitudinal location of one or more range limits has been recorded for many intertidal organisms (summarised in Helmuth et al., 2006 and Hawkins et al., 2019). The general pattern has been a poleward shift in 'leading' range edges to higher latitudes and cooler environmental temperature regimes and a contraction of the 'trailing' equatorward range edge away from warming temperatures (Firth et al., 2016). In Britain and Ireland, there have been fewer retractions in the trailing range limits of boreal species compared to expansions of southern species (Hawkins et al., 2009; Burrows et al., 2011). Many of these were reported by the Marine Biological Association of the UK MarClim project, which has documented range shifts for a wide range of rocky

intertidal invertebrates and macroalgae (Hawkins et al. 2008, 2009; Mieszkowska et al. 2014). The leading range edges of southern gastropods (*Patella depressa*, *Phorcus lineatus*, and *Steromphala umbilicalis*), barnacles (*Chthamalus stellatus*, *C. montagui*, and *Perforatus perforatus*), and kelp (*Laminaria ochroleuca*) have shifted northward around the Atlantic coastline and north-east along the English Channel coastline (Herbert et al. 2003, Mieszkowska et al. 2006, 2007, Smale et al. 2014, Yesson et al. 2015). Outside Britain and Ireland, evidence of shifts in distribution is mostly limited to recent decades, stemming from the growing awareness of the need for broad-scale long-term datasets to track and predict impacts of global environmental change (Firth et al., 2016). Similar shifts in distribution patterns have been observed in Portugal and Spain, with advances of southern species and retreat of boreal species (Lima et al., 2006, 2007). For instance, survey data indicates that the southern range boundary of the intertidal boreal barnacle *Semibalanus balanoides* has retracted poleward by 300 km along the coast of France and north-west Spain since 1872 (Wetthey et al., 2011).

The niche: how different aspects are explored through different disciplines

1. A short history of niche theory

A species' ecological position in the world has only been referred to as its niche for the past 100 years. References to concepts similar to the ecological niche can be found in the writings of Darwin and Wallace (Vandermeer, 1972), however Joseph Grinnell was the first to use the term 'ecological or environmental niche' in 1924, to describe the ultimate distributional unit of a 'species or subspecies'. A near-concurrent and independent definition of the niche was developed by Charles Elton in 1927. His 'functional niche' referred to the role of a species in a system and is often linked to the species position in the food web. In 1935, in what is perhaps the only specific law of nature to be proposed in ecology (Lawton, 1999), Georgii Gause formulated the competitive exclusion principle, which states that "no two species can occupy the same ecological niche". It was not until the end of the 1950s that G. Evelyn Hutchinson revolutionised niche theory, by developing the formal notion of

the ecological niche as a hypervolume in which each dimension represents a resource (e.g. food, material, space) or an environmental condition (e.g. temperature, humidity, pH).

The Hutchinsonian niche (Hutchinson, 1957; Holt, 2009), a cornerstone of ecology, evolution and biodiversity research, has shaped how ecologists have viewed species' distributions for decades (Palmer, 2016). Hutchinson then further refined his definition to differentiate between the fundamental niche, the range of environmental conditions a species is physiologically able to tolerate, and the realised niche, the subset of the fundamental niche actually occupied as a result of biotic interactions (Miller, 2010). These roughly correspond to parts A (fundamental niche) and parts $A \cap B$ respectively in the BAM diagram in

Figure 1. Thus the fundamental niche is determined by intrinsic properties of a species (how it responds to the environment through its physiology and behaviour) rather than by extrinsic properties of the environment independent of the species (Wiens et al., 2009), and can be obtained independently of the localities where a species is observed (Peterson et al., 2011).

The foundations for thinking about ecological niches were laid at a time when the world seemed a lot more stable, and were used at much smaller scales than the ones they are applied to now (Pinsky et al., 2020). The beginning of the 21st century marked an upsurge of interest in species niches, driven in part by the urgency of predicting ecological responses to rapid environmental change (Holt, 2009). A range of techniques are now available to assess different aspects of the niche, from the individual to the ecosystems level. The following section gives some further background on the approaches used in the following chapters, namely physiological studies at the individual level at local and regional scales, followed by a correlative modelling study at the species level across a large spatial scale.

2. Physiological traits

In order to fully grasp what allows a species to be present in a given geographic region or biotic community, it is necessary to understand when and where organisms are living at the limits of their fundamental niche (i.e. are limited by some aspect of physiological tolerance), in contrast to when their patterns of distribution are representative of realised niche space (i.e. species boundaries are affected by biotic interactions such as the presence of predators, competitors and facilitators) (Hutchins 1947; Helmuth et al., 2006).

Understanding the causes and consequences of variation in life history characteristics or traits are of great value in understanding the dynamics of an ecosystem. Functional traits are measurable features of an organism that affect fundamental processes of growth, reproduction and survival (Violle et al., 2007). Response traits are those which show a consistent response to a particular environmental factor, while effect traits are those which impact on one or several ecosystem functions (see Lavorel and Garnier 2002 and references therein). Figure 3 gives an example of response (e.g. biomass) and effect traits (e.g. stem density) in marsh plants, namely two *Scirpus* species viewed as autogenic engineers in estuarine tidal marshes (Heuner et al., 2015).

(Treurnicht et al., 2019). It has been suggested that species with high trait variation could occupy more diverse environments, have more continuity in their distributions, and consequently have larger range sizes (Violle and Jiang, 2009). In practice, geographical information on ITV is rarely available and has seldom been tested outside the field of plant ecology (Chacón-Madrigal et al., 2018).

2.1 Biochemical traits

Cells are the basic building blocks of all organisms. The core biochemical constituents of all organisms – enzymatic and structural proteins, nucleic acids, and phospholipid structures such as cellular membranes – and the interactions among them are susceptible to direct perturbation from several environmental factors such as temperature, radiation and water availability. Taking a somewhat reductionist view, a living organism and its functions can therefore be seen as the sum of chemical reactions between these biochemical constituents, the kinetics of which are governed by environmental conditions, predominantly temperature.

Each of the above essential biochemical constituents of cells must retain a delicate balance between stability and instability in order to maintain its functional properties (Hochachka and Somero, 2002). Biochemical traits are therefore key components of synthetic or metabolic biochemical pathways that are directly or indirectly linked to processes important for survival or reproduction (Dahlhoff, 2004). They give organisms the ability to persist in the face of novel conditions through phenotypic plasticity, which can be accomplished in many ways, including by a change in enzyme activity, homeoviscous adaptation (a process where cell membranes lipid composition is remodelled to maintain adequate membrane fluidity), or the synthesis of new cryoprotective molecules (Beaugrand and Kirby, 2018). Many coastal marine organisms are capable of phenotypic plasticity, resulting from and measured via underlying biochemical processes, which buffer individuals against environmental conditions that would otherwise be suboptimal (Dahlhoff and Somero 1993; Stillman and Tagmount 2009).

Biochemical traits in marine invertebrates have essentially been studied in farmed species, to assess environmental, trophic and defence dimensions (e.g. Soudant et al., 1998; Pernet et al., 2007) under aquaculture conditions. Few studies have focused on rocky intertidal communities (reviewed in Sanders, 1993; Dahlhoff 2004), and have for example shown the production of heat shock proteins occurs after exposure to temperatures experienced during low tide in mussels (Hofmann and Somero, 1996) and limpets (Dong et al., 2008), putting forward that the production of these proteins incurs some metabolic costs. A handful of studies have used heat shock proteins (e.g. Lima et al., 2016) to assess intertidal organism performance over biogeographic ranges. Using common garden experiments, geographic variation in the thermal tolerance of coastal marine invertebrates has, on rare occasions, been assessed using lipid remodelling (Muir et al., 2016) or enzyme activity (Morley et al., 2009).

2.2 Reproductive traits

Amongst the most informative functional response traits involved in distributional range-shift processes are those involved in the establishment of self-sustaining populations (i.e. the ability of dispersing individuals to reproduce and found new populations following a dispersal event) (Estrada et al., 2016). Reproductive traits therefore play an important role in species dispersal ability and the capacity to evade climate change.

In discussing the bases for temperature zonation in geographical distribution in the sea, Hutchins (1947) gave a mechanistic focus by emphasizing the important role of reproduction and recruitment (termed repopulation) in setting distributions. Species were grouped into four types of zonation: (a) poleward and equatorward limits set by inability to survive; (b) poleward and equatorward limits set by inability to repopulate; (c) heat stress (summer temperatures) setting limits both by reducing survival at equatorial margins and repopulation at poleward margins; and (d) cold stress (winter temperatures) setting limits by reducing survival at poleward margins and repopulation at equatorial margins (Figure 4). Relic populations are occasionally found beyond range limits when a year class has survived a period

of less-extreme climate, but these populations quickly become extinct when exposed to conditions that are too extreme for repopulation or survival (Helmuth et al., 2006).

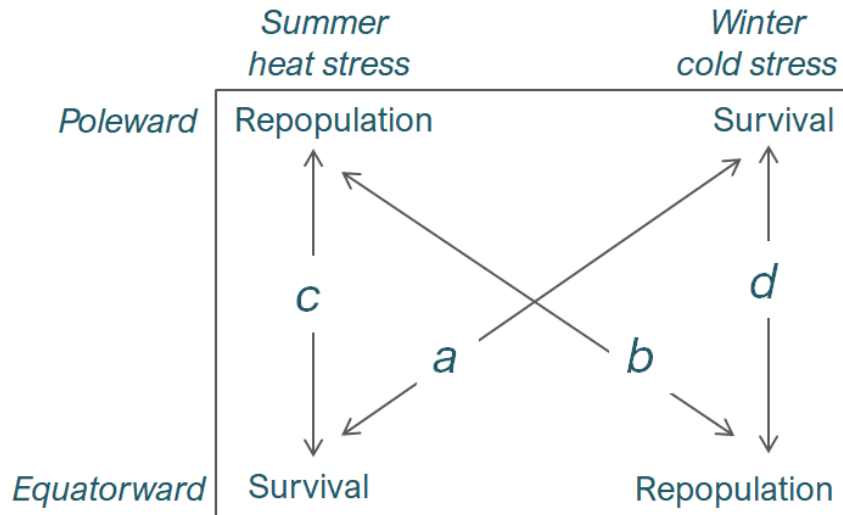


Figure 4. Diagram of the four basic types of zonation. Reprinted from Hutchinson (1947).

A more recent extension of this theory is that population abundances are expected to be highest near the centre of the species distribution, where levels of physiological stress are assumed to be lowest, and then to decrease toward the range margins (Brown, 1984). This became known as the abundant-centre hypothesis; if environmental variables tend to be spatially correlated, population abundance should be approximated by a normal distribution, with abundance declining smoothly from the range centre towards the margins (Sanford, 2014). Brown (1984) argued that a species should be most abundant at the centre of its geographic range because that is where biotic and abiotic variables are ideal for individual fitness. The multidimensional niche (Hutchinson, 1957) therefore also forms the basis for biogeographic thinking about range-wide patterns of individual performance metrics such as reproductive output (Lester et al., 2007).

3. Species distribution models

It is worth emphasizing here that the niche concept describes the distribution of a species in environmental space. Correlative species distribution models (SDMs), which estimate the ecological requirements of species by relating their known geographic distribution to a set of environmental variables, are being increasingly used (Figure 5). SDMs were first applied in the terrestrial domain. By comparison, application of SDMs to marine species is rare, although interest in their application is increasing (Robinson et al., 2011; Melo-Merino et al., 2020).

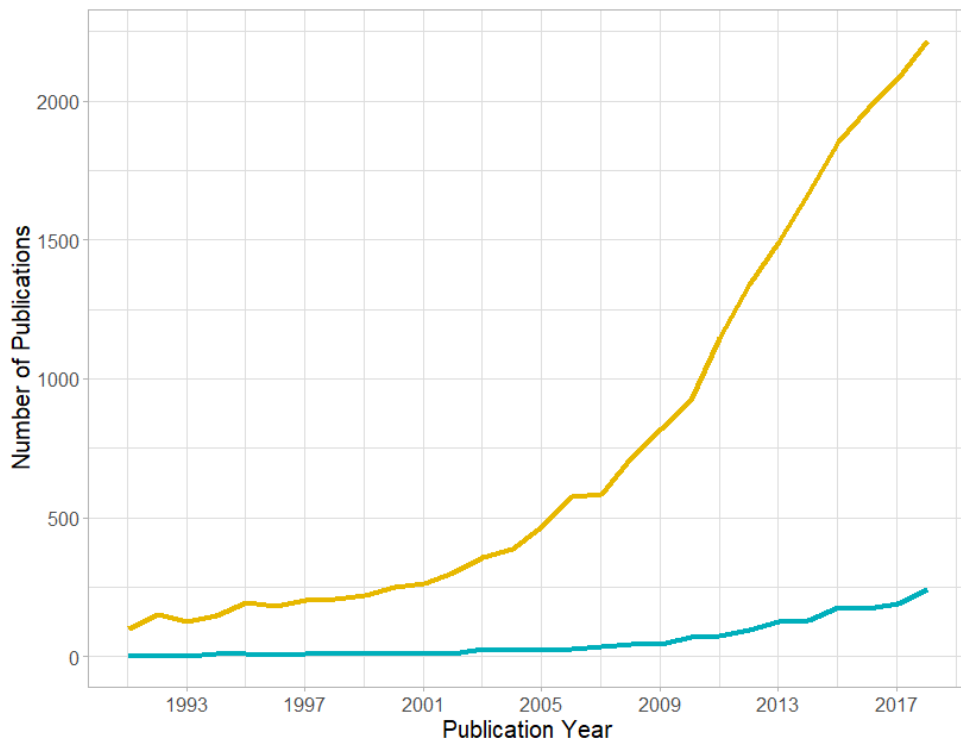


Figure 5. Trends in the number of marine (turquoise line) and terrestrial (yellow line) publications. Data derived from a Web of Science search for the years 1991 (the first year in which abstracts were included for many journals) through 2018, using topic = ‘species distribution’ OR ‘ecological niche’ OR ‘habitat preference’ OR ‘environmental preference’ OR ‘bioclimate envelope’ OR ‘environmental niche’ OR ‘habitat suitability’ AND ‘model*’. A subsearch was performed using search topic = ‘marine’ and this was subtracted from the remaining publications for each time period based upon the assumption that they would be terrestrial, although some freshwater examples may be included. Updated from Robinson et al. (2011).

The utility of SDMs lies in translating species-environment relationships into geographic space. This is illustrated in Figure 6 using data on *Acropora palmata* occurrence in the Caribbean (see Melo-Merino et al., 2020 for data description). Briefly, the distribution of *A. palmata* in geographic space (Figure 6a), is combined with environmental conditions through a statistical method to quantitatively describe its environmental profile (Figure 6b), and the resulting predicted map translates this profile into some measure of suitability in geographic space (Figure 6c).

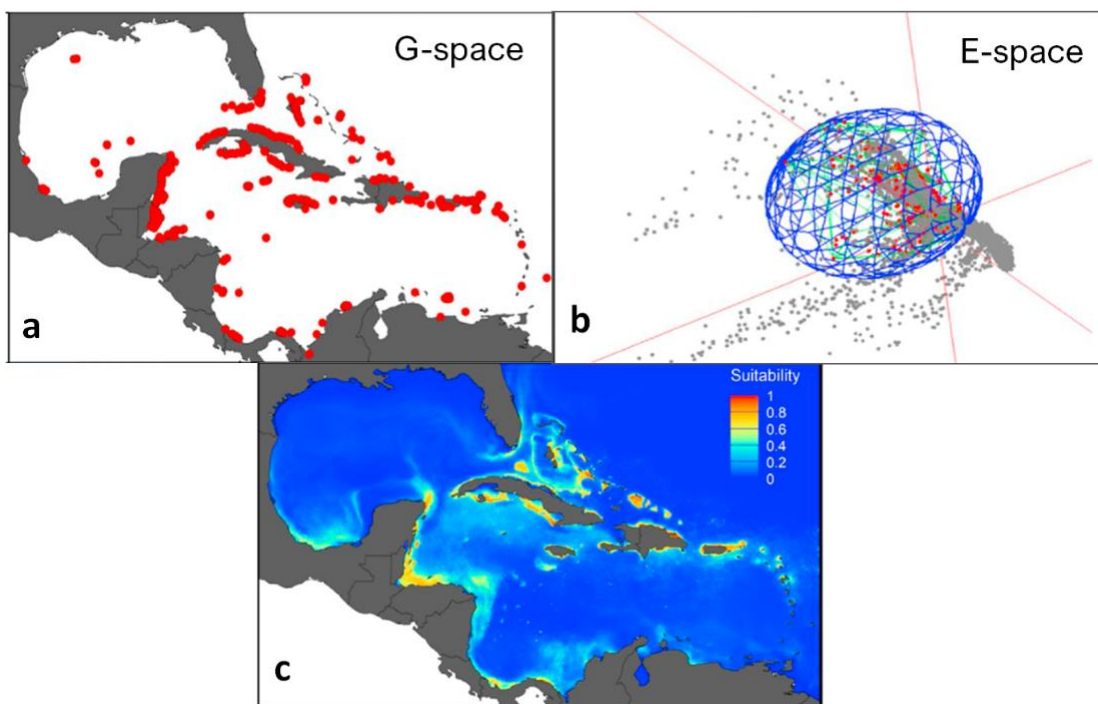


Figure 6. **a** occurrence localities for the scleractinian coral *Acropora palmata*, representing the geographical space (G-space) occupied by the species; **b** three-dimensional model of the ecological niche of *A. palmata*, where gray dots represent all the environmental conditions (E-space) available in the Caribbean, red dots represent the environments actually occupied by *A. palmata*, and the blue ellipsoid represents the fundamental ecological niche of *A. palmata*. **c** Geographic projection of *A. palmata*'s niche model and corresponding suitability values. Modified from Melo-Merino et al. (2020).

Strictly speaking, as SDMs are based on observed data, they cannot be used to map the fundamental niche of an organism, despite claims to the contrary (i.e. Soberón and Peterson 2005). This is because these approaches begin with the distribution of the organism, which is the end result of all biotic and abiotic interactions. Thus, it

implicitly incorporates any biotic interactions, disturbance, dispersal limitations, etc. that are dependent on the abiotic variables considered. Unless the models include variables that represent biotic interactions or disturbance, the mapped distribution is not exactly coincident with the realised niche either (Miller, 2010). Although the niche concept is integral to SDM, the term ‘habitat’ more accurately describes what is often modelled, as it is the distribution of suitable environmental factors that is modelled. If SDM are to be described as niche analyses at all, they are best considered as a multivariate statistical description of the Hutchinsonian niche (Kearney, 2006). Yet they are often treated as if they were fundamental niches when future species distribution scenarios are projected under environmental changes (Violle and Jiang, 2009). Since they do not include some aspect of physiological mechanisms, purely correlative approaches also run the danger of being ineffective for predicting future biogeographic patterns because projected environmental conditions can exceed those used to develop the model (Helmuth et al., 2005; Kearney, 2006; Phillips and Dudik, 2008). Despite their caveats, SDMs have emerged as a vital tool for predicting, on a spatially explicit basis, the likely impacts of climate change (Woodin et al., 2013), particularly over broad spatial extents where many biotic interactions are muted (Peterson et al., 2011).

Model organism and system

1. The intertidal reef-builder

The honeycomb worm *Sabellaria alveolata* (Linnaeus, 1767) is an allogenic ecosystem engineer, which transforms soft sediment into a hard substrate, by cementing grains of suspended sand and shell fragments together to form its tube (Le Cam et al., 2011). As a colonial species that can reach a density of 60,000 individuals.m⁻² (Dubois et al., 2002), taken as a whole, these thousands of tubes affixed to one another constitute an engineered habitat or biogenic structure (Figure 7).

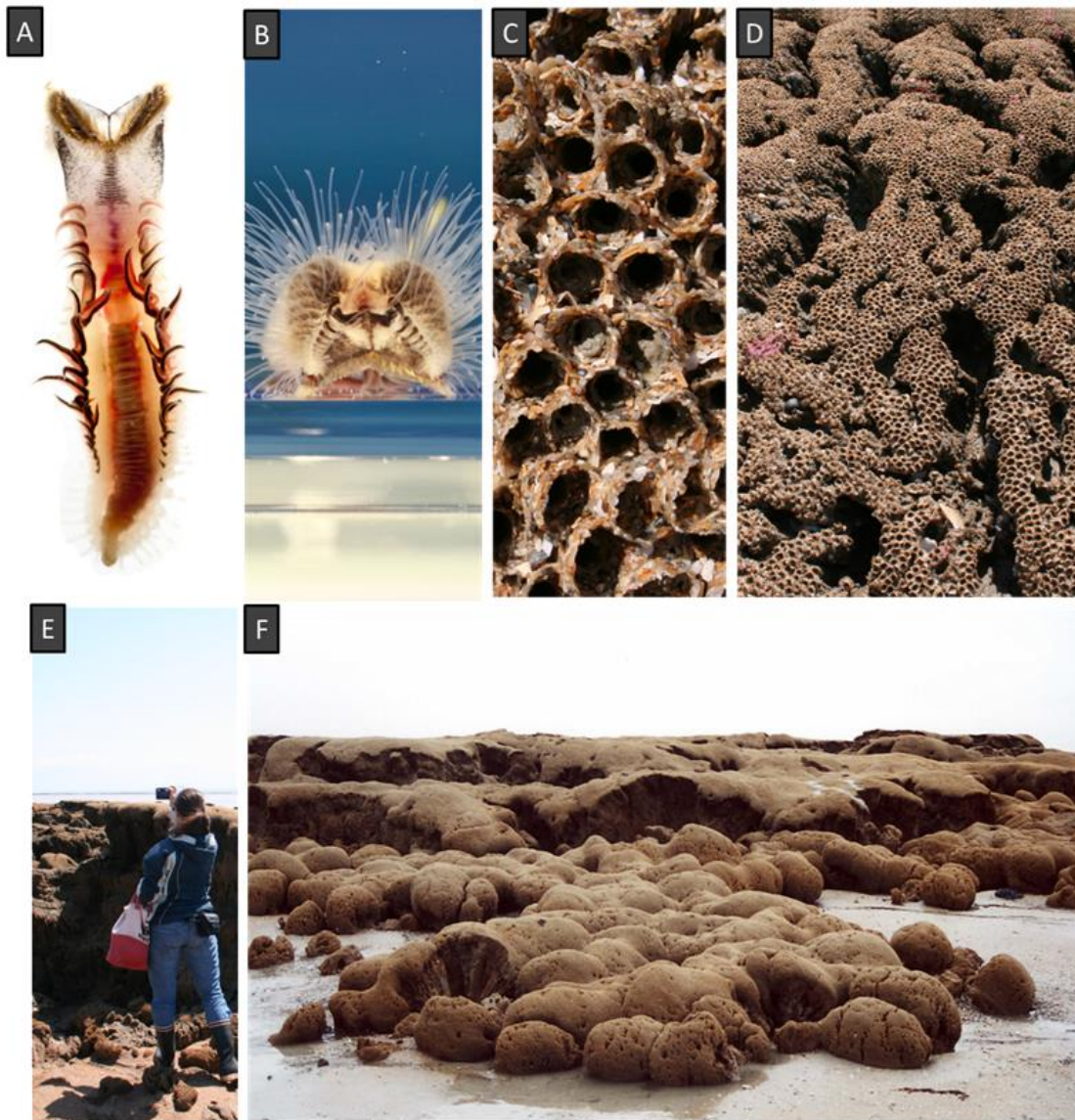


Figure 7. A: a *Sabellaria alveolata* individual. B: a close-up of *S. alveolata*'s tentacular filaments, which select resuspended sand and shell fragments from the water column to build their tubes. C: a close-up of the bioconstruction, showing the aggregation of individual tubes. Note that occupied tubes can be detected by the seal made by the worms' opercular crowns, which get covered in silt at low tide. D: zooming out from the bioconstruction, the high density of individuals and presence of epibionts (rhodophytes and trochidae) can be seen. E: reef platforms in the Mont-Saint-Michel bay showing a height of ~1.6m. F. Nunes for scale. Photo taken in 2016 F: very well-developed hummocks and platforms in the Mont-Saint-Michel bay. Photo taken in 1983. [Photo credits: A-B, A. Guérin; C-E: S. Dubois; F, Y. Gruet]

Individual colonies vary in size, and can form collections of biogenic structures ranging from small patches, hummocks, and veneers to the largest biogenic reefs in Europe found in the Mont Saint-Michel Bay, France (Holt et al., 1998; Dubois et al.,

2002) (Figure 8). These biogenic structures are important for high-biodiversity habitat provision as they are home to a unique assemblage of intertidal and subtidal species (Dubois et al., 2002). They store considerable quantities of shell debris, rock fragments and sand grains, therefore acting both as sediment reservoirs and as ‘natural’ coastal defence structures (Naylor and Viles, 2000).

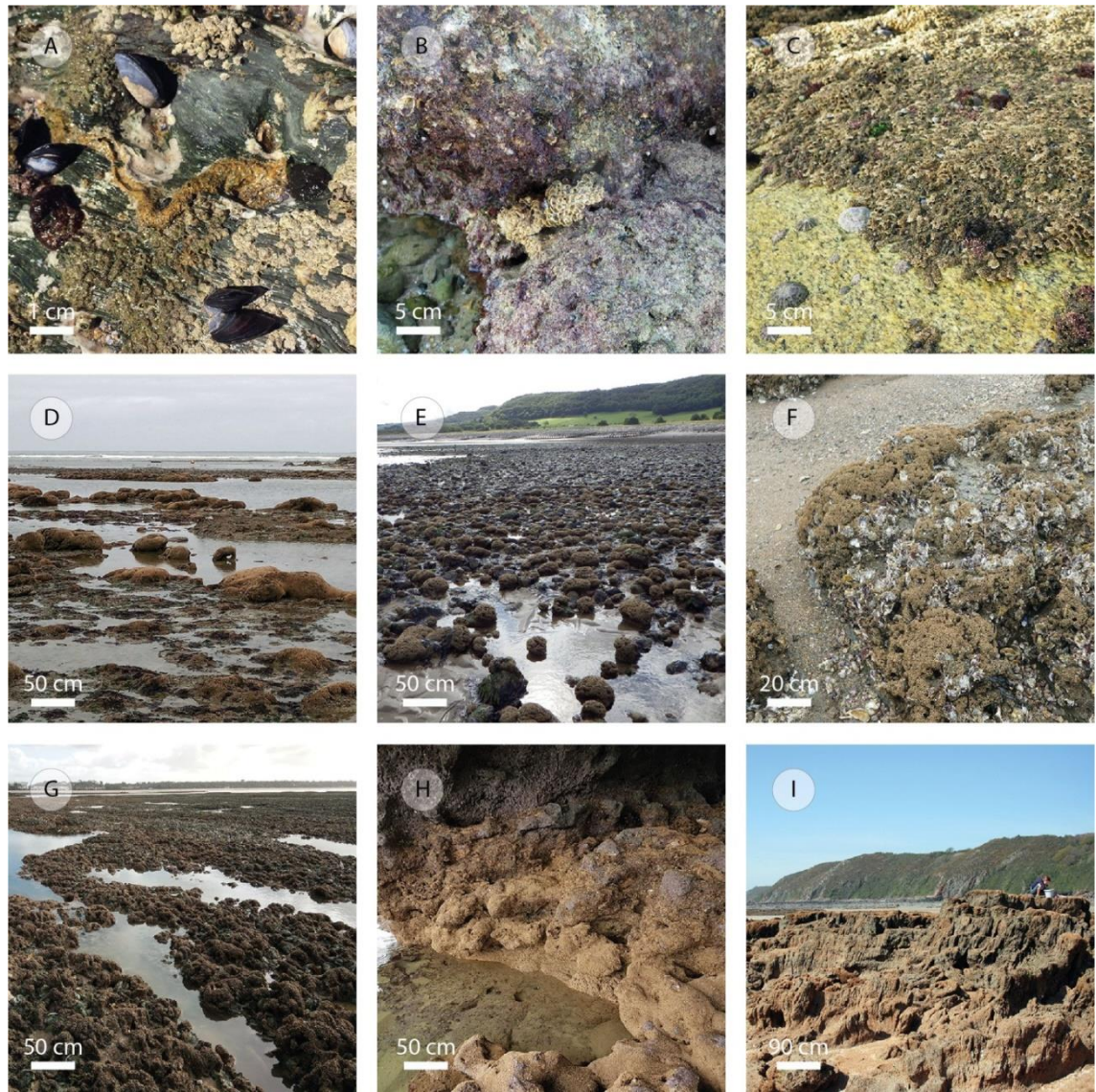


Figure 8. Photo panel illustrating the diversity of *S. alveolata* biogenic structures across Atlantic Europe. A - an isolated tube, Belle île en Mer (FR); B - a small cluster of tubes, île d’Aix (FR); C – veneer, Buarcos (PT); D - hummock forms, La Tranche (FR); E – hummocks on a cobble beach, Llanddulas (UK); F – veneers and oyster reefs, Pornic (FR); G – large veneers on oyster beds, Valière (FR); H – extensive veneers inside a sea cave, Biarritz (FR); I – the tallest present-day biogenic structures, hummocks in Champeaux (FR) [Photo credits: S. Dubois]

S. alveolata is a widely distributed Lusitanian species, extending from Auchenmalg in Scotland (Bush et al., 2016) to Dakhla in the western Sahara (Lourenço et al., 2020) and possibly even northern Mauritania (Gruet and Hawkins, pers. comm.), although as this region is underrepresented in the biodiversity literature its exact equatorward range boundary is not precisely known. In the UK, it is considered ‘nationally rare but locally abundant’ (Sanderson, 1996), as extensive reefs occur in only a handful of locations, namely the Severn Estuary and Solway Firth. Across Europe, the most extensive reefs are found in France. Along the French Atlantic coast, the densest bioconstruction coverage can be found between the Loire and Gironde estuaries (Dubois, pers. comm.), with Noirmoutier island and Bourgneuf Bay reaching particularly high abundances. Along the English Channel, the Mont-Saint-Michel Bay is home to Europe’s most extensive biogenic habitat, with the reefs of Sainte-Anne, la Frégate and Champeaux covering 300 hectares (Desroy et al., 2011).

2. Habitat importance and policy

The only legislation which affords some European-wide protection to *S. alveolata* is the European Union Habitats Directive (Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora), where it is listed under Annex I as part of the habitat 1170 ‘Reefs’. As a result, via the Natura 2000 network (the name given to the protected areas designated under the Habitats Directive), these biogenic reefs should be included in Special Areas of Conservation in which the aim is to prevent, by a series of legal measures, the deterioration of this natural habitat. However the Habitats Directive only includes intertidal reef “*where an uninterrupted zonation of sublittoral and littoral communities exist*”. Crucially, what constitutes an intertidal *S. alveolata* reef, and the significance of what ‘uninterrupted’ might mean, have yet to be defined. Despite this European framework, few member states have adopted national legislation protecting *S. alveolata* reefs. In the United Kingdom, a Biodiversity Action Plan (UK BAP) was published in 1994, pertaining to the UK Government’s response to the Convention on Biological Diversity (CBD). As part of the UK BAP, *S. alveolata* reefs were mapped,

referenced and are surveyed. Outside of the UK, some protected areas list *S. alveolata* as one of their ‘features’ in several member states, but national or European habitat distribution have not been mapped.

Despite ranging from Scotland to Mauritania, little is known about its distribution outside of the United Kingdom, where there is a strong heritage of natural history and sustained observations (e.g. Southward et al., 1995). As a result, online marine biodiversity information systems currently contain haphazardly distributed records of *S. alveolata*. Out of 2275 georeferenced stored in the Global Biodiversity Information System (accessed on the 14-05-2020), 2031 originated in the United Kingdom.

The Natura 2000 network is intended to form an ecologically coherent network at a European scale. A pre-requisite to any designation and assessment of coherence is to have accurate data on the locations of priority habitats at a regional scale. The dataset that was built as part of this thesis work fills this gap as it geographically covers Atlantic Europe and North Africa; it is presented in the first section of chapter III.

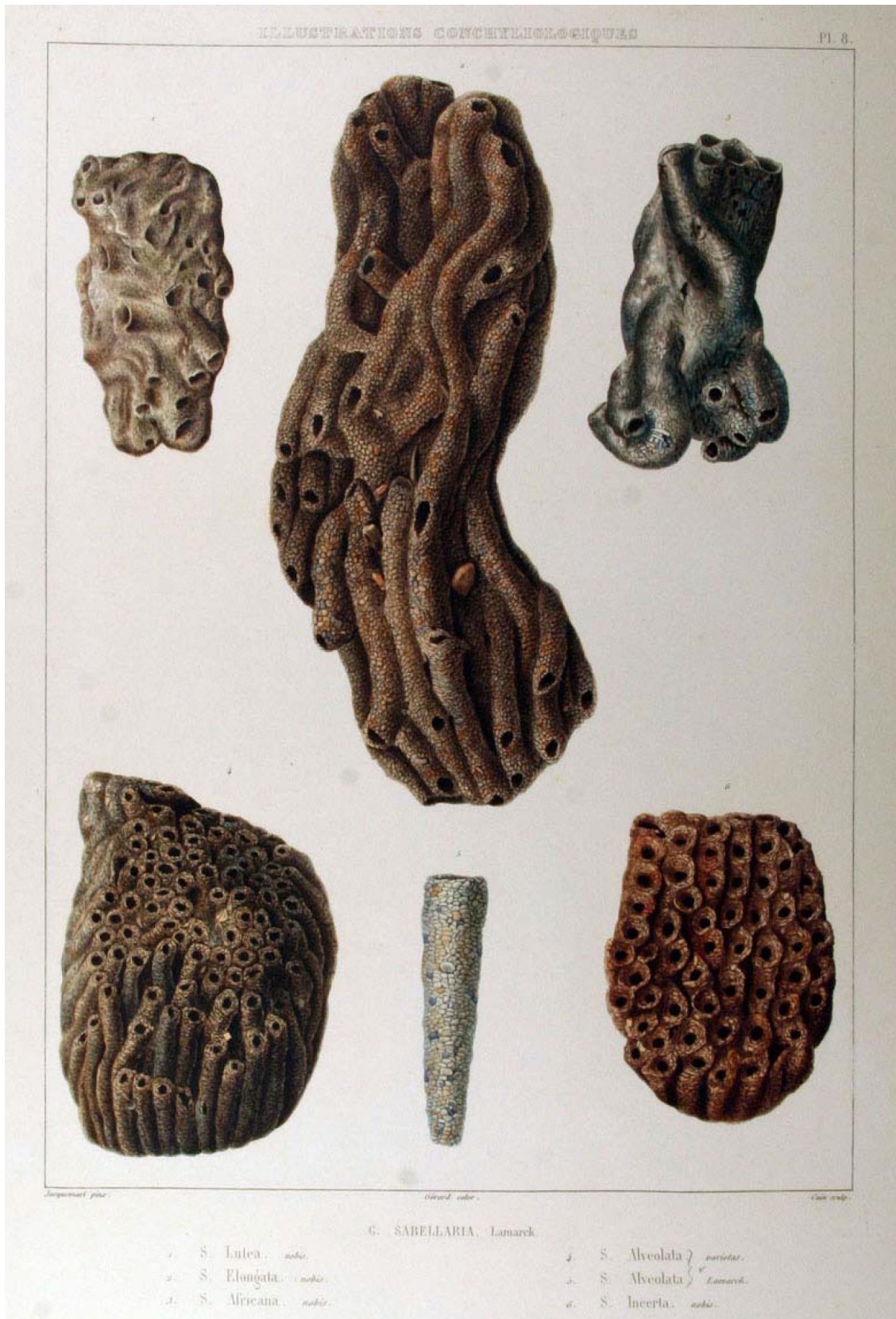


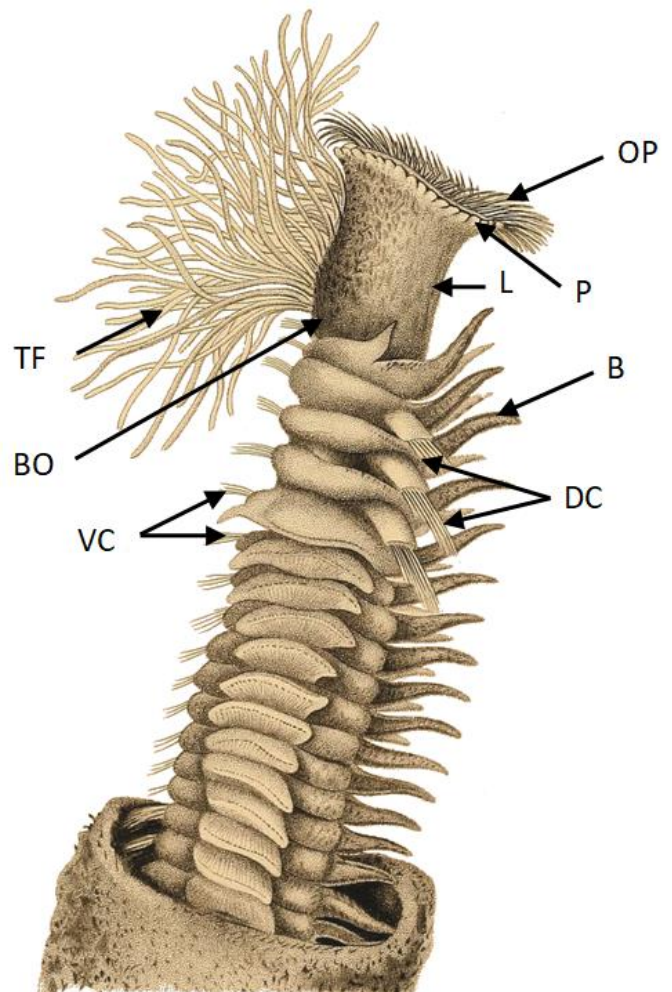
Figure 9. An illustration from Chenu (1842) of *Sabellaria* spp. biogenic reefs. Accessed via www.biolib.de

3. Body of, and gaps in, knowledge

Despite its importance as a European priority reef habitat, with rare exceptions research on *S. alveolata*'s has been conducted at a local scale. The following paragraphs are dedicated to giving a brief overview of the existing body of research, summarised in Figure 11, which presents a non-exhaustive summary of key articles in different disciplines and biological organisation levels.

Much attention has been given to the mechanisms underpinning *S. alveolata*'s biogenic reef construction, from the composition of individual tubes (Fournier et al., 2010) and the chemical properties of its biomineral cement (Gruet et al., 1987), to the morphology (Naylor and Viles, 2000) and developmental cycle (Gruet, 1984) of entire reefs. The processes through which food or mineral particles are actively selected by *S. alveolata*'s tentacular filaments (Figure 10) and transported towards the mouth or building organs have been decrypted through detailed anatomical studies (Dubois et al., 2003, 2005 and 2009).

Figure 10. Left side-view of *Sabellaria alveolata* anterior region. TF = tentacular filaments, BO = building organ, OP = opercular paleae, L = peristomial lobe, P = papillae forming a ring around the base of the operculum, B=branchia, DC=dorsal chaetae, VC=ventral chaetae. Modified from Cuvier (1836) and Ebling (1945).



As with many coastal benthic invertebrates, *S. alveolata* features a complex life cycle, with several planktonic larval stages, in addition to a sessile bottom dwelling juvenile and subsequent adult stage (Wilson, 1929; Cazaux, 1964). Settlement stage larvae are known to be attracted to conspecific reef structures, both alive and dead (Wilson, 1968; Pawlik, 1988). Studies of larval duration and peak reproductive periods have yielded variable results. Planktotrophic larvae have been reported to persist in the water column for 4-12 weeks (Wilson, 1968; Ayata et al., 2009). Contradictory information is available regarding peak reproductive periods, with spawning reported for just one summer month (e.g. Wilson, 1971) or extended over several summer months (e.g. Culloty et al., 2010), to bimodal peaks in spring and autumn (Gruet and Lassus, 1983; Dubois et al., 2007), to semi-continuous trickle spawning throughout the year (Gruet and Lassus 1983; Dubois et al., 2003; 2007; Culloty et al., 2010). These variable larval durations and spawning periods imply that larval dispersal models have many different scenarios to contend with (Muir et al., 2020), and ultimately yield vastly different scenarios for protected area network coherence and connectivity.

Prior to this thesis, no *in-situ* physiology studies had been conducted, and the physiological response of *S. alveolata* to environmental stressors was limited to two experimental studies on the impact of seawater temperature and pH. Muir et al. (2016) looked at lipid remodelling in *S. alveolata* through common garden experiments using individuals sampled from five locations along the north-east Atlantic coastline, in response to acclimation and adaptation to temperature. They found *S. alveolata* to be tolerant to heat stress, being able to acclimatise to sustained high temperatures by modulating its cellular membrane lipids, although this ability appears to be limited to temperatures below 25°C (Muir et al., 2016). Experimental work on *S. alveolata*'s tolerance to increasing seawater temperatures and acidification has shown it can tolerate warm acidic conditions for several weeks (Faroni-Perez, unpublished data). How environmental stressors other than seawater temperature, such as air temperature and hydrodynamic factors - known to be

important for intertidal, filter-feeding, engineer species - affect organismal performance, had not been studied. Equally, prior to this thesis nothing was known about broad-scale spatial variation in *S. alveolata* reproduction and physiology in relation to environmental stressors.

Biology and physiology

Physiology : fatty acid profiles acclimatisation and local adaptation to temperature (Muir et al. 2016)

Feeding mechanisms (Dubois et al. 2003, 2005, 2009), feeding ecology and trophic inter-species competition (Lefebvre et al. 2009, Dubois and Colombo 2014)

Tube composition

Tube composition (Gruet et al., 1987 ; Naylor & Viles 2000) and change with growth (Gruet 1984)

Mechanical resistance (Le Cam et al. 2011) and biochemical cement composition (Gruet et al. 1987, Flammang et al. 2009, Fournier et al. 2010)

Egg development (Wilson 1968) and composition (Peaucellier et al. 1984), larval behaviour (Pawlik 1988, Dubois et al. 2007, Ayata et al. 2009) and reproduction period (Gruet & Lassus 1983, Culloty et al. 2010)

Worm parasites (Leander 2008, Leander et al. 2006)

Biodiversity

Diversity of reef associated fauna in France (Dubois et al. 2002, Schlund et al. 2016, Jones et al. 2018), Spain (Porras et al. 1996), Portugal (Dias & Paula 2001, Bertocci et al. 2012, Plicanti et al. 2017), Italy (Bonifazi et al. 2019, Bertocci et al. 2017), Morocco (Chouikh et al. 2020)

Anthropogenic direct (Plicanti et al. 2016) and indirect (Dubois et al. 2006) effects on associated fauna



Biogeography

Decadal spatial changes in bioconstructions in Britain (Firth et al. 2015) or local temporal changes (Lecornu et al. 2016)

Seascape ecology

Estimates of reef volumes and sediment pool (Noernberg et al. 2010)

Local bioconstruction mapping in France (Schlund et al. 2016), Italy (Ingrosso et al. 2018), Spain (Anadon 1981). Experimental high resolution mapping using airborne optical imagery (Collin et al. 2018) and laser scanning and photogrammetry (d'Urban Jackson et al. 2020)

Local conservation status and survey protocol (Desroy et al. 2011)

Figure 11. Diagram summarising key *S. alveolata* research papers and topics.

The bulk of this research has been concentrated in three locations, by three researchers: (1) Duckpool in Cornwall UK, by Douglas Wilson (2) Bourgneuf Bay near the Loire Estuary in France, by Yves Gruet (3) the Mont-Saint-Michel Bay, by Stanislas Dubois (see references in above paragraphs and figure 10). The reefs in the Mont-Saint-Michel in particular have been the subject of many subsequent studies building on previous biological descriptive work to increasingly explain ecological processes that drive patterns in *S. alveolata* population dynamics and community structure (e.g. Ayata, 2010; Jones, 2018). Given the special nature of this location (a mega-tidal bay where reefs have formed atop of soft sediments), it is unknown how transposable these research results are to other locations.

The alpha diversity of the reef associated fauna has been described in many locations across France (Dubois et al., 2002; Jones et al., 2018), Spain (Porrás et al., 1996), Portugal (e.g. Dias and Paula, 2001), Italy (e.g. Bertocci et al., 2017) and Morocco (Chouikh et al., 2020). The effects of direct (human trampling – Plicanti et al., 2016) and indirect (epibiont presence due to eutrophication and aquaculture – Dubois et al., 2006) local anthropogenic impacts have been studied. The development of an (super-abundant) reef health status index has shown continuous deterioration of the Mont-Saint-Michel reef's state of health, which correlates with the colonisation of the Pacific oyster *Magallana gigas* and with increasing silt deposits linked to shellfish farming (Desroy et al., 2011).

The Mont-Saint-Michel has also been the testing ground for a number of high-resolution remote-sensing mapping methods, namely LiDAR (light detection and ranging – Noernberg et al., 2010), drone imagery (Collin et al., 2018) and most recently hyperspectral imagery (Bajjouk and Dubois – unpublished data). Spatial ecologists have also newly tested laser scanning and structure-from-motion photogrammetry on Welsh *S. alveolata* reefs as promising new three-dimensional mapping tools (d'Urban-Jackson et al., 2020).

The broadest-scale studies to date have gone from studying five-year reef dynamics along the western Cotentin peninsula in France (Lecornu et al., 2016), to decadal-scale shifts spanning the length of Britain (Firth et al., 2015). In

summary, prior to this thesis, occurrence records and mapping studies were mainly local and did not stretch beyond the national level in the United Kingdom. Range-wide distribution and abundance was unknown, and biogeographic studies of future climate change scenarios covering the entire species distribution area had not been carried out.

4. Model organism, biogeography and climate change

As a Lusitanian warm-water species that responds positively to warming temperatures (i.e. population increase, Frost et al., 2004) and negatively to severe winters (Crisp, 1964; Firth et al., 2015), towards its northern range boundary, *S. alveolata* is considered a climate change indicator species in Britain and Ireland (Hiscock et al., 2004; Mieszkowska et al., 2006; Merder et al., 2018). Evidence is however currently lacking to determine whether the poleward range boundary is set by the inability to survive cold stress or because of the inability to repopulate (i.e. lack of larval recruitment or survivorship of juvenile phases) (Hutchins, 1947).

Up until now, the broadest-scale, longest-term studies of *S. alveolata* distributional shifts have spanned the length of Britain over a decadal time scale (Cunningham et al., 1984; Firth et al., 2015, Bush 2016). Whether it can be considered a climate change indicator species in the southern part of its range, and whether its distribution is predicted to shift under future climate change scenarios, are questions that had not been answered (or even asked) prior to this thesis.

Thesis outline

The general aim of this PhD thesis is to gain a better understanding of where and why *S. alveolata* is distributed, by investigating different dimensions of its ecological niche through three different approaches, organisational levels and scales.

The first chapter provides a snapshot link between the physiological condition of the organism, and the outward physical appearance of the bioconstruction, on *S. alveolata* sampled in the Mont-Saint-Michel Bay. By learning more about the physiological condition of the species at the individual level, insight was gained into the limits of its fundamental niche. Exploratory research was conducted in order to identify which biochemical indicators could subsequently be used as response traits in ensuing *S. alveolata* physiology studies.

In the second chapter, response traits are explored on a regional scale, by integrating information on physiological and reproductive condition with knowledge of temporal and spatial patterns in the physical environment across ten sites, from Criccieth in North Wales to Buarcos in central Portugal. We link these biochemical and reproductive response traits to emergent patterns in *S. alveolata* populations and allude to how these may be affected by environmental stressors, namely extreme temperature and storm events. This macrophysiological study, which focuses on the variation of reproductive traits and adult physiological condition across 14.5° latitude, confers the ability to directly assess the abundant-centre hypothesis (aka Brown's principle) which proposes that species have decreased performances towards their range edges.

The third chapter uses a species distribution modelling approach to estimate *S. alveolata* habitat suitability on the basis of environmental gradients across the near-entirety of its geographic range. This thesis is the first 'range-long' study of *S. alveolata*, and was made possible by the compilation of occurrence records across six countries spanning two decades. As a species which provides

a high-biodiversity habitat, climatic impacts could result in sweeping community-level changes. Based on future projections of environmental predictors, the predicted emergent response to climate change was analysed, in the form of range contractions and expansions forecast by the mid and end of the 21st century. Taken as a whole, these three chapters provide different pieces to the integrated view puzzle of *Sabellaria alveolata*'s niche, summarised in Table 2.

Table 2. Summary overview of hypotheses tested, data types and analytical methods applied to *Sabellaria alveolata* in the three chapters.

	Chapter I	Chapter II	Chapter III
H₀	The outward structural appearance of the bioconstruction is not linked to the physiological condition of the resident individuals.	(i) There are no differences in reproductive and biochemical traits in individuals at the centre or edges of the distribution range; (ii) Extreme or fluctuating abiotic conditions do not increase intra-specific trait variation.	Statistical distribution models (i) present day distribution cannot be predicted by broad-scale environmental variables; (ii) climate change will leave the future biogeographical distribution unaltered.
Study scale and time frame	1 site in FR (100s of meters) February 2016	10 sites in UK, FR & PT (100s of km) Summer 2017 & Winter 2018	North-east Atlantic (1000s of km) 1970-2019 Projections for 2040s, 2090s
Response variables	Biochemical physiological indicators (fatty acids and enzymes)	Univ.: Total egg diameter, egg symmetry, egg circle fit, relative fecundity Multiv.: Biochemical physiological indicators	Occurrence records (presence/absence data)
Sources of variation	Bioconstruction types (Hummock or Veneer), phases (Prograding or Retrograding) and shore level (High or Low) Random factor: sampling location	Meteorological variables (30 day mean): Air and seawater temperature, Chl-a, suspended particulate inorganic matter, tidal amplitude, wave exposure,	Climate variables (pluri-annual mean): Sea surface temperature, sea surface salinity, air temperature, fetch, significant wave height, tidal amplitude
Applied statistical methods	Univ.: T-test Multiv.: GLM, GLMM, PCA	Univ.: linear regressions Multiv.: CoIA, RDA, MLR, varcomp, varpart	Multiv.: GAM, RF, ensemble models

Univ. = univariate; **Multiv.** = multivariate; **Chl-a** = Chlorophyll a; **GLM** = General Linear Models; **GLMM** = General Linear Mixed Models; **PCA** = Principal Component Analysis; **CoIA** = Co-inertia Analysis; **RDA** = Redundancy Analysis; **MLR** = Multiple Linear Regression; **varcomp** = variance component analysis; **varpart** = variance partitioning; **GAM** = Generalised Additive Models; **RF** = Random Forest.

It is worth noting here that the physiological processes presented in chapters I and II are not explicitly included in the determination of *S. alveolata*'s large-scale habitat in the third chapter. Moving towards integrating mechanistic knowledge into successful biogeographic forecasting is discussed in the final thesis chapter.

CHAPTER I

The first chapter of this thesis focuses on biochemical traits in *S. alveolata*. This work was published in March 2019 in 'Ecological Indicators.' The overall objective of this study was to investigate the relationship between the physical appearance of the reef or bioconstruction and the physiological state of the individual worms. Biochemical markers are frequently used to assess the physiological condition of aquaculture species but have yet to be routinely used in intertidal field ecology. The focus of this study was on a single site and sampling event: the Mont-Saint-Michel Bay, sampled in February 2016.

This study tested a whole suite of biochemical markers to see which stood out as being relevant proximate response traits for *S. alveolata*. Importantly, it also proposed a clear terminology for the bioconstruction type (vaneer, hummock or platform) and phase (progradation vs. retrogradation) from which the worms were sampled. Both the biochemical markers and terminology were selected to be widely applicable across *S. alveolata*'s range.

The polar lipid fraction of arachidonic acid (20:4n-6) was selected, together with the activity of two metabolic enzymes (citrate synthase and superoxide dismutase) as three informative biochemical stress markers for this species. Our key finding was that worms sampled from retrograding reefs (i.e. displaying signs of erosion and colonisation by epibionts such as oysters or mussels), were less physiologically stressed than worms sampled from prograding bioconstructions. Lower intraspecific competition, increased micro-habitats and hence greater food availability is the suggested reason. Whilst prograding bioconstructions, with their rounded shapes, crisp porches and low number of epibionts, are often considered as having a greater aesthetic value, retrograding bioconstructions may ensure a greater number of ecological functions. It is therefore essential that conservation measures encompass multiple *S. alveolata* bioconstruction types and phases.

ARTICLE I - CONNECTING ORGANIC TO MINERAL: HOW THE PHYSIOLOGICAL STATE OF AN ECOSYSTEM-ENGINEER IS LINKED TO ITS HABITAT STRUCTURE

Amelia Curd^{1,*}, Fabrice Pernet², Charlotte Corporeau², Lizenn Delisle², Louise B. Firth³,
Flavia L.D. Nunes¹ and Stanislas F. Dubois¹

Article published in *Ecological Indicators*

¹ IFREMER, Centre de Bretagne, DYNECO LEBCO, 29280 Plouzané, France

² IFREMER, Centre de Bretagne, LEMAR UMR 6539, 29280 Plouzané, France

³ School of Biological and Marine Sciences, University of Plymouth, Drake Circus, PL4
8AA, Plymouth, United Kingdom

Abstract

The honeycomb worm *Sabellaria alveolata* is capable of building extensive bioconstructions, including what are currently considered Europe's largest biogenic reefs. The size and volume of these bioconstructions, however, vary greatly, such that not all habitats engineered by *S. alveolata* may be easily identified as reefs. Given that European environmental legislation protects marine habitats that are classified as "reefs", it is important to identify a clear set of definition criteria. Furthermore, quantifiable and unequivocal criteria are also needed to evaluate the ecological (health) state of these reefs, in order to best monitor and protect them. Here we propose new terminology to describe the physical appearance of these bioconstructions and attempt to link these physical criteria to the physiological state of the tube-building polychaete. We tested whether a bioconstruction displaying outward signs of growth is built by "healthy" worms devoid of physiological stress by analysing three macromolecules (carbohydrates, proteins, lipids), four polar lipid fatty acids, six neutral lipid fatty acid markers and three metabolic enzymes (citrate synthase, catalase and superoxide dismutase). The worms were sampled in

bioconstructions of different “Type” (venerer vs. hummock), “Phase” (progradation vs. retrogradation), and “Shore Level” (high shore vs. low shore) at Champeaux in Mont-Saint-Michel Bay, France. Our results show that worms sampled in retrograding reefs (i.e. displaying signs of erosion and colonisation by epibionts such as oysters or mussels), were less physiologically stressed than worms sampled in prograding bioconstructions, possibly due to lower intraspecific competition and hence greater food availability. We therefore suggest management measures should encompass the whole mosaic of biogenic construction Types and Phases. We propose the inclusion of the polar lipid fatty acid arachidonic acid, in combination with the activity of two metabolic enzymes, citrate synthase and superoxide dismutase, as the three key biochemical markers to consider for quantitative information on the physiological state of this particular ecosystem engineer. Our results also revealed the influence of both sex and size on fatty acid and enzyme levels, highlighting the importance of taking into account both these variables when sampling and subsequently pooling individuals by sex and size category for laboratory analyses. Once seasonal and site variation have been addressed, these biochemical indicators could be examined in parallel with *S. alveolata* bioconstruction physical criteria as part of a European-wide protocol for monitoring ecological status in this potential reef habitat.

1. Introduction

Biogenic reefs are among the most biologically diverse and functionally important habitats on Earth (Goldberg, 2013). Their physical structure is known to provide numerous provisioning and regulating services, such as unique habitat provision and coastal protection (Hattam et al., 2015). Tropical coral reefs are often the first image that springs to mind upon hearing the term ‘reef’, and are the subject of enormous literature. Scleractinian corals, however, are only one of many marine taxa capable of building biogenic reefs, which can be defined as follows: “*solid, massive structures which are created by*

accumulations of organisms” and “*clearly forming a substantial, discrete community or habitat which is very different from the surrounding seabed*” (Holt et al., 1998). In temperate waters, shellfish and tube-dwelling polychaetes also fall under this definition (Bartol et al., 1999; Dubois et al., 2006).

The term “healthy reefs” is ubiquitous throughout the literature on marine conservation; healthy reefs are often the focus of protection efforts (Abelson et al., 2017). Yet when it comes to assessing reef health status, the metrics most commonly described assess either ecological (i.e. species richness and presence of species of interest), or landscape characteristics (i.e. elevation, extent, coverage). It is unknown whether these assessments are indicative of the health of the engineering organism itself.

Reef-building sabellariid worms are ubiquitous globally in both intertidal and shallow subtidal zones. The species responsible for building what are currently considered as Europe’s largest biogenic reefs (Gruet, 1986) is the honeycomb worm *Sabellaria alveolata* (Linnaeus, 1767). This sedentary colonial polychaete creates tubes of coarse sand grains and shell fragments cemented together; dense aggregations of which may be regarded as reefs (Holt et al., 1998). This Lusitanian species is widely distributed from southwest Scotland to Morocco where it inhabits the low- to mid-shore (Gruet, 1986; Dubois et al., 2002). As an ecosystem engineer, *S. alveolata* generates small to large scale topographic complexity, creating numerous spatial and trophic niches for other species to colonise (Dubois et al., 2002; 2006; Dubois and Colombo 2014; Jones et al., 2018). Their bioconstructions buffer physical and chemical stresses, protect from predators and competitors, and alter resource availability (Porrás et al., 1996). Consequently, these bioconstructions host highly diverse and unique communities, composed of species originating from hard, muddy and sandy substrates, in addition to both subtidal and intertidal habitats (Dubois et al., 2002; 2006; Schimmenti et al., 2015), and are broadly considered as local hotspots of biodiversity (Jones et al., 2018).

Honeycomb worm bioconstructions constitute a highly dynamic habitat subject to numerous natural (e.g. cold winters or storms) and anthropogenic disturbances (e.g. trampling, harvesting, shellfish farming, coastal development) (Dubois et al., 2002; Firth et al. 2015; Plicanti et al., 2016). These bioconstructions may take on three main structural types (see e.g. Cunningham, 1984 and Holt et al., 1998, Figure 12). Gruet (1982) described a cycle whereby a bioconstruction evolves from (1) “veneers” in which the tubes overlap and lie at an acute angle to the substratum, to (2) “hummocks” in which the tubes radiate out from the initial settlement point before reaching (3) “platforms” formed of extensive areas of hummocks fused together. In the majority of locations throughout Europe, however, neither the “hummock” nor “platform” type is ever reached. Any one of these bioconstruction types can display outward signs of being in a “progradation” or “retrogradation” phase (Figure 12a). Gruet (1982) was the first to refer to *S. alveolata* reef phases, which he referred to as “growth” and “destruction”. Here we propose new terminology for *S. alveolata* bioconstruction development. The engineered structure is constantly in a delicate balance between these two phases, and can therefore display some or all of the characteristics listed in Figure 12b. Patches can undergo cyclic or erratic changes whereby they prograde or retrograde either partially or totally through resettlement, as *S. alveolata* larvae, as with all sabellariid species, preferentially settle on conspecific adult tubes (Pawlik, 1986).

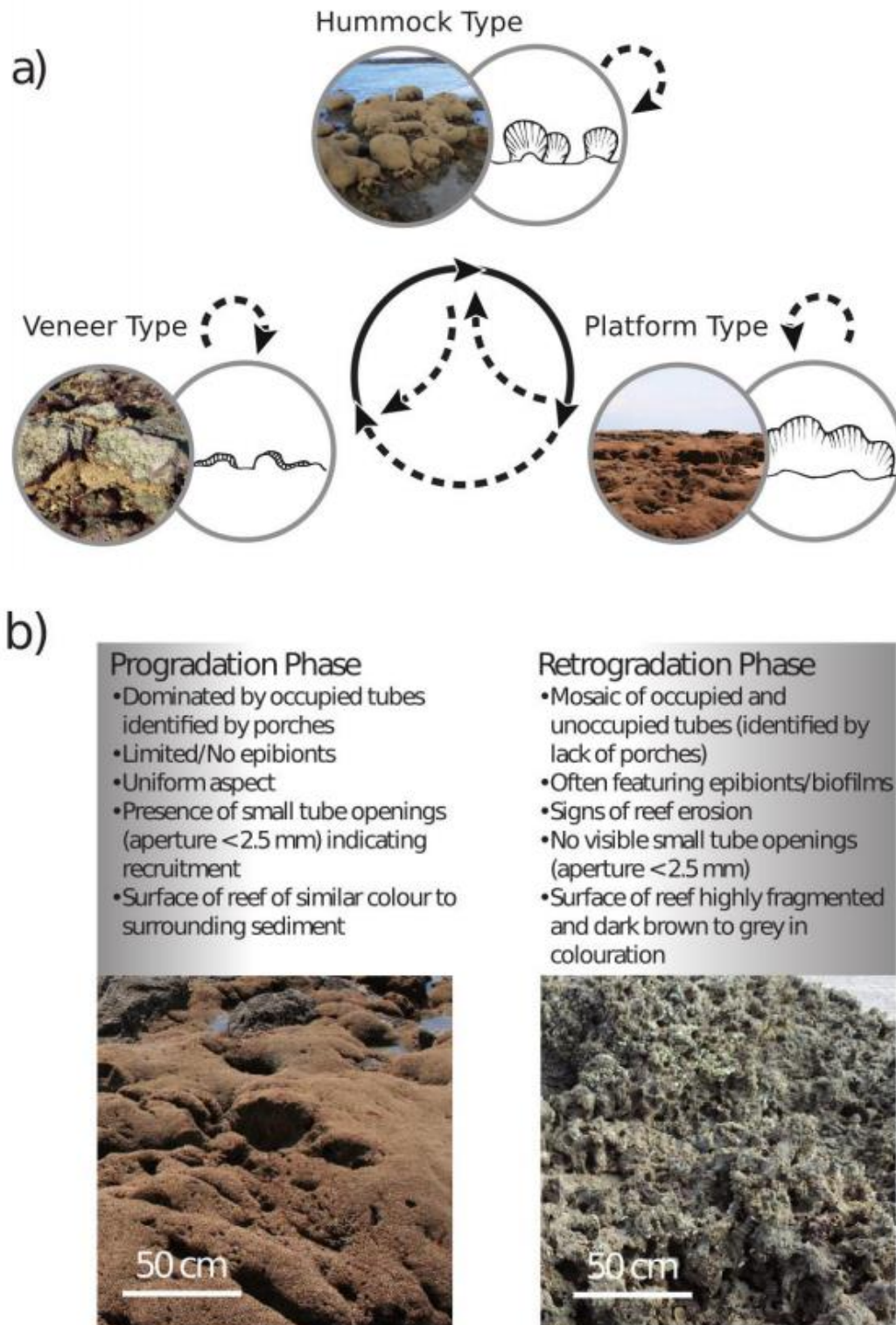


Figure 12. Conceptual diagram of a) the different bioconstruction Types of *S. alveolata* (adapted from Gruet, 1986). Progradation and Retrogradation, as defined in b), are represented by full versus hatched arrows respectively. Note that a bioconstruction can cycle between the two Phases – as represented by the circular arrows – within the same bioconstruction Type. Images © Ifremer.

Currently there is no single definition or guidance of what constitutes a *S. alveolata* “reef”. Far from being a semantic dispute, this has far-reaching implications in terms of management and conservation, as throughout the majority of its distribution (*i.e.* Europe) the sole legislative instrument affording any protection is the Habitats Directive (Council Directive 92/43/EEC), which only protects the “reef” form of biogenic constructions. A “reefiness” scoring system in the context of the Habitats Directive was developed by Hendrick and Foster-Smith (2006) for subtidal *Sabellaria spinulosa* reefs, based on a series of physical, biological and temporal characteristics weighted according to data quality of and perceived importance of each feature. Desroy et al. (2011) developed a Health Status Index for *S. alveolata* bioconstructions at the Bay of Mont-Saint-Michel, based on fragmentation, proportion of different bioconstruction morphological types and coverage by three key epibionts (*i.e.* oysters, *Magallana* (formerly *Crassostrea*) *gigas*, mussels, *Mytilus* spp., and green macroalgae, *Ulva* spp.). Existing rapid assessments of intertidal *S. alveolata* “quality” (*i.e.* Cunningham, 1984; Firth et al., 2015) are based on visual evaluations of the bioconstructions, and do not consider environmental characteristics of the site. Whilst all of these scoring indices are very useful, they may not easily translate beyond the species or biogeographic regions that they were developed for. Due to differences in morphology between the two species, the “reefiness” score for *S. spinulosa* developed by Hendrick and Foster-Smith (2006) is more helpful as a means of comparing the relative values of two different areas of *S. spinulosa* reef. The Health Status Index developed by Desroy et al. (2011) is only applicable in areas where *S. alveolata* bioconstructions reach the platform type and become colonised by *M. gigas* or *Mytilus* spp., thus restricting its application. Furthermore, not only do both of these indices require a considerable amount of field and laboratory work with numerous field experts, they also rely entirely on the physical looking-aspect of the bioconstruction. For example, muddy and fragmented bioconstruction patches have a low score on Desroy et al. (2011) health scale, disregarding the actual physiological state of the worm. The main objective of the present study

was to develop a generic tool that would be applicable across the entire geographic range of *S. alveolata*, able to help linking the physical state of the bioconstructions with the physiological state of the individuals.

Biochemical proxies may provide generic health indicators well suited for *S. alveolata*. Cell health and survival rely on a series of biochemical fluxes and reactions that are highly conserved among species and biogeographic regions (Hochachka and Somero, 2002). Therefore, biochemical indicators can be used as a snapshot of the physiological condition of the individual at the time it was sampled (Fraser, 1989; Dahlhoff, 2004), and could potentially have similar applicability across a variety of taxa. In order to understand how the physiological condition of *S. alveolata* ties in with their bioconstruction structure (*i.e.* type, phase and shore level), we focused on a suite of metabolic parameters that reflect several key physiological processes.

Information on the organic macromolecules of a species is fundamental to understanding its biochemical characteristics. Carbohydrates and neutral lipids constitute major energy reserves for fuelling growth, reproduction, and defence against stressors in many marine invertebrates (e.g. Gallagher et al., 1986; Berthelin et al., 2000; Rivest et al., 2017). Glycogen is the primary polysaccharide (polymeric carbohydrate) in annelids (Scheer, 1969) and has long been recognised as the principal energy reserve in juvenile and adult bivalves (Lucas and Beninger, 1985). It serves both as an energy reserve under unfavourable environmental conditions, and also for the formation of gametes (Gabbott, 1975). Quantifying glycogen levels may therefore provide an indication of the level of energy reserves in *S. alveolata*.

Fatty acids, which are key constituents of the lipid compartment, vary with environmental factors such as temperature (e.g. Pernet et al., 2007) or salinity (Fuhrmann et al., 2018), trophic sources (Winder et al., 2017) and life history stage (e.g. Soudant et al., 1999; Lourenço et al., 2017). On one hand, the fatty acid composition of neutral lipids, which generally consists of triglycerides, reflects the fatty acid profile of the food consumed, thus revealing useful information about quality and assimilation of trophic sources (Dalsgaard,

2003). On the other hand, the fatty acid composition of polar lipids, which mainly originate from cell membranes (phospholipids), is altered to enable physiological adaptation of organisms to their physical environment (Hazel and Williams, 1990; Hochachka and Somero, 2002). The best example of this is the remodelling of membrane lipids by ectothermic animals, including *S. alveolata*, to counteract the effect of temperature on membrane fluidity (Hazel, 1995; Muir et al., 2016). Some fatty acids are particularly informative. The fatty acid 20:4n-6 (arachidonic acid) is a precursor of hormones involved in stressful or energetically expensive situations, namely gametogenesis and spawning (Osada, Nishikawa and Nomura, 1989), stimulation of immune functions in marine invertebrates (Delaporte, 2003) and acclimation to increasing seawater temperatures in *S. alveolata* (Muir et al., 2016). Therefore, fatty acid composition acts as a good stress bioindicator in marine organisms.

Metabolism is the biological processing of energy and materials through a series of biochemical reactions catalysed by enzymes (Brown et al., 2004). Metabolic enzymes are proteins which help maintain physiological homeostasis. Citrate synthase is a central enzyme in the process of sugar oxidation involved in adenosine triphosphate (ATP) generation. It is the first step of the citric acid or Krebs cycle, consisting of a series of chemical reactions which generate energy through the oxidation of acetyl-Coenzyme A derived from carbohydrates, lipids and proteins. Citrate synthase activity (CS) is correlated with respiration rate in marine invertebrates and can be used as indicator of oxidative stress (Dahlhoff et al., 2002). Reactive oxygen species (ROS) are generated through cell respiration and their production is exacerbated by environmental stressors such as contaminants, pathogens and dietary restrictions (e.g. Abele and Puntarulo, 2004 for review). Accumulation of ROS in aerobic cells can result in oxidative stress in the host (Lesser, 2006) which is normally prevented by an enzymatic antioxidant system. Studies have highlighted the importance of the enzymes superoxide dismutase (SOD) and catalase (CAT) in the prevention of tissue damage from oxidative stress in marine invertebrates (Abele and Puntarulo, 2004 for review).

The overall objective of this study was to investigate the relationship between the outward structural appearance of the bioconstruction and the physiology of the resident individuals. From a practical standpoint, we tested the effect of the physical appearance of the bioconstructions in terms of their structural Type (vener vs. hummock, but not platform due to this type being absent from the majority of locations), Phase (progradation vs. retrogradation) and shore level (high vs. low-shore) on several well-known biochemical indicators of health. Key macromolecules, enzyme activity and fatty acid composition of neutral and polar lipids may change between different bioconstruction phases of growth and deterioration and are likely to modulate the individual's response to environmental stressors.

2. Materials and Methods

2.1. Study location: Champeaux Reef

Our study took place in the Bay of Mont-Saint-Michel (north-western France), a megatidal (>14m) ecosystem with one of the highest maximum spring tidal range values in the world (Levoy et al., 2017). It is home to the largest and most extensive biogenic constructions in Europe, namely the Saint-Anne reef (2.25 km²) and the Champeaux reef (0.29 km²) (Desroy et al., 2011). The current study focused on the Champeaux reef affixed to rocky substrate in the upper intertidal zone, situated in the southeastern part of the Bay (48.7318, 01.5520; Figure 13). The tidal amplitude in a megatidal regime implies that the water column is very well mixed. The surrounding substrate is known as '*tangue*', a heterolithic sediment displaying an alternate structure of sandy and silty-muddy beds which represent the deposit of each semi-diurnal tidal cycle (Tessier, 1993).

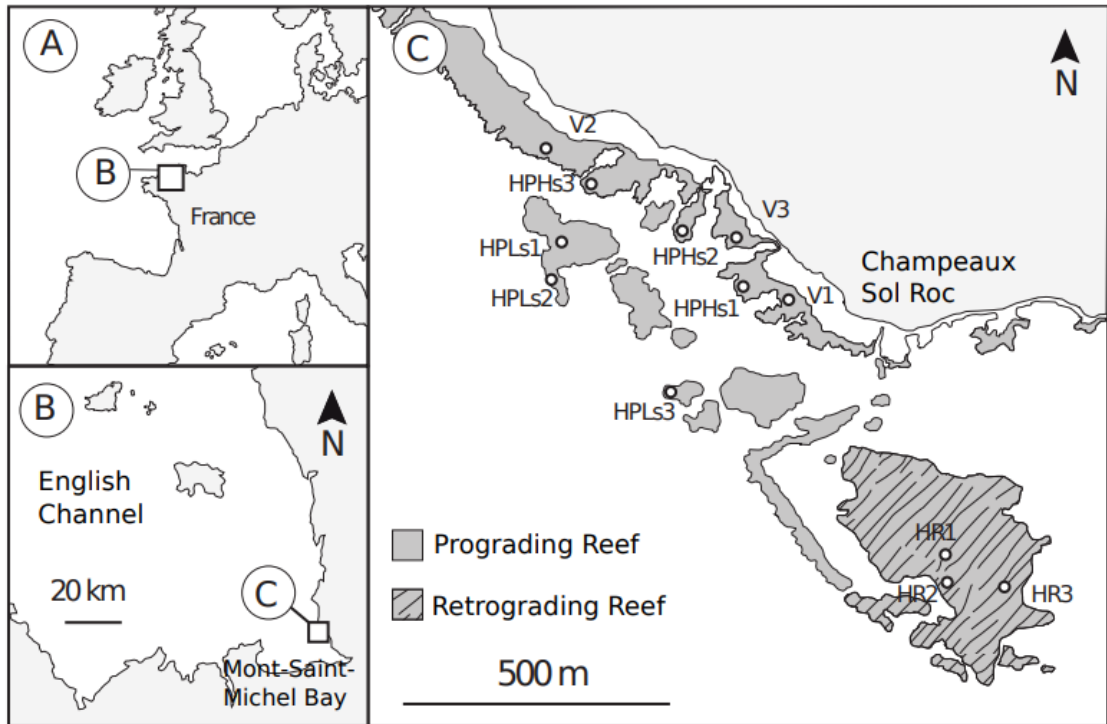


Figure 13. Map of the study site with the twelve sampling points. V=Vener, HR= Retrograding Hummock, HPHs=Prograding Hummock High Shore, HPLs=Prograding Hummock Low Shore.

2.2. Sampling design

Twelve patches of *S. alveolata* were sampled on the bioconstruction during low water on the 22nd February 2016. Five individual worms were extracted from each patch of either vener or hummock type (Table 3). For hummocks, the distinction was made between formations presenting outward signs of either progradation or retrogradation. Most treatments were well interspersed over the study area, but within ~50 m from each other. Although we would have ideally wished to sample all shore heights and phases for all types, our study location only allowed for prograding hummocks to be sampled both on the high and low shore, whilst retrograding hummocks were only present in the eastern part of the study site (Figure 13).

Small clumps of tubes were broken off, and five females were gently extracted from their tubes for each sampling point. In addition, five males were sampled from one low-shore hummock patch located in the centre of the reef. Worms were randomly sampled within mature individuals. Maturation stage was

assessed by visual examination of the extracted worms. Unspent (*i.e.* those that had not shed their gametes) worms are creamy white for males and purplish/rose-violet for females, while spent worms are thin-bodied brownish (see Wilson, 1971, Gruet and Lassus, 1983, Wilson, 1968 cited in Culloty et al., 2010). All sampled worms were placed in cryotubes and immediately flash frozen in liquid nitrogen *in situ* before they could start releasing their gametes. Samples were then long-term stored at -80°C until laboratory analyses.

Table 3. Summary of the sampling design. Abbreviations: nc, not considered for analysis; F, Female; M, Male.

Bioconstruction		Shore level	Sex	Patch	Number of individuals	Code
Type	Phase					
Hummock	Retrogradation	nc	F	1	5	HR1
Hummock	Retrogradation	nc	F	2	5	HR2
Hummock	Retrogradation	nc	F	3	5	HR3
Hummock	Progradation	High	F	1	5	HPHs1
Hummock	Progradation	High	F	2	5	HPHs2
Hummock	Progradation	High	F	3	5	HPHs3
Hummock	Progradation	Low	F	1	5	HPLs1
Hummock	Progradation	Low	F & M	2	5 & 3	HPLs2
Hummock	Progradation	Low	F	3	5	HPLs3
Veneer	nc	nc	F	1	5	V1
Veneer	nc	nc	F	2	5	V2
Veneer	nc	nc	F	3	4	V3

2.3. Laboratory analyses

Individual worms were weighed and ice-cold milliQ water was added at ¼ mass volume ratio. Then, samples were grinded and homogenised 2×20 seconds at 4.5 m sec⁻¹ using the FastPrep-24™ 5G Instrument (MP Biomedicals SARL, Illkirch, France). Tissue samples were aliquoted in one tube containing 100-200 µL for lipid analyses and in six tubes containing 180 µL for carbohydrate and protein extraction.

2.3.1 Carbohydrates

An aliquot of 180 µl of tissue sample was used for determination of total carbohydrate concentrations. Briefly, samples were diluted 10 times by addition of 820 µL MilliQ water. Carbohydrate concentrations were determined by colorimetric method according to DuBois (1956). Then, samples (250 µL) were mixed with phenol (0.5 ml, 5% m/v) and sulfuric acid (2.5 ml, 98%), and incubated for 40 min. Absorbance was read at 490 nm with a UV 941 spectrophotometer (Kontron instruments, San Diego, California, USA). Carbohydrate concentrations were determined using a standard calibration curve and expressed as mg of carbohydrates per g of wet weight.

2.3.2 Lipids

2.3.2.1 Extraction

One aliquot tube of 180µl was used for determination of fatty acid profiles of neutral and polar lipids. The sample was transferred into a 6 mL glass vial. Lipids were extracted according to Bligh and Dyer (1959). A mixture of CHCl₃:MeOH 1:2 (v/v, 750 µL) was added to the sample. Then, the sample was vortexed before adding pure CHCl₃ (250 µL), vortexed again, diluted with MilliQ water (250 µL), vortexed again, and centrifuged at 3000 rpm for 5 minutes. The lower organic phase was transferred into another clean 2-mL glass vial. The remaining aqueous phase was washed with 500 µL CHCl₃, vortexed, and centrifuged again. The lower phase was recovered, pooled with the first one and evaporated under a nitrogen flow. The sample was stored at -20°C in 1 mL of CHCl₃:MeOH 98:2 (v/v).

2.3.2.2 Neutral and Polar Lipid Separation

Subsamples (250 µL) were then placed on the top of a silica gel micro column (30×5 mm internal diameter; Kieselgel; 70–230 mesh (Merck, Lyon, France); previously heated to 450°C and deactivated with 5% water) (Marty et al., 1992). Neutral lipids were eluted with 10 ml of CHCl₃:MeOH (98:2, v/v) and the polar

lipids were recovered with 15 ml of MeOH. A known amount of tricosanoic acid (23:0) was added to both fractions as an internal standard. The lipid fractions were evaporated to dryness under nitrogen, re-suspended in CHCl₃:MeOH 2:1 (v/v) before transesterification.

2.3.2.3 Transesterification

Neutral and polar lipids were transesterified at 100°C for 10 min with 1 mL of boron trifluoride-methanol (12% MeOH) (Metcalf and Schmitz, 1961). This transesterification produces fatty acid methyl esters (FAME) from the fatty acid esterified at the sn-1 and sn-2 position of diacylphospholipids, and the sn-2 position of plasmalogen phospholipids. It also produces dimethyl acetals (DMA) from the alkenyl chains at the sn-1 position of plasmalogens (Morrison and Smith, 1964). FAME and DMA were analysed in a HP6890 gas-chromatography system (Hewlett-Packard) equipped with a DB-Wax capillary column (30 m × 0.25 mm; 0.25 µm film thickness; Agilent technologies). Peaks were analysed by comparison with those of a standard 37 component FAME mix (Supelco® 37, Merck) together with other known FAME mixes from marine invertebrates. Each fatty acid was expressed as the peak area percentage of the total fatty acid content. Total DMA was used as an indicator of the plasmalogen level.

The fatty acid trophic markers investigated in this study were the ratio of 16:1n-7/16:0 and 16:4n-1 both of which indicate the contribution of diatoms to the diet; the ratio of 22:6n-3/20:5n-3 which is used as an indicator of dinoflagellate contribution relative to diatoms, all of the sum of 18:2n-6 and 18:3n-3, which is generally considered as a marker of terrestrial inputs; the ratio of 18:1n-9/18:1n-7, which is generally used as an indicator of carnivory; the ratio of polyunsaturated/saturated fatty acid (PUFA/SFA), which is an indicator of food freshness; and the sum of iso- and anteiso-branched chain fatty acids and unbranched 15:0 and 17:0, which reflects the contribution of bacteria to the organic matter. These fatty acid food web markers are routinely used in trophic ecology (Dalsgaard, 2003). The ratio of neutral to polar lipid content was also

calculated, as this proxy reflects the relative contribution of reserve to structural lipids and is used as a nutritional condition index that is scaled to body size (Hentschel, 1998).

2.3.3 Enzymes

2.3.3.1 Protein extraction and quantification

Tissue samples of 150µl were diluted by 2/3 in ice-cold lysis buffer solution and homogenized with a Polytron® PT 2500 E (Kinematica, Luzernerstrasse, Switzerland). The buffer solution was made of 150 mM NaCl, 10 mM Tris, 1 mM EDTA, 1 mM EGTA, 1% Triton X-100, 0.5% Igepal, 1 tablet of complete EDTA free protease inhibitor cocktail (Roche Diagnostics, Risch-Rotkreuz, Switzerland) in 25 ml of buffer, phosphatase inhibitor cocktail III (Merck KGaA, Darmstadt, Germany) all at pH 7.4 (Le Foll et al., 2006). Homogenates were incubated for 1 hour before being centrifuged twice at 4000 rpm for 1 hour at 4°C and at 11700 rpm for 45 min at 4°C to eliminate the lipid fraction of the samples, using GR412 and MR22 Jouan centrifuges (Thermo Scientific, Waltham MA, USA), respectively. The resulting supernatants were aliquoted and stored at -80°C until protein quantification and enzyme assays.

To determine total protein concentration, an aliquot of protein extract was diluted by 1/10th and quantified according to Lowry et al. (1951) using the DC_{tm} protein assay kit (Bio-Rad, Hercules, California, USA). Absorbance was read at 750 nm and protein concentrations were determined by comparison with a calibration curve of Bovine Serum Albumin provided with the kit. Results were expressed as mg of proteins per g of dry tissue weight.

2.3.3.2 Citrate synthase

Enzyme assays were performed in triplicate at room temperature and enzyme activities were expressed and related to the total protein concentration for each sample.

Citrate synthase activity (CS; EC 4.1.3.7) was assayed at room temperature according to Childress and Somero (1979). Protein extract (20 µL) was added in

wells containing an assay buffer solution (160 μL) which consisted of 100 mM Tris-HCl, 0.2 mM acetyl-coenzyme A, 0.1 mM 5, 5' -dithio-bis-[2-nitrobenzoic] acid (DTNB). The reaction was initiated by adding oxaloacetate (0.5 mM; 20 μL). Absorbance was recorded for 10 min at 412 nm using a Synergy HT microplate reader (BioTek, Winooski VT, USA). Results were expressed in mU mg^{-1} protein, where 1 U is the amount of enzyme to catalyze 1 μmole of TNB per minute (using $\epsilon_{\text{TNB},412} = 13.6 \text{ mM}^{-1} \text{ cm}^{-1}$).

2.3.3.3 Superoxide dismutase

Total superoxide dismutase activity (SOD; EC 1.15.1.1) was determined using an assay kit (Merck KgaA, Darmstadt, Germany), following the manufacturer's instruction. Superoxide dismutase activity (SOD) was measured by adding 200 μL of Water-Soluble Tetrazolium salt (WST-1) to 15 μL of total protein lysates 10 times diluted, and the reaction was initiated by adding 20 μL of xanthine oxidase (XO) and xanthine mix. After a 20 min incubation at 37°C, absorbance was read at 450nm using a Synergy HT microplate reader (BioTek, Winooski VT, USA). SOD is quantified by comparing the decrease in the colour development at 450nm to a standard inhibition curve, performed using SOD from bovine erythrocytes. Results were expressed in units per mg of protein (U/mg), where 1 U of SOD is the amount of enzyme necessary to inhibit by 50% the xanthine/XO complex formation.

2.3.3.4 Catalase

Catalase activity (CAT; EC 1.11.1.6) was assessed at room temperature following Aebi (1984). Briefly, 5 μL of 10 times diluted protein supernatant were added to 195 μL of hydrogen peroxide solution (10 mM) to initiate the reaction. Absorbance was immediately recorded for every 15 s for 4 min using a Synergy HT microplate reader (BioTek, Winooski VT, USA). CAT is expressed in U/mg protein where 1 U is the amount of enzyme necessary for catalysing 1 μmole of H_2O_2 per min (using $\epsilon_{\text{H}_2\text{O}_2}, 39.4 \text{ mM}^{-1} \text{ cm}^{-1}$).

2.3.4 Statistical analyses

Mixed design analyses of covariance (ANCOVA) were used to compare lipid, carbohydrate, and protein contents, enzyme activities and relative fatty acid concentration of the *S. alveolata* samples among the different bioconstruction types, phases and shore level. In the model, the random factor was the patch where the samples were taken and the covariate was individual worm mass (*i.e.* wet weight measures for 59 individual females). The individual worm mass did not vary with bioconstruction characteristics (ANOVA F -test=2.35, $p=0.148$) and can therefore be used as an independent factor. The categorical fixed variables were the four combinations of bioconstruction types and phases: veneer (V), retrograding hummock (HR) and prograding hummock located either on the high-shore (HPHS) or low-shore (HPLs). Interactions between bioconstruction characteristics and worm mass were systematically not significant and therefore omitted from the model (Table 4). When F -tests were significant the following *a priori* null hypotheses (H_0) were tested using contrasts:

$$H_{0_1}: \mu_V = \frac{\mu_{HR} + \mu_{HPHS} + \mu_{HPLs}}{3}$$

$$H_{0_2}: \mu_{HR} = \frac{\mu_{HPHS} + \mu_{HPLs}}{2}$$

$$H_{0_3}: \mu_{HPHS} = \mu_{HPLs}$$

To compare males and females, the unequal variance T -test was used. The normality of residuals and homogeneity of variances were investigated using Box-Cox transformations (Box and Cox, 1964). When necessary, data were log-transformed. All statistical tests were performed with SAS software (SAS 9.4, Carry NC, USA).

Table 4. Summary of the mixed analyses of covariance (ANCOVA) model used for comparing females. df = degrees of freedom

Sources of variation	df
Main-plot analysis	
Bioconstruction characteristics	3
H0 ₁ : Veneer (V) = Hummock (H)	1
H0 ₂ : Retrograding H (HR) = Prograding H (HP)	1
H0 ₃ : HP High-shore (HPHs) = HP Low-shore (HPLs)	1
Error a: Patch (Bioconstruction characteristics)	8
Subplot analysis	
Individual worm mass	1
Error b: Individual worm mass × Patch (Bioconstruction characteristics)	47
Total	59

3. Results

We investigated the effect of bioconstruction characteristics, worm mass and sex on 16 different parameters grouped into four categories (Figure 14 to Figure 17). We report that bioconstruction characteristics were associated with variations in three out of four indicator categories, whereas both individual mass and sex drove differences in all four categories.

3.1. Organic Macromolecules

There was a significant relationship between the neutral:polar lipid ratio and bioconstruction characteristics (Figure 14c), where the two bioconstruction phases contrasted significantly ($F_{1,8}=20.1$, $p=0.002$), with a higher neutral:polar lipid ratio found in the retrogradation phase. Individual wet weight was negatively correlated with both carbohydrate and protein concentration, and positively correlated with neutral:polar lipid ratio (Figure 14d-f). Females had a neutral:polar lipid ratio that was 5.9 times higher than males (Figure 14i),

however sex had no effect on either proteins or carbohydrates (Figure 14g and h).

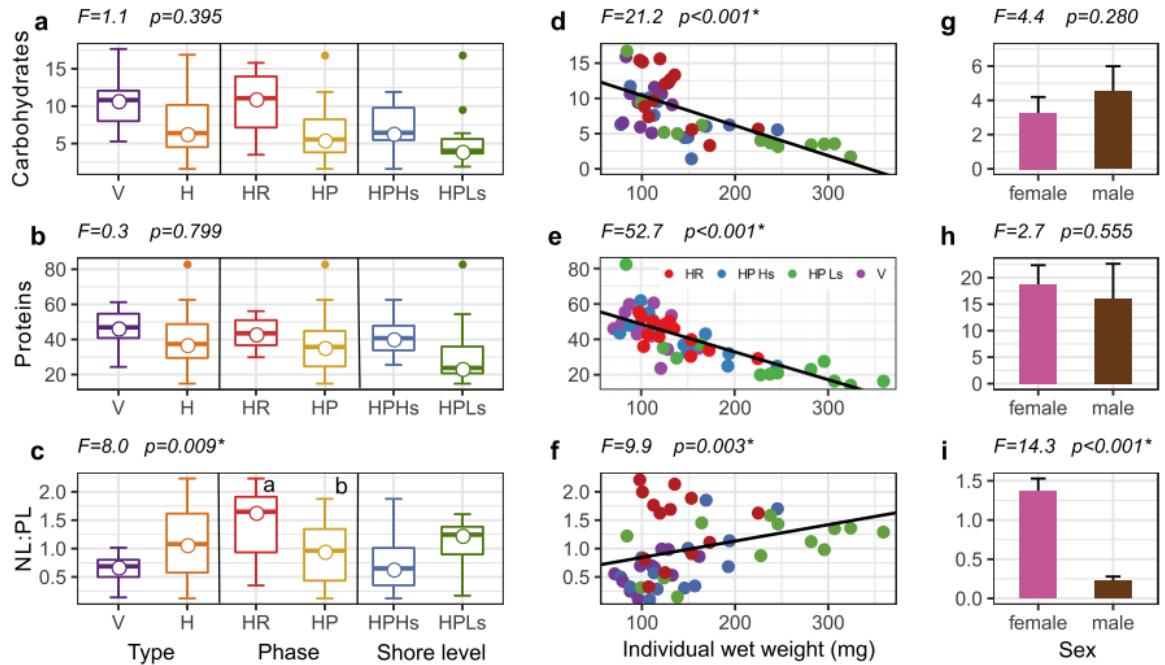


Figure 14. Organic macromolecules in the honeycomb worm *Sabellaria alveolata* as a function of bioconstruction type, bioconstruction phase and shore level (a-c, n=59), worm mass (d-f, n=59) and sex (g-i n=8 (5 female, 3 male)). All y axis units are mg.g⁻¹ tissue. V=Veneer, H=Hummock, HR=Retrograding Hummock, HP=Prograding Hummock, HPHs=Prograding Hummock High shore, HPLs=Prograding Hummock Low shore. Carbohydrate statistical test results are log-transformed. The letters “a” and “b” represent a significant difference in the contrast test ($p=0.002$). * = $p\leq 0.05$.

3.2. Fatty acids

3.2.1. Polar lipids

There was a significant effect of bioconstruction characteristics on both gadoleic (20:1n-11) and arachidonic (20:4n-6) acid after controlling for individual worm mass. Gadoleic acid varied with bioconstruction type and was significantly higher in worms sampled in hummocks than in worms from veneers ($F_{1,8}=12.0$, $p=0.009$) (Figure 15a). Arachidonic acid levels varied with bioconstruction phase and were significantly lower in retrograding hummocks ($F_{1,8}=7.8$, $p=0.024$) (Figure 15b). 20:4n-6 levels were near-significantly lower on the low shore ($F_{1,8}=4.8$, $p=0.059$) at 1.9%, compared to 2.2% on the high shore.

Both eicosapentaenoic acid (20:5n-3) and docosahexaenoic acid (22:6n-3) were not influenced by bioconstruction characteristics (Figure 15c and d). 22:6n-3 was the only polar lipid fatty acid to be significantly negatively correlated with individual wet weight (Figure 15h). Sex clearly influenced levels of 20:1n-11 and 22:6n-3 content but had no effect on the other markers (Figure 15i and l); the former is present in greater quantity in females than in males whereas the latter is present in greater quantity in males than in females.

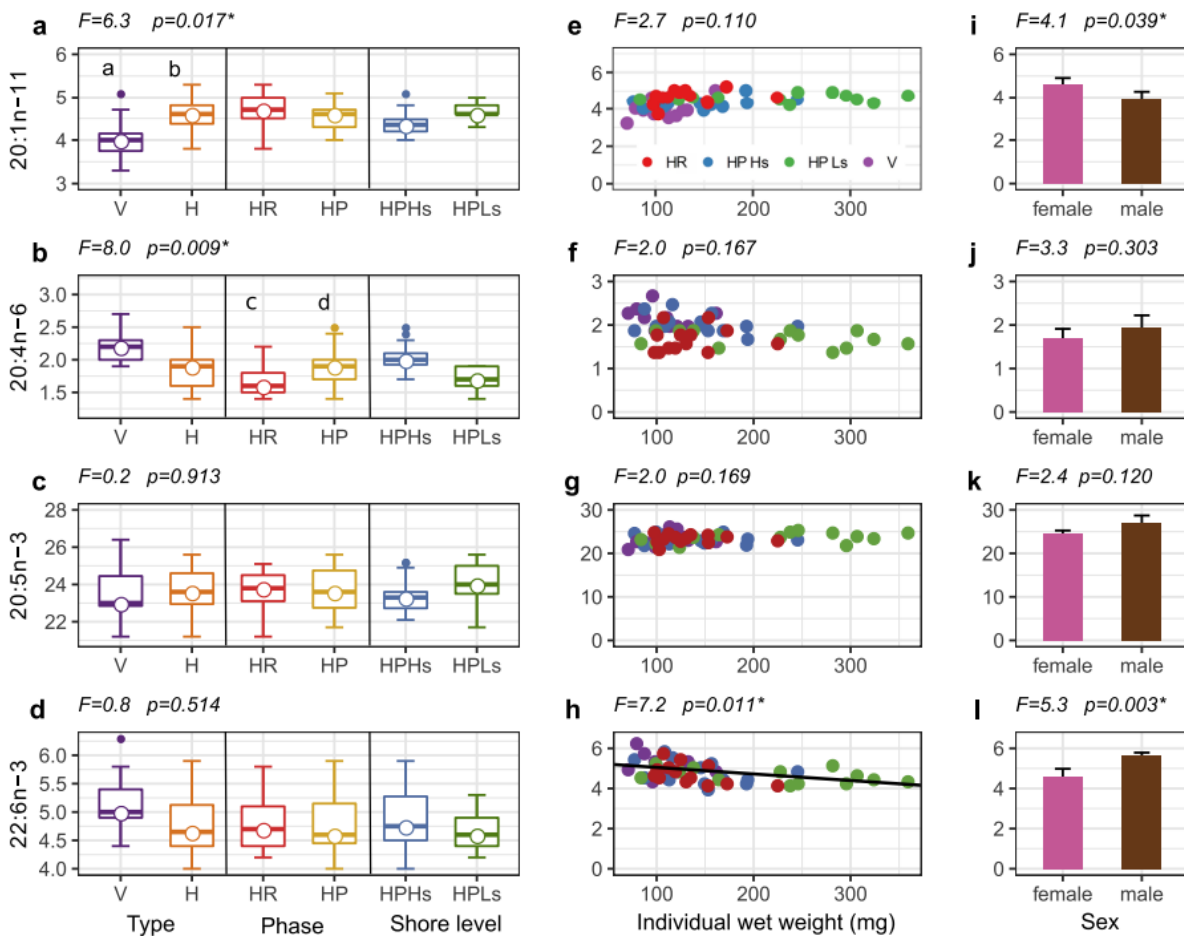


Figure 15. Polar lipids in the honeycomb worm *Sabellaria alveolata* as a function of bioconstruction type, bioconstruction phase and shore level (a-d, n=59), worm mass (e-h, n=59) and sex (i-l, n=8 (5 female, 3 male)). All y axis units are a percentage of total phospholipids. Note that the y axis scale varies between fatty acids. V=Veneer, H=Hummock, HR=Retrograding Hummock, HP=Prograding Hummock, HPHs=Prograding Hummock High shore, HPLs=Prograding Hummock Low shore. 22:6n-3 statistical test results are log-transformed. The letters “a” and “b” represent a significant difference in the bioconstruction type contrast test ($p=0.009$), and the letters “c” and “d” in the bioconstruction type contrast test ($p=0.024$). * = $p\leq 0.05$.

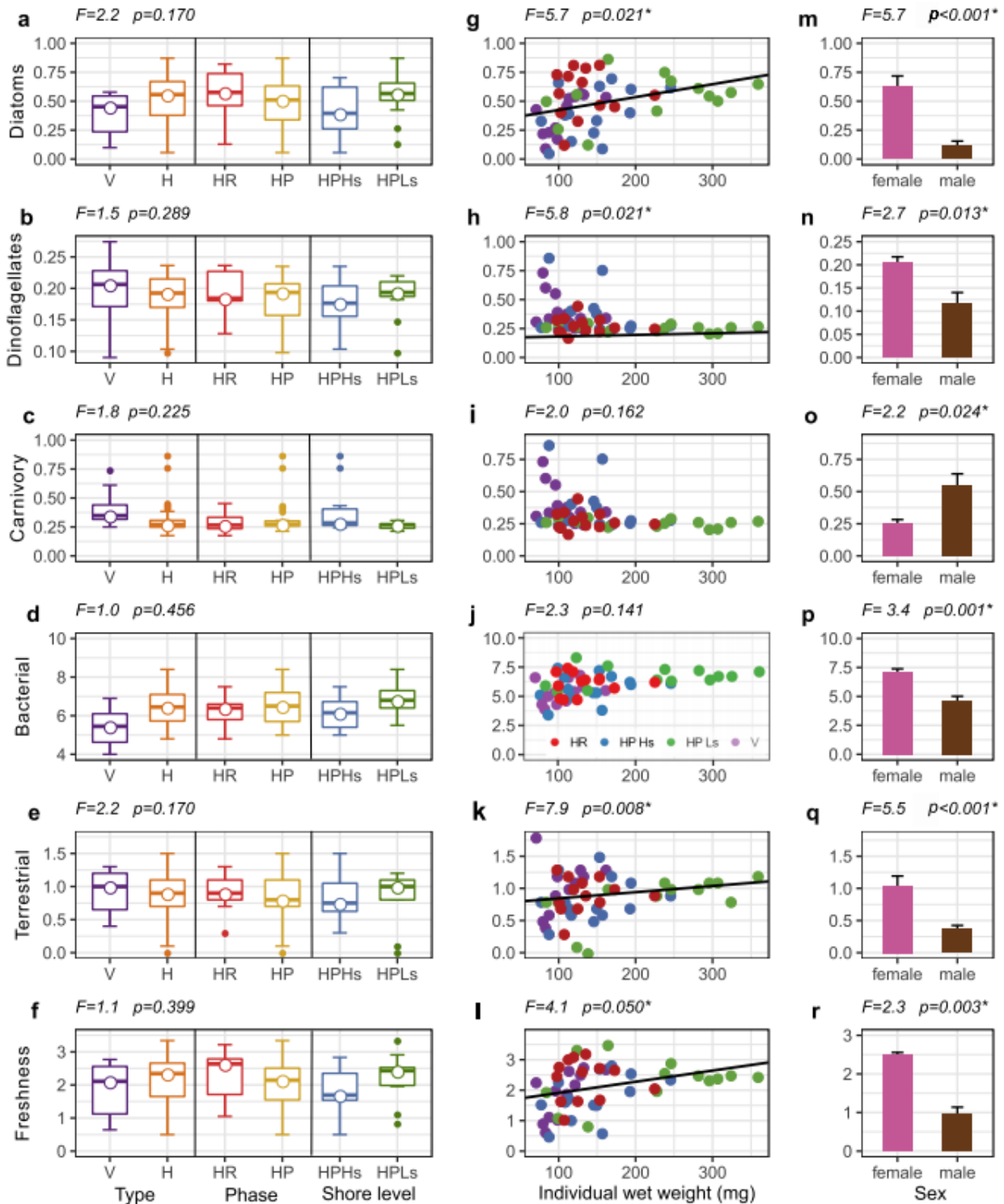


Figure 16. Neutral lipids in the honeycomb worm *Sabellaria alveolata* as a function of bioconstruction type, bioconstruction phase and shore level (a-f, n=59), worm mass (g-k, n=59) and sex (m-r, n=8 (5 female, 3 male)). All y axis units are a percentage of total neutral lipids. Note that the y axis scale varies between fatty acids. Diatoms=16:1n-7/16:0; Dinoflagellates=22:6n-3/20:5n-3; Carnivory=18:1n-9/18:1n-7; Bacterial = 15:0 + 17:0 + branched fatty acids; Terrestrial= 18:2n-6 + 18:3n-3; Freshness= PUFA/SFA. V=Veneer, H=Hummock, HR=Retrograding Hummock, HP=Prograding Hummock, HPHs=Prograding Hummock High shore, HPLs=Prograding Hummock Low shore. * = p≤0.05

3.2.2. Neutral lipids

Fatty acid composition in neutral lipids was not influenced by bioconstruction characteristics (Figure 16a-f). With the exception of bacterial and carnivory markers, all neutral lipids were positively influenced by individual wet weight (Figure 16gh and kl). A strong difference between male and female was observed for all trophic markers, with female worms exhibiting higher values for all markers except for carnivory, where males have 18:1n-9/18:1n-7 levels twice as high as those found in females (Figure 16o). The 16:1n-7/16:0 ratio (Figure 16a), which is used as a diatom tracer, was corroborated by a second diatom tracer, 16:4n-1 (Appendix 1, Figure 37), whose concentration was significantly influenced by both individual wet weight and sex.

3.3. Enzyme assays

Citrate synthase activity (CS) was significantly affected by bioconstruction characteristics (Figure 17a); average CS was near significantly higher in worms sampled in hummocks than in veneers ($p=0.054$), and twice as high in worms sampled in the retrogradation phase compared to the progradation phase ($F_{1,8}=10.1$, $p=0.013$). Although superoxide dismutase activity (SOD) was not significantly influenced by bioconstruction characteristics (Figure 17), SOD positively correlated with CS (Appendix 1, $CS=0.95+3.17\times SOD$, $r^2=0.400$ $p<0.001$). Individual wet weight was negatively correlated with CS, but not with catalase activity (CAT) or SOD (Figure 17). Sex clearly influenced CS activity but had no effect on either CAT or SOD (Figure 17cfi). Mean CS was 3.8 times higher in males than in females (Figure 17c). Relationships among all variables measured in our study were represented in a principal component analysis biplot (Appendix 1).

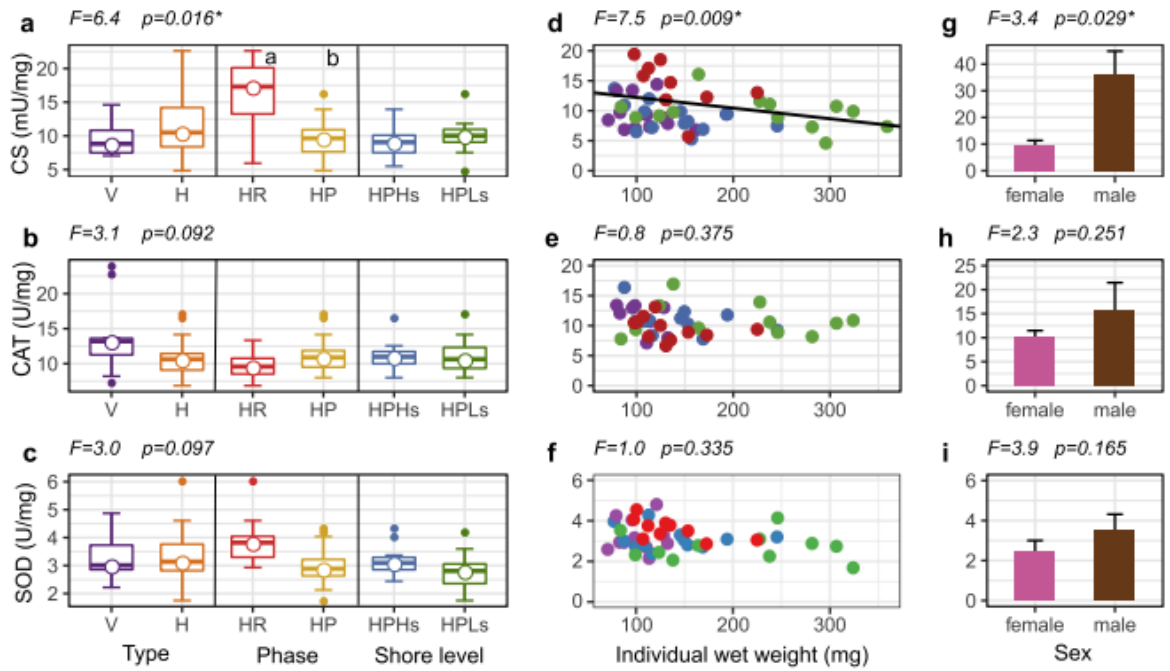


Figure 17. Enzyme levels in the honeycomb worm *Sabellaria alveolata* as a function of bioconstruction type, bioconstruction phase and shore level (a-c, n=59), worm mass (d-f, n=59) and sex (g-i, n=8 (5 female, 3 male)). CS y axis units are micro Units $\text{mU}\cdot\text{mg}^{-1}$ of protein, whereas CAT and SOD units are $\text{U}\cdot\text{mg}^{-1}$ of protein. CS= Citrate synthase, CAT=Catalase, SOD=Superoxide dismutase. V=Veneer, H=Hummock, HR=Retrograding Hummock, HP=Prograding Hummock, HPHs=Prograding Hummock High shore, HPLs=Prograding Hummock Low shore. All statistical test results are log-transformed. The letters “a” and “b” represent a significant difference in the contrast test ($p=0.013$). * = $p\leq 0.05$.

4. Discussion

Our study revealed that a retrograding *Sabellaria alveolata* bioconstruction does not necessarily equate with reserve-depleted worms. Indeed, carbohydrate levels did not vary between retrograding and prograding bioconstructions, and the ratio of neutral:polar lipids was in fact higher in the retrogradation phase. Neutral lipids are essential energy reserves for sustaining early life stages and play a key role in settlement, habitat selectivity and recruitment in marine invertebrates (e.g. Tremblay et al., 2007). Also, higher levels of energetic reserves are associated with a better ability to cope with stressful situations such as pathogen resistance (Lochmiller and Deerenberg

2000, Pernet et al., 2014, Ellis et al., 2011). It is therefore likely that worms living in retrograding reefs are better equipped to face stressful situations.

We also found that levels of 20:4n-6 in the polar lipids of worms sampled in the retrogradation phase were lower than in the progradation phase, unexpectedly compounding the fact that worms are more stressed in progradation phase bioconstructions. Arachidonic acid is a precursor of hormones involved in stress response and levels increase for example with increasing temperature in *S. alveolata* (Muir et al., 2016). These authors found that across six sampling stations spanning Scotland to Morocco, the level of 20:4n-6 was lowest in worms collected in the Bay of Mont-Saint-Michel where environmental conditions were perceived to be the most favourable (e.g. hydrodynamics and sediment supply). Indeed, this is a central population within the geographic distribution of *S. alveolata* and supports the largest living biogenic reefs in Europe. Differences in 20:4n-6 observed between the two bioconstruction phases in our study were however weak (0.25%) compared to existing natural variability across the range (1-5%, Muir et al., 2016). Membrane 20:4n-6 is therefore a good indicator of stress, as it can detect differences locally as well as across a species distribution range and is therefore applicable at several scales.

Citrate synthase activity (CS) was twice as high in worms sampled in the retrogradation phase compared to the progradation phase. The CS involved in ATP generation reflects the oxygen consumption rate of animals and has been used in community ecology to evaluate the physiological status of rocky intertidal invertebrates (Dahlhoff et al., 2002). CS varies in response to multiple variables. For example, CS in marine invertebrates increases with food availability (Dowd et al., 2013), growth rate (Garcia-Esquivel et al., 2002), maintenance costs and mitochondrial density (Moyes, 2003). Therefore, the elevated levels of CS presented here require interpretation in conjunction with other markers. In our study, the observed increase in CS in retrograding bioconstructions coincided with higher levels of stored lipid reserves, as

reflected by the higher neutral:polar lipid ratio. Therefore, it may reflect a feeding-induced increase in aerobic metabolism as reported in fish larvae (Ferron and Leggett, 1994) and intertidal invertebrates (Dahlhoff, 2002). Although superoxide dismutase activity (SOD) was not significantly influenced by overall bioconstruction characteristics, SOD correlated with CS and was higher in the retrogradation phase. This also points towards worms sampled in retrograding bioconstructions having a faster metabolism, as SOD processes the ROS metabolic by-products produced through aerobic respiration (Abele and Puntarulo, 2004).

To sum up, high neutral:polar lipids, low 20:4n-6, high CS, high SOD and undepleted carbohydrates all indicate that worms sampled in retrograding bioconstructions were not stressed, but rather had either a higher quantity or quality of food source. As all trophic markers were remarkably similar between the two bioconstruction phases, worms sampled in the retrogradation phase reef probably had access to food of the same quality but in greater quantity. Intraspecific competition in a densely-populated progradation-phase bioconstruction is a source of physiological stress due to limited food availability (Connell, 1983). Alternatively, retrograding bioconstructions harbour more small cracks and crevices filled with deposited sediment on top of which microphytobenthos can grow and that can be made available through resuspension processes (Dubois et al., 2007a; Lefebvre et al., 2009; Jones et al., 2018). Microphytobenthos is mostly composed of benthic diatoms, which are of great dietary value, compared to phytoplankton (Miller et al., 1996).

Existing assessments of the health of biogenic habitats depend primarily on visual criteria. Certain aspects of the health of tropical coral reef polyps have made use of biochemical markers, by assessing the size of energy stores (as lipid content) as a proxy for physiological condition (Anthony, 2006) or by using CS and energy-storage lipids to see how scleractinian coral larvae respond to ocean acidification and warming (Rivest and Hoffmann 2014; Rivest et al., 2017). However, none of these studies made a link between the coral polyps and their calcareous skeleton. Attempting to join the physical appearance of a

bioconstruction with the physiological status of the engineering species is surprisingly new.

Our study confirms that designating a given *S. alveolata* bioconstruction as retrograding or prograding leaves room for interpretation, as shown for coral reefs (Abelson et al., 2017). Health criteria based on the physical appearance of the bioconstruction did not yield any information on the processes regulating individuals. Yet our results show that worms present in retrogradation phase bioconstructions are in a better physiological state compared to progradation phase worms. In a recent study, Jones et al. (2018) demonstrated the ecological value of retrograding (referred to as “degraded reef”) *S. alveolata* bioconstructions which, due to their increased micro-habitat availability, act as biodiversity and recruitment promoters and harbour more diversified food sources. *S. alveolata* colonies, in their role as habitats, may be of considerable value to certain species of very small animals (Wilson, 1971), with retrograding bioconstructions showing high numbers of associated species (Porrás et al., 1996; Dubois et al., 2002; Jones et al., 2018).

Although further work is needed to address large-scale variation over time, our results suggest that *S. alveolata* sampled in retrograding bioconstructions were in fact healthier. The only signs of ecosystem distress in the retrogradation phase are value judgments about the bioconstruction appearance. Prograding bioconstructions, with their rounded shapes and crisp porches, are often considered more aesthetically appealing than silty, pitted retrograding bioconstructions. Although visual beauty correlates with ecosystem health for tropical coral reefs (Haas et al., 2015), this does not appear to be the case for other *S. alveolata* bioconstructions.

The majority of shorelines where *S. alveolata* are present host a mosaic of bioconstruction types of varying heights and surface areas. With the exception of 20:1n-11, all of the examined parameters did not vary between bioconstruction types. Hummock and veneer sampling points were well interspersed and, due to the Mont-Saint-Michel’s bay megatidal regime, were

subjected to a homogeneous water mass. None of the biochemical parameters varied significantly between the high and low shore. Although the intertidal zone is a stressful environment (Helmuth et al., 2002; Bertness et al., 2009; Firth and Williams 2009; Firth et al., 2011), the buffering role that *S. alveolata* bioconstructions play diminishes fluctuations in temperature and humidity to the point where they are able to host a number of subtidal species (Dubois et al., 2002; Jones et al., 2018 and unpublished temperature data). It is worth mentioning that the bathymetric differences between the high and low shore sampling points were minor (*ca.* 1.5 m) compared to the tidal amplitude in the Mont-Saint-Michel (>14 m). This could explain why shore level had no effect in our sampling design. Hummocks found lower down the shore reach a greater height relative to sea level. However, this feature is common for *S. alveolata* bioconstructions which develop around the mid-tide level, with the bioconstructions located highest on the shore being submerged at least one hour less than the bioconstructions in the low intertidal zone. In an area experiencing a semidiurnal tide cycle, this translates as four less hours to filter-feed per lunar day, hence explaining why the largest individuals are typically found in the bioconstructions lowest down the shore.

There was a five-fold difference in individual wet weight across sampled individuals, with specimens ranging from ~70 to ~350 mg. We found that energetic reserves, CS, 22:6n-3 in phospholipids and four out of six trophic markers were correlated with size. It is therefore vital to take *S. alveolata* individual size into consideration when analyzing biochemical variables, something that is not systematically done in marine invertebrate biochemical studies. Carbohydrate and protein concentrations diminished with individual mass whereas neutral lipids increased, reflecting a size-specific biochemical composition. All of the sampled individuals were mature and collected at the adult stage. Therefore, size may be confounded with age, and differences in biochemical composition could reflect either. Both CS and 22:6n-3 decreased with increasing individual mass. Body mass and basal metabolic rates are allometrically related (Hochachka and Somero, 2002). Our results suggest that

differences in respiration rate in *S. alveolata* relate to cell membrane fatty acid composition. This is consistent with Hulbert's theory of membranes as metabolic pacemakers (Hulbert et al., 2005).

We found that the neutral:polar lipid ratio and five out of six neutral lipid fatty acid trophic markers were higher in female worms, whereas 22:6n-3, the carnivory trophic marker and CS were all significantly higher in male worms. Docosahexaenoic acid (DHA – 22:6n-3) is abundant in spermatozoa (Masuda, 2003), and hence is the only polar lipid fatty acid significantly higher in males. Invertebrate eggs typically contain few carbohydrates and are mainly composed of energy dense proteins and lipids, hence explaining higher neutral lipid contents in females (Pernet and Jaekle, 2004). Female worms stored four times more neutral lipids than males. The neutral lipid fatty acid composition is transferred more conservatively than the polar lipid fraction and therefore mirrors more closely that of the diet. Females containing high neutral lipid levels are more susceptible to dietary change than males which contain mostly polar lipids. This renders neutral lipid-rich female *S. alveolata* more suitable than males for representing trophic-related changes in the environment, especially when investigating diets or changes in food source composition. In order to use biochemical indicators for studying trophic interactions, it is therefore important to be able to distinguish the two sexes and to sample and analyse female *S. alveolata*.

Our study examined a one-time sampling event at a single study location. Increased spatio-temporal sampling may further clarify differences between the long-term physical changes of the bioconstruction and the short-term physiological state of the worm. In the progradation phase, *S. alveolata* individuals displayed biochemical stress markers. However, this may be considered as temporary stress due to, for example, momentarily lacking sufficient food. A bioconstruction can move rapidly between progradation and retrogradation phases and is therefore an inherent or “natural” fluctuation. An alternative scenario is that the worm population is physiologically stressed beyond recovery. When resilience is exceeded, the future of the

bioconstruction is entirely dependent on primary or secondary settlement, thus reflecting some kind of fundamental change in underlying dynamics (Johnson, 2009). Although retrograding bioconstructions support worms in a better physiological condition, the high diversity this phase supports may have a negative effect both on adult worms through interspecific competition, and on *S. alveolata* larval recruitment, as epiflora can lower successful recruit density due to the mechanical action of algal fronds sweeping the reef surface (Dubois et al., 2006). Bioconstructions will no doubt naturally undergo a cycle of progradation and retrogradation. However, when resilience is exceeded the balance between these two phases is upset and may cause the system to “flip” to an alternative state (Fung et al., 2011). An ecosystem’s health can be defined in terms of system vigour, organisation and resilience (Costanza, 1992). Whilst existing ecological studies attest to retrograding *S. alveolata* bioconstruction vigour and organisation (Dubois et al., 2002; Jones et al., 2018), further work is needed to quantify their resilience.

The European Habitats Directive, and the overarching Marine Strategy Framework Directive (MSFD, 2008/56/EC) give statutory significance to the definition of a “reef”. Crucially, the distinction between what is considered as “reef” and what is not, is imprecise. Which *S. alveolata* bioconstruction type, and which progradation/retrogradation phase criteria are of conservation value, are yet to be defined. This has far-reaching implications in terms of environmental management and conservation. The offset between the physical state of the bioconstruction and the physiological state of the worm makes it vital to analyse the two together, and to understand the natural history and physiology of one’s study organisms when using biochemical indicators for ecological studies (Dahlhoff, 2004). Seasonal, broad-scale studies are therefore warranted to further our understanding of the link between the engineer species and the engineered habitat it creates.

5. Conclusion

The metabolic enzymes citrate synthase and superoxide dismutase, when analysed in conjunction with the polar lipid fatty acid 20:4n-6, serve as stress markers for the physiological state of *S. alveolata*. Once seasonal and inter-site variation have been addressed, these three biochemical indicators could be looked at in priority, in concurrence with *S. alveolata* bioconstruction physical criteria, as part of a European-wide monitoring protocol. Member states will be updating their MSFD monitoring programme and measures in the coming years and are being urged by the European Commission for a coherent and coordinated approach within and between marine regions. Although exploratory biochemical analyses time and money costs are high, they greatly diminish with subsequent routine screening of a few key indicators. Furthermore, few worm specimens are needed and their collection is substantially less destructive than the sediment core sampling typically used for obtaining biodiversity metrics. Whereas physical bioconstruction parameters are site-specific, biochemical indicators are applicable across a species range and therefore serve as large-scale, quantitative metrics, provided that sex and size are controlled for.

CHAPTER II

In the second chapter of this thesis, the focus was on geographical patterns in the reproductive traits of *S. alveolata*: how these are linked to their individual physiological condition, and how they are shaped by their local environment. This chapter bridges the disciplines of reproductive biology, physiological ecology and biogeography by using a blend of field studies, biochemical markers, remotely-sensed products and novel instruments, each of which comes with their own suite of analytical tools and literature.

By sampling individuals from 10 sites, in summer and in winter, across a significant portion of its distribution area (from Criccieth in northern Wales to Buarcos in central Portugal – 14.5° in latitude), we were able to test whether variable abiotic conditions were responsible for intraspecific trait variation. We further verified two theories making contrasting predictions on how reproductive traits should vary, both within and among populations. On one hand, biogeography predicts that populations with high individual performance and abundance decrease from optimal conditions at the centre of their range towards marginal conditions at the periphery where populations are increasingly stressed. On the other hand, evolutionary biology makes predictions based on resource allocation and the ensuing life-history trait trade-offs. Stressful conditions, regardless of the position within a range, could for example lead to higher reproductive output, because of a low probability of surviving to the next reproductive event.

Our results show that intraspecific reproductive trait variation was indeed highest in locations subjected to extreme hydrodynamic or temperature events, and demonstrate that both biogeographic and evolutionary biology theory apply to *S. alveolata* reproductive traits, depending on the trait and time scale being studied. As part of an integrated approach to studying spatial variation in reproductive traits, we make the case for using the variability in innovative reproductive response traits (circularity and symmetry of eggs), as well as biochemical traits of physiological condition.

ARTICLE II – AN EGG-CENTRIC PERSPECTIVE INTO THE REPRODUCTIVE TRAIT VARIABILITY OF A FOUNDATION SPECIES

Amelia Curd¹, Aurélien Boyé¹, Céline Cordier¹, Fabrice Pernet², Louise B. Firth³, Laura Bush⁴, Andrew J. Davies⁵, Fernando Lima⁶, Claudia Meneghesso^{6,7}, Claudie Quéré², Rui Seabra⁶, Mickaël Vasquez¹ and Stanislas F. Dubois¹

Article prepared for Ecology

¹ IFREMER, Centre de Bretagne, DYNECO LEBCO, 29280 Plouzané, France.

² IFREMER, Centre de Bretagne, LEMAR UMR 6539, 29280 Plouzané, France.

³ School of Biological and Marine Sciences, University of Plymouth, Drake Circus, Plymouth, PL4 8AA, , United Kingdom.

⁴ FUGRO GB Marine Limited, Gait 8, Research Park South, Heriot-Watt University, Edinburgh EH14 4AP, United Kingdom.

⁵ Department of Biological Sciences, University of Rhode Island, Kingston, RI 02881, USA.

⁶ CIBIO-InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto, Campus Agrario de Vairão, 4485-661, Vairão, Portugal.

⁷ Departamento de Biologia, Faculdade de Ciências da Universidade do Porto, R. Campo Alegre, s/n, 4169-007 Porto, Portugal

Abstract

Elucidating the key dimensions of an ecosystem engineers' reproductive traits is critical for understanding, predicting and ultimately managing the high-biodiversity biogenic habitat they create. The fields of biogeography and evolutionary biology make different predictions for how reproductive traits should vary, both within and among populations. We empirically investigated two contrasting theoretical approaches by determining geographic patterns in

the reproductive traits and physiological condition of intertidal individuals of the reef-forming worm, *Sabellaria alveolata*, across the near-entirety of its latitudinal range along the European coastal fringe of the north-east Atlantic. By integrating broad-scale meteorological data with *in-situ* biochemical and physiological data, we identified and ranked the drivers of variability in two reproductive traits (relative fecundity and total egg diameter). Our results show that intraspecific reproductive trait variation was highest in locations subjected to extreme hydrodynamic or temperature events. We make the case for using the variability in selective biological traits (circularity and symmetry of eggs), as well as biochemical indicators of the physiological condition of the individuals (enzymatic activity of citrate synthase and superoxide dismutase, and the polar lipid fraction of three essential fatty acids) as an integrated approach to studying spatial variation in reproductive traits. Our work demonstrates that both Brown's abundant-centre hypothesis and evolutionary biology theory apply to *S. alveolata* reproductive traits, depending on the trait and time scale (i.e. a single sampling or a pluri-annual event) being studied. Improving our understanding of species reproductive traits and physiological condition across their range lays the foundations for understanding the factors controlling their distribution.

1. Introduction

Variation within a species can have as great an effect on ecological processes and ecosystem services as variation between species (Des Roches et al., 2018). The phenotypic variability of a trait within a population is known as intraspecific trait variation (ITV) (Hofmann et al., 2019). Species traits can be described as any morphological, physiological, phenological or behavioural feature measurable at the individual level (Violle, 2007). ITV may vary due to heritable differences between individuals, or because of phenotypic plasticity across varying environmental conditions (Moran et al., 2016). While ITV across large geographic areas can often be related to environmental gradients (Violle

et al., 2012), it is yet poorly understood whether it is associated to environmental heterogeneity at the local scale (Stark et al. 2017).

The environmental factors determining the distribution of a species have traditionally been viewed from either an evolutionary or a biogeographical perspective (Connallon and Sgrò, 2018). On one hand, evolutionary biology makes predictions based on resource allocation and the ensuing life-history trait trade-offs, whereby a beneficial change to one trait is linked to a detrimental change in another (Stearns, 1992). Stressful environmental conditions for adult stages, regardless of their position within the distribution range, could for example, lead to the production of a large number of gametes, because of a low probability of surviving to the next reproductive event (Siems and Sikes 1998). On the other hand, biogeography, which is underpinned by the ecological niche theory (*sensu* Hutchinson 1957), makes predictions based on a species' relative position within its range. According to Brown's abundant-centre hypothesis (Brown, 1984), physiological constraints limit the distribution of a species at the edge of their range, where environmental conditions are sub-optimal for survival and reproduction, leading to predictions based on a species' relative position within its range (Lester et al., 2007).

Testing these opposing theories requires appropriately broad-scale data. Particularly suitable to this type of study are intertidal invertebrates, which typically have broad latitudinal ranges and narrow tidal and longitudinal ranges (Sagarin and Somero, 2006). Intertidal invertebrates live on the edge of two worlds (Carson, 1955) and are thus exposed to environmental challenges posed by both the terrestrial and marine realms (Helmuth et al., 2006). Their unique position means they are doubly exposed to climate stressors, with combined effects of rising and fluctuating air and seawater temperatures (and indeed other factors) having a large impact on many natural assemblages (Sagarin et al. 1999, Hawkins et al. 2009). Abiotic environmental changes have direct impacts on response traits, which govern how species respond to different environmental filters (Lavorel and Garnier, 2002). For sessile intertidal

organisms, where adults are unable to escape unfavourable abiotic conditions, the importance of reproductive life-history traits determines the viability of local adult populations, which in turn can have community-level consequences as many sessile species act as ecosystem engineers (Pineda et al., 2012). These alterations to organismal-level processes can scale-up to changes in community structure, which ultimately lead to ecological responses such as biogeographic shifts (Harley et al., 2006). In other words, in order to apprehend how patterns of species distribution and abundance will manifest in a changing world, we must first undertake the challenging task of understanding the organismal condition and physiological performance across a species' range (Osovitz and Hofmann, 2019).

The factors shaping a species' distribution should be reflected in the geographic variation of their life-history traits (Rivadeneira et al., 2010). Hutchins (1947) underlined the roles of seawater temperature and repopulation (defined as the combination of reproduction and recruitment), in setting poleward and equatorward distribution limits. While it is widely accepted that biotic and abiotic factors spatially alternate in setting range limits, reproduction is generally acknowledged to be a critical factor in determining a species range edge (Hutchins, 1947; Lewis, 1986).

It has long been known (e.g. Darwin 1859) that ITV reflects the ability of a species to exist in a more diverse range of environments. Outside of the plant ecology field, the patterns and drivers of ITV, and their link to species resilience, remain for the most part unknown (Stein et al., 2014). The number and size of offspring are arguably the two most important and variable life-history traits (Bernardo, 1996). ITV in egg number and size in female marine invertebrates is common (Foo and Byrne, 2017). Understanding the effect of environmental stressors on ITV in female egg traits is important for understanding potential adaptation strategies in a changing world. Studies reviewed in Dahlhoff (2004) have investigated the effects of temperature, food availability, or other physical factors on the physiology of marine animals and have led to the development of biochemical indicators of metabolic condition,

and physiological stress. Some biochemical indicators are particularly informative of the organismal stress generated by gametogenesis and egg production (Soudant et al., 1999). Brown's abundant-centre hypothesis has commonly been tested on populations, but rarely on individual traits. Very few studies in marine ecology (e.g. Lester et al., 2007; Rivadeneira et al., 2010) have examined how reproductive traits vary spatially at the scale of species' ranges, and to our knowledge none have quantified the amount of ITV attributable to local vs. latitudinal-scale environmental variables.

Study system

The honeycomb worm *Sabellaria alveolata* is a broadly distributed intertidal species that engineers a unique high-biodiversity habitat (Dubois et al., 2002; Jones et al. 2018) by cementing together coarse sand grains and shell fragments into tubes. Dense aggregations of these tubes form biogenic reefs (Holt et al., 1998), which are afforded statutory protection by the European Union's Habitat Directive (Council Directive 94/43/EEC). *S. alveolata* ranges from Scotland to Morocco and, as a warm-adapted Lusitanian species, is known to suffer from cold weather spells (Crisp 1964; Firth et al., 2015). Environmental impacts on ecosystem engineers may result in cascading effects on the community composition and structure (Wetthey et al., 2011). We therefore chose this influential foundation species as a pragmatic first step towards gaining insight into the ecological impacts of proximate reproductive responses to environmental stressors.

Species have different reproductive phenologies across their geographic range. *S. alveolata* is a continuous broadcast trickle spawner, meaning that a varying proportion of ripe worms can always be found within a reef (Dubois et al., 2007). This prolonged trickle spawning is overlaid with unimodal summer spawning events in northern Europe (Wilson, 1971; Culloty et al. 2010) and bimodal spring/autumn spawning events in southern Europe (Gruet and Lassus, 1983, Dubois et al., 2006). Time and technological constraints have led to the number and size of gametes being the two commonly studied fertility metrics (Moran and McAlister, 2009), and a vast body of theoretical and

empirical research exists on the intuitive trade-off between these two traits (Bernardo, 1996).

Using biochemical and microscopic imagery analyses, we examined the phenotypic responses in the reproductive traits and physiological condition of intertidal *S. alveolata* to meteorological variables, over two seasons (winter and summer) and across ten sites, encompassing almost its entire latitudinal range along the Atlantic coast of Europe. We explored patterns in several reproductive traits before focusing on egg size and number; their supposed trade-off, and their environmental and physiological drivers. We tested two differing theories: (i) the biogeographic theory with Brown's abundant centre hypothesis, which posits that reproductive trait metrics would be higher, and biochemical physiological condition of the adults would be best at the centre of the range, versus (ii) the evolutionary biology theory, according to which reproductive metrics would be higher in locations where biochemical physiological condition of the adults is poorer, which leads to predictions unrelated to relative position within the species range. We quantified the proportion of variation governed by site-scale meteorological and biochemical predictors. Finally, we tested the hypothesis that ITV would be highest in the locations where adult *S. alveolata* are subjected to environmental stressors, such as in sites with extreme or fluctuating abiotic conditions.

2. Materials and Methods

We measured reproductive traits and biochemical indicators of physiological conditions in individuals from ten populations of *S. alveolata*, distributed from northwest England to central Portugal (14.5° latitude, Figure 18). The northernmost site is very close to its northern range limit and the southernmost site is relatively close to the known southern range limit in Morocco (Gruet, 1986). We focused on female individuals, more sensitive to environmental stressors than males due to the higher energetic cost in producing eggs when compared to sperm (Foo and Byrne, 2017).

On the Macroecology and Global Distribution of the Ecosystem Engineer;

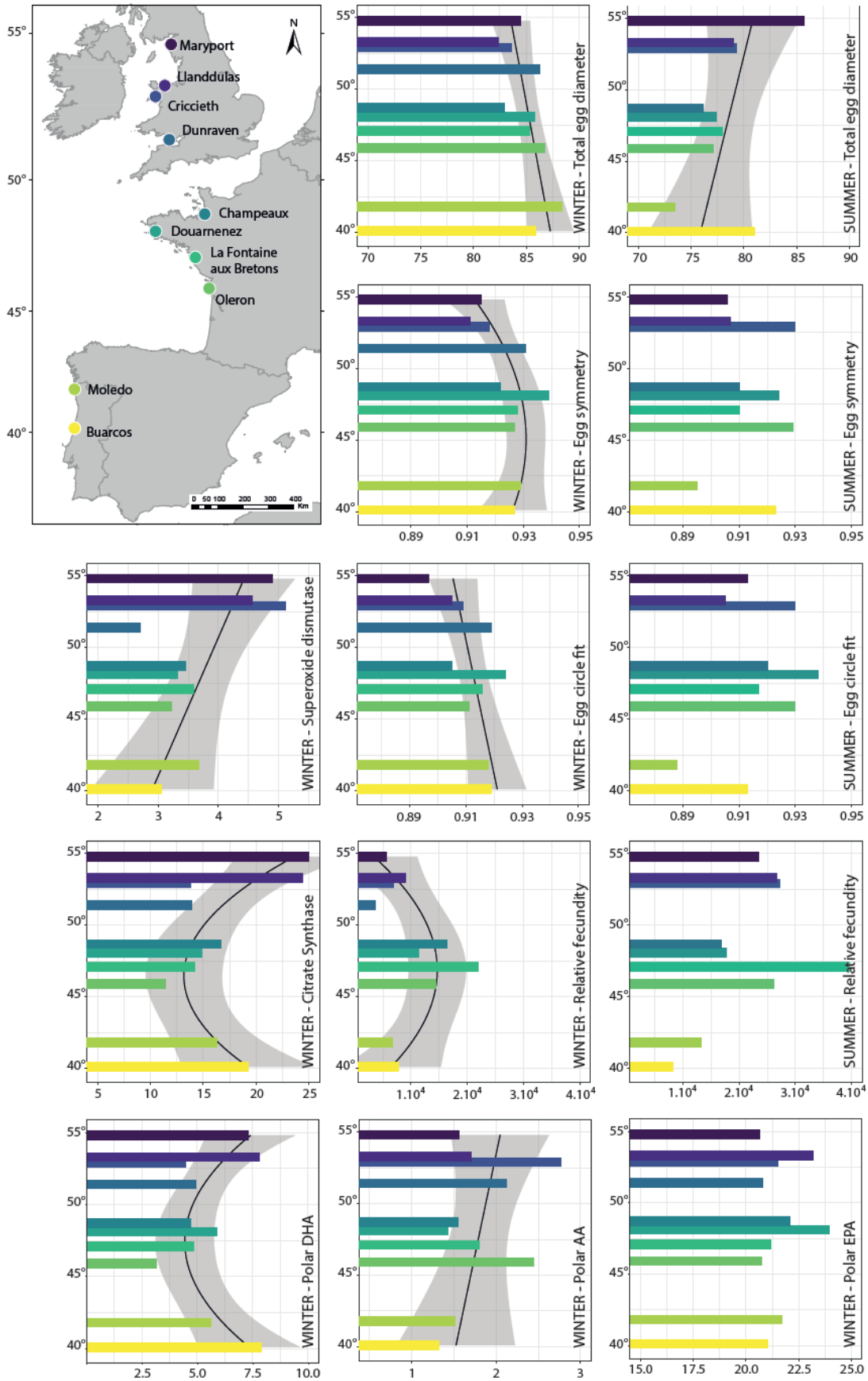


Figure 18. Sampling sites and barplots of key reproductive and biochemical *S. alveolata* traits vs. latitude measured over summer and winter. Latitude was treated as x and the axes were then flipped for presentation purposes. When the relationship with either linear or quadratic latitude was significant, regressions with standard errors were plotted. x-axis units and abbreviations are as follows: total egg diameter = μm ; relative fecundity = the number of eggs divided by the opercular crown diameter of the adult female worm ; egg circle fit = [0-1], index, where 1 is a perfect circle; egg symmetry = [0-1], index, where 1 is perfect symmetry; citrate synthase = micro Units of protein ($\text{mU}\cdot\text{mg}^{-1}$); superoxide dismutase = Units of protein ($\text{U}\cdot\text{mg}^{-1}$); Polar DHA = docosahexaenoic acid in the polar lipid fraction = % of total phospholipids. Polar AA = arachidonic acid in the polar lipid fraction = % of total phospholipids. Polar EHA = eicosapentanoic in the phospholipid fraction = % of total phospholipids.

2.1 Animal collection

All sites were sampled during summer 2017 and winter 2018 spring tides, with the exception of Dunraven in summer 2017 (Appendix 2; Table 13). Small clumps of tubes were broken off mid-tide level reefs and 60 ripe female individuals were removed from their tubes. Ripe females are externally recognizable as the abdominal segments are swollen and appear pink (Costello and Henley, 1971). Half of the individuals were immediately placed in Falcon tubes containing 9 ml filtered seawater, agitated and left for 1 hour, before adding 1 ml buffered 39% formalin solution (i.e. made up to 10 ml of 4.0% formaldehyde) (Bush, 2016). The other half of the individuals had their rigid opercular crowns separated from their abdomen and posterior segments with a sharp blade. Opercular crowns were preserved in individual Eppendorf tubes containing 39% formalin solution for subsequent size measurements, while the corresponding abdomen and posterior segments were placed in individual cryotubes and immediately flash frozen in liquid nitrogen in situ. The opercular crown diameter measurement of each worm (the only hard morphological structure) was used as a size proxy. The cryotubes were then long-term stored at -80°C until laboratory biochemical analyses.

2.2 Meteorological variables

For each of the ten study sites, meteorological variables were extracted from several sources of modelled or remotely sensed data (fully described in Appendix 2). Chlorophyll-a (Chl-a, $\mu\text{g}\cdot\text{m}^{-3}$) and suspended particulate inorganic matter ($\text{mg}\cdot\text{m}^{-3}$) were extracted from SeaWiFS, MODIS and MERIS remotely-sensed products. Daily concentrations at 1 km^2 resolution were provided as a merge of multiple-satellite data (Saulquin et al., 2011) using an algorithm that has been validated against in-situ coastal observations for the English Channel and Bay of Biscay (Gohin, 2011). Hourly records of air and seawater temperatures, and salinity were obtained respectively from Météo France ARPEGE and CMEMS products (Appendix 2; Table 14) and were averaged over the 30-day period preceding survey dates. The performance of air and seawater temperature products was tested by comparing their values with temperatures recorded in-situ over a period of 22 months (Gandra et al., 2015). Three thermal sensors were deployed in the intertidal area of each of the ten sampled sites, however it was only possible to retrieve data from eight of these locations in summer and seven in winter (see Appendix 2, Figure 38). Heat waves and cold spells (number and mean event duration) for both air and seawater were calculated by using the “heatwaveR” package (Schlegel and Smit, 2018). Tidal amplitude data was obtained at the Atlantic scale ($1/12^\circ$) – see Egbert et al. (2010) for details. A modified version of the Burrows et al. (2008) wave exposure index was also calculated, where the hourly square of the wind speed (extracted from ARPEGE outputs) was multiplied by the wave fetch in the direction of the wind. Wave fetch was calculated for each sampling location for all 360 degrees using coastline polygon data from NOAA (Wessel and Smith, 1996) and the “fetchR” package (Seers, 2018). The maximum distance for fetch segments was set to 300 km, and fetch was then standardized between 0 and 1 (with 0 representing a completely closed and 1 a completely open point), by dividing by the maximum fetch possible ($360^\circ/300\text{km}$). For each data layer,

values within a 9 km buffer zone around the sampled site were averaged to get an accurate point estimate. All variables were then integrated (min, mean, max and 5, 25, 50, 75 and 95 quantiles) over the 30-day period preceding sampling dates (Appendix 2; Table 14). This time interval was specifically selected as this is known to be important for environmental conditions affecting egg size and number in marine invertebrates (Crean and Marshall, 2008).

2.3 Biochemical metrics

Five biochemical indicators of *S. alveolata*'s physiological condition were selected based on two previous studies on the same species (Muir et al., 2016; Curd et al., 2019) and analysed in individuals collected during winter 2018 only. The polar lipid fatty acid composition of an organism reflects its physiological adaptation to its environment (Hazel and Williams, 1990, Hochachka and Somero, 2002). The long-chain polyunsaturated fatty acids 20:4n-6 (arachidonic acid, AA), 20:5n-3 (eicosapentaenoic acid, EPA) and 22:6n-3 (docosahexaenoic acid, DHA) are all considered essential for the survival, growth and reproduction of marine organisms (Soudant et al, 1999). Citrate synthase activity (CS), an enzyme involved in mitochondrial activity, is an indicator of aerobic metabolic rate and overall physiological condition (Hochachka and Somero, 1984). Superoxide dismutase activity (SOD) is an anti-oxidant enzyme involved in the prevention of tissue damage from oxidative stress in marine invertebrates (see Abele and Puntarulo, 2004 for review). In order to have sufficient organic material for lipid analysis, all individuals were pooled into batches of five individuals of similar size, as determined by the opercular crown diameter. Worm tissues were ground in liquid nitrogen with an MM400 homogenizer (Retsch, Eragny, France). The resulting worm powder aliquots (100 mg) were homogenized in 2 ml chloroform-methanol (2:1, v/v, Folch et al. 1957), then sonicated and stored at -20°C. Neutral and polar lipid fatty acids, together with CS and SOD activity, were analysed following the protocol detailed in 2. Materials and Methods section of Chapter I.

2.4 Reproductive metrics

The Flow Cytometer and Microscope (FlowCAM®) system (Fluid Imaging Technologies, Scarborough, ME, USA) works by drawing fluid into a flow cell where all individual particles are counted and analysed using high-speed digital imaging (Sieracki et al. 1998). Observations were made using a Benchtop B3 Series FlowCAM with a 4x objective lens and a 300 µm-thick flow cell (FC 300). Worms were removed from the Falcon tubes and had their opercular crown diameter recorded. The 10 mL of spawning solution was vortexed before 0.75 mL were sampled to run through the FlowCAM. In order to prevent clogging of the flow cell, samples were pre-filtered through a 200 µm gauze placed on top of the sample funnel. It is important to note that unfertilised *Sabellaria* spp. eggs elevate a vitelline membrane immediately after contact with seawater, (Novikoff, 1939; Pasteels, 1965). We therefore define ‘total egg diameter’ as the diameter of the egg including the ovicell and vitelline membrane. When the number of particles per image exceeded 100, the sample was diluted by half with Milli-Q water and three diluted sub-samples were then dispensed. The instrument was run in auto image-mode, capturing all particles in the range of 15–1,000 µm. Based on this analysis, a minimum of 50 ovocytes was chosen for concentration values, thus modulating the number of ‘viable’ individuals sampled from a range of 2-34 individuals per site (Appendix 2, Table 13. Field locations and sampling dates. Numbers in italic represent the number of). A preliminary Principal Component Analysis of the 40 measurements taken by the software package VisualSpreadSheet® version 4.3.55 showed that the following four parameters captured 62% of the variation in over 400 000 ovocytes: a) total egg diameter [µm], b) concentration [particles.ml⁻¹], c) best circle fit (deviation of the particle edge from a perfect circle, normalized to the range [0-1]) and d) symmetry (real [0-1]).

2.5 Statistical analyses

Clutch size is expressed as relative fecundity, i.e. the total number of eggs (calculated as the particle concentration in the 10 mL of spawning solution) standardized by opercular crown diameter. Total egg diameter >120 μm were excluded from the analyses as they were assumed to be sample contamination from other broadcast spawning species. One individual sampled from La Fontaine aux Bretons, collected in winter 2018 and presenting an extremely high relative fecundity (>400 000 eggs.mm⁻¹) was also removed from analyses so as not to distort multivariate and regression results.

2.5.1 Latitudinal structures in reproductive and biochemical traits

Linear or quadratic relationships between the reproductive and biochemical variables and latitude were tested using linear (with only latitude as an explanatory variable) and polynomial (with only the second degree polynomial of latitude) Model I regressions and are summarized in Figure 18.

2.5.2 Relationship between reproductive traits and biochemical variables

Common spatial structures between biochemical descriptors and mean reproductive traits of each site were searched through a co-inertia analysis (Dolédec and Chessel, 1994), where a Principal Component Analyses (PCA) was computed on each dataset (Figure 19). The RV coefficient (Robert and Escoufier, 1976), a multivariate generalization of the squared Pearson correlation (Legendre and Legendre, 2012), was used to quantify the relationship between these two sets of descriptors.

2.5.3 Drivers of variation in reproductive traits

The individual and combined contribution of local meteorological conditions, biochemical variables and latitude in explaining variation in total egg diameter and relative fecundity were quantified through a variance partitioning method (Borcard et al., 1992; Peres-Neto et al., 2006) applied to samples collected during winter (Figure 20). Prior to the analysis, collinear meteorological

predictors were removed using a variance inflation factor threshold of 10 (Dormann et al., 2017). A stepwise selection of the remaining variables was performed based on adjusted R^2 , with p-values for adding and dropping variables of 0.05 and 0.1, respectively. These explained fractions were put in perspective with the amount of inter- vs. intra-site variation found at each sampling season (Appendix 2, Figure 39). As different numbers of viable individuals were sampled at each site, we used a re-sampling procedure to balance the dataset when quantifying the amount of inter- vs. intra-site variation. We excluded measures taken at Buarcos in summer as there were only two viable individuals. We used the lowest number of individuals measured within the remaining different sites to subsample the original data set, by drawing randomly 1000 data subsets with 5 individuals per site. Variance component models were performed on each subset to quantify, for each season, the variance in total egg diameter and relative fecundity across two nested scales (inter- and intra-site variation; see Messier et al., 2010 for details).

We additionally performed a redundancy analysis (RDA; Rao, 1964) to better understand the role of environmental drivers. Analyses were based on data collected during both seasons (Figure 21) to understand the variation and covariation of all reproductive variables to meteorological conditions during winter and summer. We included the mean and standard deviation of the total egg diameter, best circle fit, symmetry and mean relative fecundity as response variables, which we centred and standardized to unit variance, together with latitude (both linear and quadratic) and linear meteorological predictors selected through the step-wise procedure described above.

For the two reproductive traits which responded the most to seasonal variation, namely total egg diameter and relative fecundity, stepwise multiple linear regressions were carried out separately for each season in order to determine which combination of meteorological factors best accounted for their variation. Using variance inflation factors and scatterplot correlations, a selection of 5-7 meteorological predictors were retained for each regression.

Due to air and seawater temperature being significantly correlated, we chose to retain seawater as a temperature variable in our regressions due to prior knowledge on its relevance for explaining ecological and/or physiological responses of the species (Muir et al. 2016). Interactions between meaningful variables and quadratic transformations of seawater temperature and chlorophyll-*a* were tested for all four regressions. We selected among candidate models through comparison of Akaike's Information Criterion with small-sample correction. Model residuals were checked for consistency with stochastic error. Regression coefficients and confidence intervals of the best-fit models were plotted (Figure 22). All analyses were carried out with R 3.5.1 (R Core Team, 2018) and relied on the *vegan* package (Oksanen et al., 2018).

3. Results

3.1 Latitudinal structures in reproductive and biochemical traits

Comparing clouds of points in traits to latitude yielded four possible distribution patterns, which Sagarin and Gaines (2002) referred to as 'ramped south' (positive linear), 'ramped north' (negative linear), 'abundant edge' (negative quadratic) or 'normal' (positive quadratic). Summer total egg diameter SOD and polar lipid AA were ramped south, winter total egg diameter and egg circle fit were ramped north, CS and polar lipid DHA followed an abundant edge pattern, whilst winter relative fecundity and egg symmetry followed a normal pattern (Figure 18). Summer egg symmetry, egg circle fit and relative fecundity, together with polar lipid EPA bore no relationship to latitude.

3.2 Relationship between reproductive traits and biochemical variables

Sites with a high egg symmetry and best circle fit in winter had low levels of metabolic enzyme activity (SOD and CS), and were found in the centre to southern part of the range (Figure 18; Figure 19), as illustrated by the opposite vectors in panels Figure 19b and Figure 19c, and the positioning of the sites

from Douarnenez (RIS) to Buarcos (BUA) in the left part of panel Figure 19a. Despite a moderate relationship between reproductive trait variation and changes in mean biochemical composition (RV coefficient of 0.38), these two sets of variables are both strongly structured along the first co-inertia axis (Figure 19), which represented 91.3% of their co-inertia. The three northernmost sites were isolated from the remaining seven sites due to their high CS, SOD and polar lipid DHA levels in combination with eggs with low symmetry and circle fit indices. The sites showing the least agreement between biochemical and reproductive variables, as depicted by the longest vectors in Figure 19a, are located in the centre to southern part of the range, namely Champeaux (CHA), Douarnenez (RIS), la Fontaine aux Bretons (LFB) and Moledo (MOL). Conversely, the three northernmost sites, together with the southernmost site Buarcos (BUA) had the highest agreement between the two sets of variables.

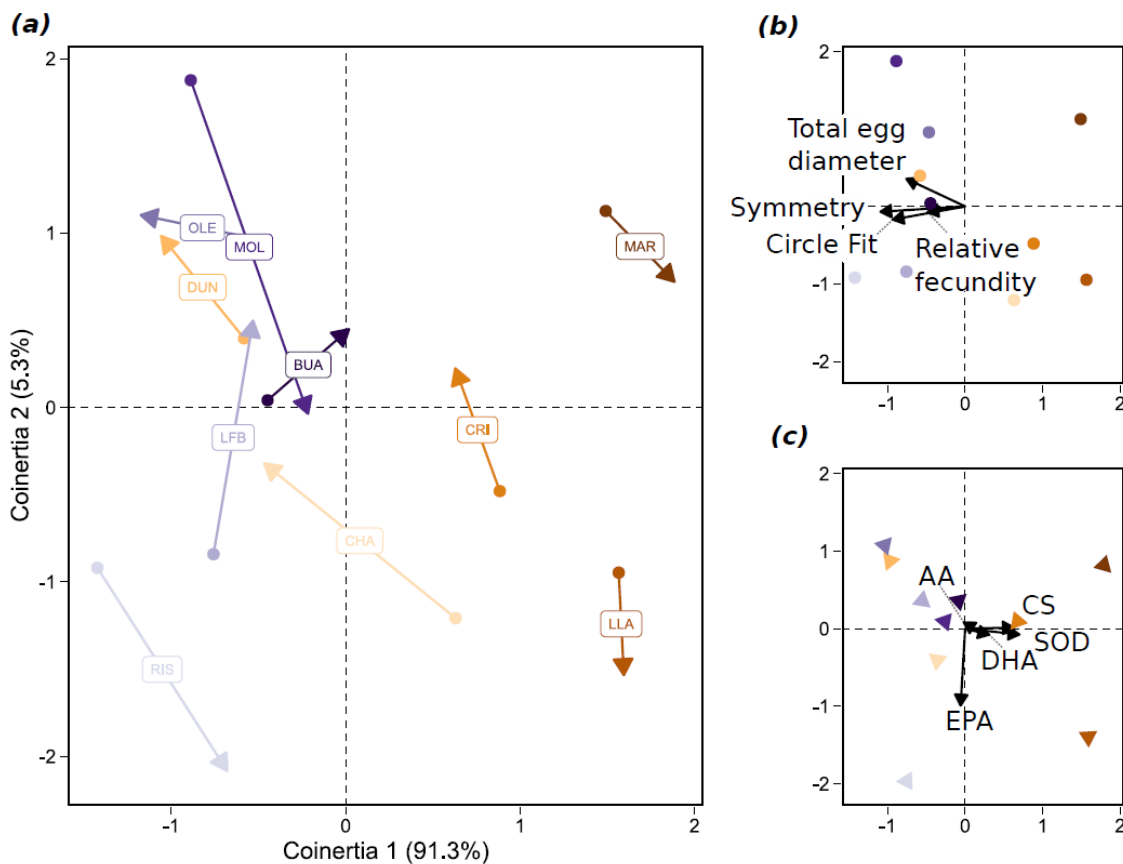


Figure 19. Graphical results of the co-inertia analysis of the reproductive and biochemical variables for winter 2018. The left-hand plot (a) (normed site-scores)

shows the position of the sites on the co-inertia axes using the reproductive (origins of the arrows) and biochemical (arrowheads) co-inertia weights. The shorter the arrows, the better the match between the two projections. The right-hand pair of plots shows the contribution of the two groups of variables to the canonical space (reproductive traits (b) on the top; biochemical variables on the bottom (c)). Vectors pointing in the same direction are correlated and longer vectors contribute more to the structure. Site name abbreviations are as follows: MAR = Maryport, LLA = Llanddulas, CRI = Criccieth, CHA = Champeaux, RIS = Douarnenez, plage du Ris, LFB = La Fontaine aux Bretons, OLE = Oléron, MOL= Moledo, BUA = Buarcos. Biochemical abbreviations as in Figure 18.

3.3 Drivers of variation in reproductive traits

Twenty-one percent of the variation in total egg diameter and 28% of the variation in relative fecundity in winter is explained by our selected meteorological, biochemical and spatial predictors. For total egg diameter, 12% of the variation explained by meteorological variables was linearly structured along the latitudinal gradient (Figure 20a), with 10% being shared with biochemical variables. For relative fecundity, 18% of the variation explained by meteorological variables was spatially structured (shared here with the quadratic polynomial of latitude), with 6% being shared with biochemical variables (Figure 20b).

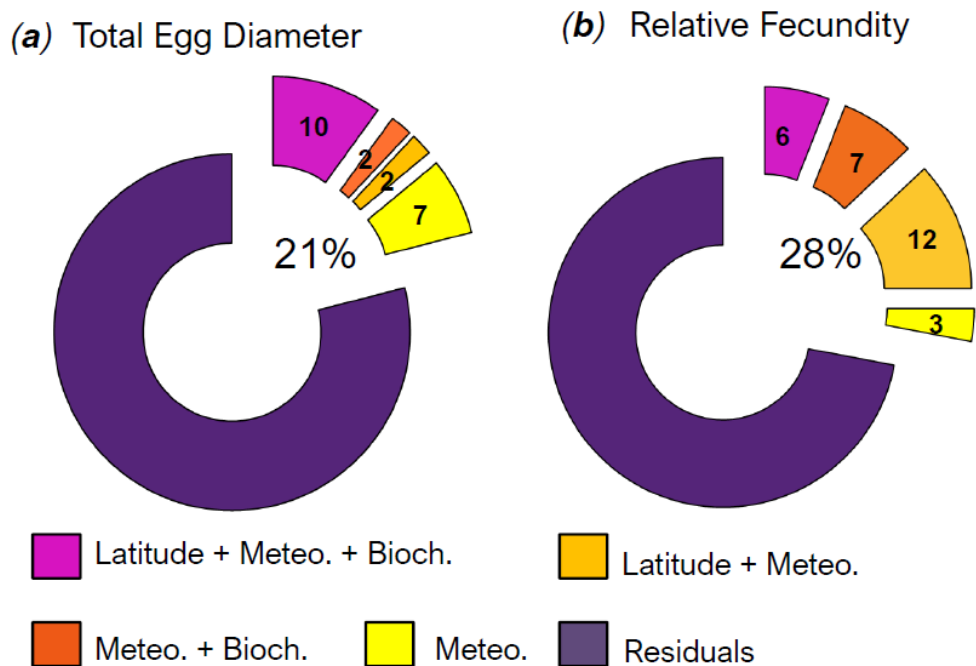


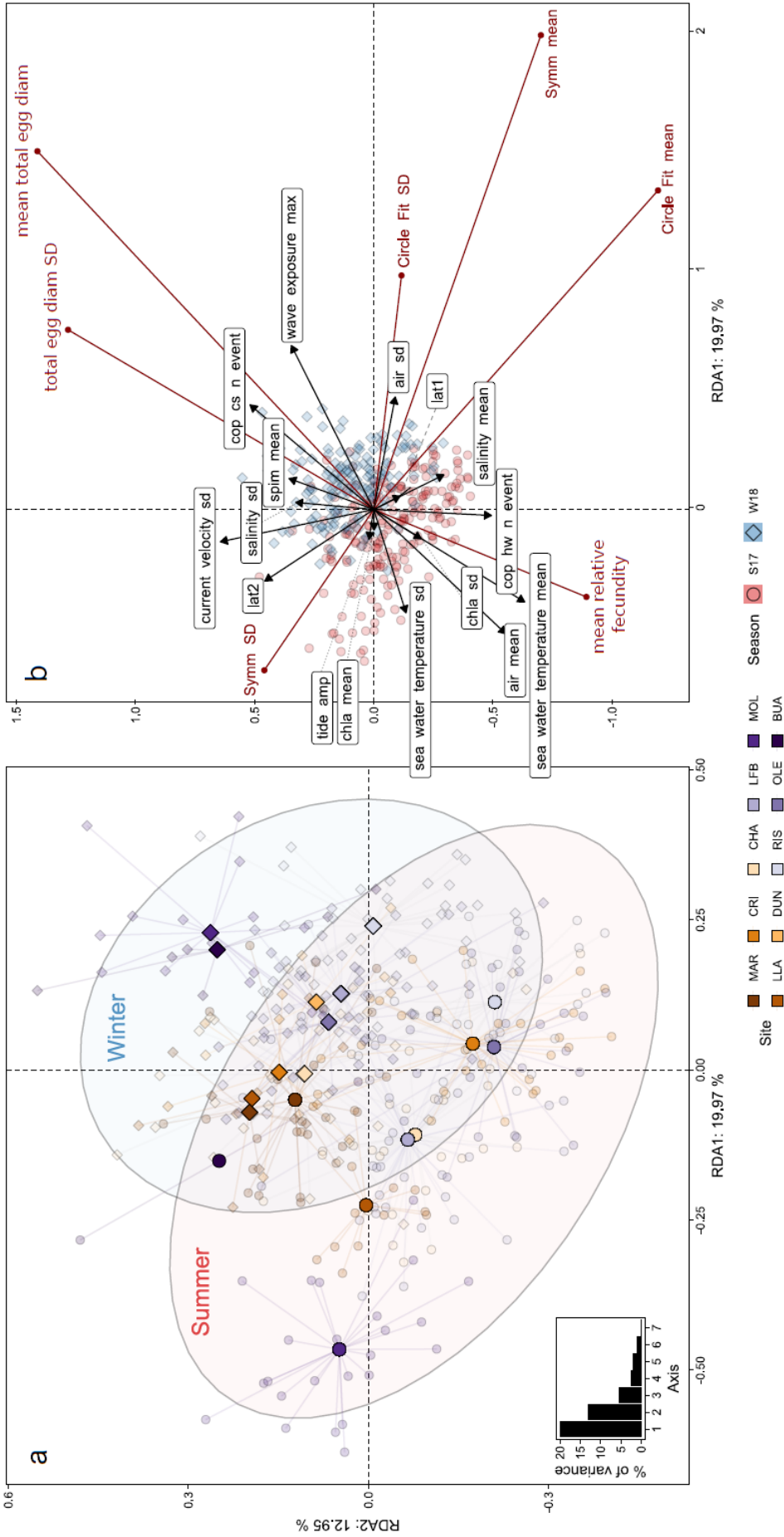
Figure 20. RDA variance partitioning of egg size and relative fecundity during winter among meteorological, biochemical and latitude predictor groups. Numbers indicate R_{adj}^2 values. Only the non-null fractions and residuals are represented. The four non-null fractions were: a) meteorological predictors alone (Meteo.), b) the shared effect of meteorological predictors with latitude (Latitude + Meteo.), c) the shared effect of biochemical and meteorological predictors (Meteo. + Bioch.) and d) the shared effect of biochemical and meteorological variables together with latitude (Latitude + Meteo. + Bioch). Latitude is linear for total egg diameter, and quadratic for relative fecundity. Meteorological variable selection for each trait was based on the regression results presented in Figure 22.

When looking at all reproductive traits and both sampling seasons, winter and summer separated out along the first axis (Figure 21a and Figure 21b). Our set of meteorological variables explained 33% of their variation and co-variation. Winter conditions, namely higher maximum wave exposure, number of cold spells, suspended particulate inorganic matter concentrations and stronger variance in current velocities, were linked to higher mean and standard deviation in total egg diameter and lower relative fecundity. Conversely, summer conditions, characterized by higher air and seawater temperatures and with number of heat wave events, were associated with lower total egg diameter but higher relative fecundity. Egg best circle fit and symmetry were more weakly correlated to available meteorological variables, although higher variance in air temperature and mean salinity, as well as lower variance in current velocity, seem to promote more symmetrical and circular eggs (Figure 21b).

Figure 21 (following page). Redundancy analysis (RDA) of selected centred and standardized reproductive traits (displayed as red vectors in the right-hand panel b; Scaling 2) constrained by selected standardized meteorological variables (displayed as black vectors panel b; Scaling 2). The left-hand panel a shows the centroid scores for each sampling site and season, linked to each individual (Scaling 1). 95% confidence dispersion ellipses are represented for the seasons. In both panels, summer scores are displayed by circles, winter scores as diamonds and colors correspond to the sampling sites. Axes values represent the % of explained variance per axis, the two axes representing altogether 33% of the total variance. The inner figure of panel a corresponds to the eigenvalues of the first 7 RDA axes. Panel b meteorological variable abbreviations are as follows: 'spim mean' = mean suspended particulate inorganic matter; 'lat1' = linear latitude; 'lat2' = quadratic latitude; 'chla' = chlorophyll-a; 'tide amp' = mean tidal amplitude; 'cop cs n event' = number of cold spells in seawater over 30 days; 'cop hw n event' = number of heatwaves in seawater

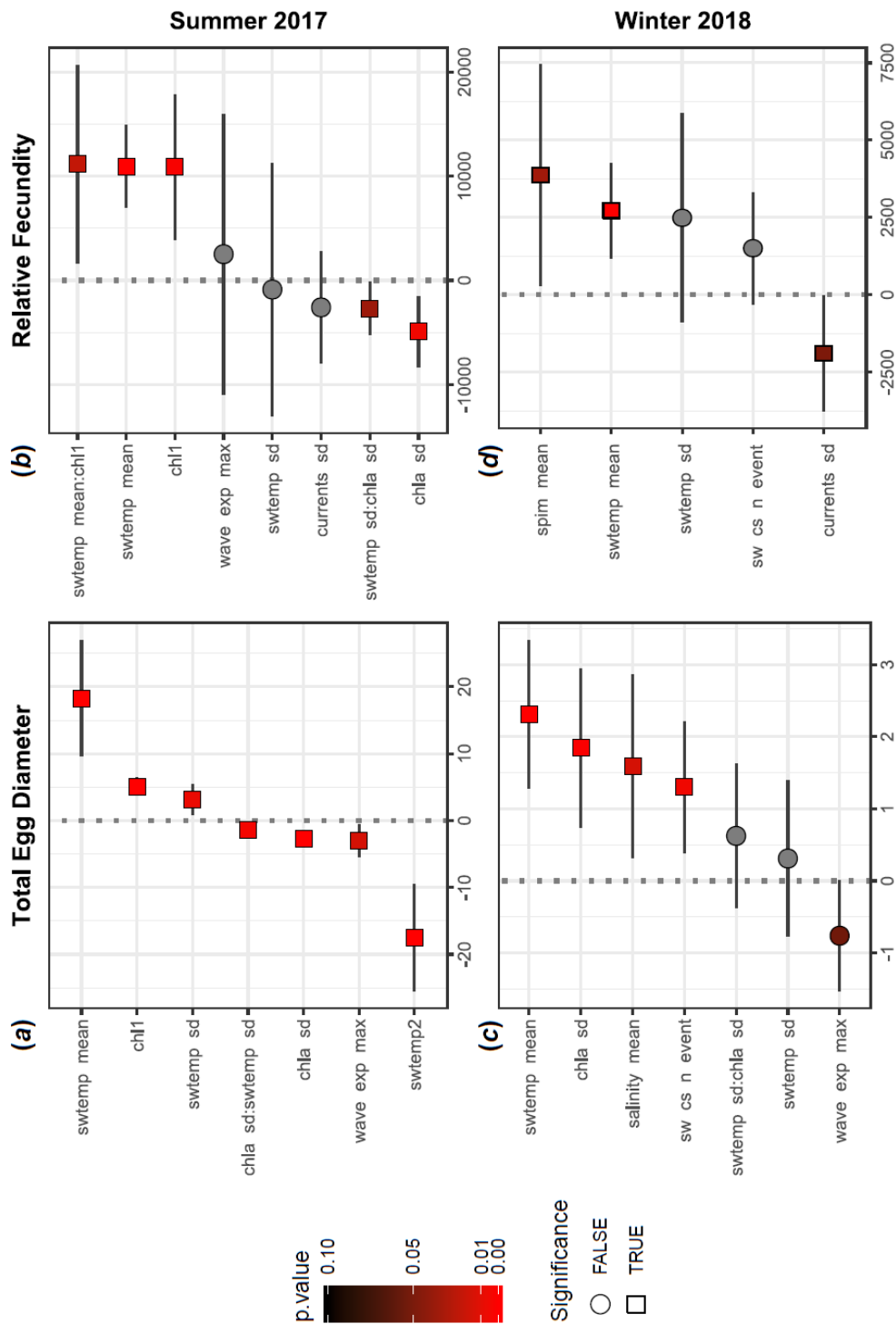
over 30 days; 'air mean' = air temperature mean. All 'sd' suffixes represent the variation (standard deviation) of different variables. Site abbreviations as for Figure 19.

On the Macroecology and Global Distribution of the Ecosystem Engineer;



The mean and standard deviation of seawater temperature were the only two parameters retained to explain variation in total egg diameter and relative fecundity in both winter and summer (Figure 22). Mean seawater temperature was the predictor with the greatest effect on total egg diameter for both seasons (Figure 22a and Figure 22c). The fact that both linear (swtemp) and quadratic (swtemp²) seawater temperature were significant with high absolute coefficients indicates a strong non-linear effect of seawater temperature on total egg diameter. In summer, chlorophyll-*a* also had a significant effect on total egg diameter, with both following a ramped south pattern (Figure 18; Appendix 2, Table 15).

Figure 22 (following page). Regression coefficient plots for the best linear regression models, as determined by AIC comparisons, for total egg diameter and relative fecundity in summer 2017 and winter 2018. All input variables were centred and standardized. Effect estimates are marked as squares when significant and circles when non-significant at the threshold $\alpha=0.05$. Point colours represent the estimated p values. Lines indicate the width of the 95% confidence interval for each effect. For each model, the R^2_{adj} values are (a) = 0.53, (b) = 0.24, (c) = 0.21, (d) = 0.28. Plot units are μm for (a) and (c), and total number of eggs divided by opercular crown diameter for (b) and (d). Meteorological variables were ranked and plotted in decreasing order based on their coefficient estimates. Abbreviations are the same as those used in Figure 21.



Summer relative fecundity is driven primarily by an interaction between chlorophyll-*a* and seawater temperature (Figure 22b), whereas the most important meteorological variable for winter relative fecundity was suspended particulate inorganic matter (spim mean, Figure 22d). For three of the four season/variable combinations, the percentage of variance explained by our set of site-scale meteorological variables matched the mean percentage of

variance found between sites in the variance component models (Appendix 2; Figure 39), indicating that most of the broad-scale, inter-site structures in the two variables were captured by the regressions. The winter relative fecundity variation was the exception (Figure 22d), with only 28% of variance explained by our site-scale predictors, compared to a mean inter-site variance of 41%. The unexplained variance in the four models varied between 47 and 78% (Appendix 2; Figure 39).

4. Discussion

By combining the partitioning of environmental variation between broad and local scales across a wide latitudinal gradient with how it corresponds to independently measured *in-situ* adult physiological condition, we discuss how reproductive ITV is collectively shaped.

4.1 Latitudinal structures in reproductive and biochemical traits

Different reproductive and biochemical traits in the engineer species *S. alveolata* seem to follow different biogeographic or evolutionary biology theories that vary in intensity depending on the sampling period. Our initial linkage to latitude found that on one hand *S. alveolata* relative fecundity and egg symmetry in winter followed Brown's abundant-centre hypothesis, with unimodal distributions along the latitudinal gradient similar to those observed for CS enzyme activity and polar lipid DHA levels. On the other hand, total egg diameter and egg circle fit seem to conform to evolutionary biology, as suggested by their linear or non-significant relationship with latitude, which are similar to those observed for stress-markers such as SOD enzyme activity and polar lipid AA and EPA. The fact that we now have the possibility to perform near-exhaustive analyses of physiological markers and reproductive traits provides a more nuanced background against which ecological theories should be tested and challenged.

4.2 Relationship between reproductive traits and biochemical variables:

linking physiological condition to latitude

Our overall data suggests that meteorological conditions in the northern sites were physiologically more stressful for *S. alveolata* than those encountered in the centre or southern sites. The three northernmost sites display the least circular eggs together with the highest levels of SOD enzyme activity and polar lipid AA. SOD activity reflects oxidative stress levels, which in our study, despite being often linked to thermal stress in marine bivalves (Rahman et al., 2019), rises with increasing latitude. AA is a precursor of eicosanoids, known to be associated in other invertebrates with stressful or energetically expensive situations such as gametogenesis, spawning or immune function stimulation (Osada et al., 1989; Stanley and Howard, 1998). Customarily, AA increases with increasing seawater temperature, however the underlying reasons are not currently understood (Pernet et al. 2007 ; Muir et al. 2016).

The four centre sites display the most symmetrical eggs, the highest relative fecundity, and the lowest levels of CS activity and DHA. Both CS and DHA are highly correlated ($R^2_{\text{adj}}=0.76$) and related to aerobic metabolic rate (Hulbert and Else, 1999). A study on tropical scallops found levels of CS to decrease during gonadal maturation and after spawning (Brokordt et al., 2000). Given the high relative fecundity displayed in the four centre sites, depleted CS levels could also be an indicator of high spawning activity in *S. alveolata*.

Overall, our biochemical metrics indicate the best physiological conditions as being in the southern range sites, thus corroborating the Lusitanian nature of *S. alveolata*, whilst the individuals investing the most in reproduction, with the highest relative fecundity by far yet not the smallest eggs, are situated in the centre of the range. Biochemical indicators can aid in forecasting climate-related changes by enhancing our knowledge base of (1) environmental stress levels across species' ranges, (2) the physiological condition of local individuals and (3) the effects of physiological condition on individual performance (Sorte and Hofmann, 2004).

Our results make the case for using the symmetry and circularity of *S. alveolata* vitelline membranes as indicators of egg quality. With the advent of high-speed imaging flow cytometers, it is now possible to analyse dozens of physical gamete parameters and link these to their viability, opening the way for the use of many more reproductive traits. Very few studies on the biochemical quality of marine invertebrate gametes exist, and those that do concern either echinoids or molluscs (see Marshall and Keough (2007) for review). This study is the first to examine variability in reproductive traits and link these to biochemical indicators of maternal physiological condition across a species range.

4.3 Drivers of variation in reproductive traits: a major role of environmental variability and extreme events

In our study, most of the spatial variation in total egg diameter and relative fecundity occurred within- rather than among sites, except for total egg diameter in summer. This intra-site heterogeneity suggests many local habitat factors operate to a greater effect than latitudinal factors (Lewis, 1986) and cannot therefore be elucidated by site-scale predictors. Nonetheless, our selected broad-scale meteorological and biochemical predictors captured most of the explicable fraction of inter-site variability in total egg diameter, although they performed more poorly for relative fecundity. Only 28% of ITV (out of 41% of inter-site variance on average) was captured for this trait, signifying either that our data has missed some of its potential drivers of variation, or that our meteorological data sources did not adequately capture the localized weather patterns responsible for phenotypic plasticity (Helmuth et al., 2006). Whilst they are the result of daily model outputs and can be considered to be at a high temporal resolution, their spatial coarseness does not perfectly reflect localized weather patterns (Seabra et al., 2011).

Although several biochemical and reproductive variables indicate optimal winter conditions to be found in the centre of *S. alveolata*'s range, no single meteorological variable had a significant relationship with quadratic latitude along Europe's Atlantic coast. Our results suggest, as hypothesized, that higher

variability in environmental conditions leads to more ITV in reproductive traits: variation in chlorophyll-*a* production and episodes of cold spells or heat waves led to more variability in total egg diameter, variation in air temperature and maximal wave exposure positively influenced variability in *S. alveolata* eggs circularity, and surface current variation is positively correlated with variation in egg symmetry. As chlorophyll-*a* production follows phytoplankton blooms, variable spikes in its concentration are an indicator of productivity (Racault et al., 2012). Greater variation in phytoplankton bloom phenology is predicted under future global warming scenarios (Henson et al., 2013) which may have repercussions for *S. alveolata*, and indeed many marine filter-feeders. Despite large uncertainty in climate projections, across Europe the overall adverse extreme weather event frequency is much more likely to increase than to decrease (Trnka et al., 2014). Several studies (reviewed in Aviz et al. 2016), found sabellariids to have facultative breeding peaks following major storms and wave-related disturbances (McCarthy et al. 2003), a phenomenon also observed in other intertidal species (Bowman and Lewis, 1977). This conforms to evolutionary biology theory (Ramirez-Llodra, 2002), where hydrodynamic disturbances increase mortality risk whereby sabellariids respond by investing their energy in reproductive output. Additionally, the number of seawater temperature cold spell events over the preceding 30 days positively influenced both the diameter and variability in total egg size in winter. Whilst the majority of studies assessing the impacts of extreme weather events focus on heat stress (e.g. Sagarin and Somero, 2006; Wernberg et al., 2013; Muir et al., 2016), relatively little work has been carried out on cold stress (but see Urian et al. 2011). Intertidal species, and warm-adapted species such as *S. alveolata* in particular, could suffer increased mortality due to the extreme winter cold, particularly in embayments (Crisp, 1964, Firth et al. 2011) or in locations where spring low tides occur at night time when air temperatures drop (Mislán et al., 2009).

Broad-scale comparisons of physiological traits between individuals separated across geographic space are valuable in highlighting important ecological features (Osovitz and Hofmann, 2007), however, the general conclusions reached by this approach can be influenced by a number of confounding variables; phylogeny is one such constraint (Clarke et al., 1992). Furthermore, although some local-scale variation may partly be due to phenotypic plasticity, fine-scale abiotic factors and biotic interactions not captured by our data, some may be genotypic. Further studies that explicitly consider the genetic divergence among populations (and individuals) are needed to fully understand how phenotypic variation is ultimately generated and maintained in *S. alveolata* at geographic scales (Barboza et al., 2019). It will also be important to determine the heritability of changes to reproductive traits induced by exposure to climate change stressors (Foo and Byrne, 2017).

4.4 Intraspecific trait variability in an engineer species: laying the foundations for understanding their distribution drivers

Marine invertebrate populations have traditionally been viewed as being strongly structured by the quantity of offspring; however offspring quality has an equally important effect (Marshall and Keough, 2007). The widespread use of mean values for the functional traits of a species sampled in a given location signifies an implicit assumption that ITV is negligible compared to interspecific trait variation (Violle et al., 2012). While often regarded as ‘noise’ ITV is key to the fundamental processes of natural selection and speciation (Ridley, 2004), and should therefore be examined in trait-based research in both species-specific and community ecology (Albert et al., 2010). As observed when grouping *S. alveolata* reproductive ITV results across both summer and winter, marine invertebrates generally exhibit trade-offs, whereby they either produce many small eggs with high mortality or fewer, larger eggs that may experience reduced planktonic mortality (Marshall and Keough, 2007). In both seasons, total egg diameter variability was lowest and relative fecundity peaked in the centre of the range. If conditions during larval development and maturation

are favourable, many small offspring are probably the best reproductive strategy, however if conditions are unexpectedly harsh the whole clutch can be lost (Olofsson et al., 2009). As an iteroparous species, *S. alveolata* effectively has several chances throughout its lifetime to reproduce and therefore does not require as much intra-clutch variability in egg size as semelparous species, which tend to select for higher variability as a more cautious “bet-hedging” strategy (Olofsson et al., 2009).

Broad-scale empirical field studies of biogenic habitat-forming species must continue, for they allow us to detect general patterns over large scales and are vital for informing policy (Helmuth et al., 2006, Hawkins et al. 2017). For habitat-forming species, small environmentally induced shifts in metabolic activity, brought on by non-lethal but highly stressful conditions such as those experienced cold spells may lead to disproportionate large impacts on ecosystem functioning and the associated biodiversity via changes in reproduction, growth and survival of the engineer species (Dahlhoff et al., 2002).

Our work demonstrates that both Brown’s abundant-centre hypothesis and evolutionary biology theory apply to reproductive traits, depending on the trait and time scale (i.e. a single sampling or a pluri-annual event) being studied. We argue that reproductive ITV does not solely occur due to constraints on producing offspring of uniform size and may be an adaptive emergent response to environmental variability. A better understanding of which environmental variables play a primary role in the physiological response of intertidal organisms will however only come with further integration of controlled experimental studies (Sagarin and Somero 2006). Only by carrying out fine-scale studies that capture local conditions and proximate ecological responses in concert with regional scale studies will we gain an understanding of emergent responses, and reproductive ITV in particular.

CHAPTER III

The third chapter of this thesis focuses on the emergent response to climate displayed by many marine species: a predicted distributional range shift.

The first section of this chapter briefly presents the data curation that went into building a range-wide occurrence dataset, as no accurate ‘off-the-shelf’ *S. alveolata* dataset was available at a biogeographic range scale. As the dataset spans two centuries, older references brought to light the shift in human perception in the value of *S. alveolata* reefs; some examples are given.

In the second section, structured as a manuscript, we modelled present-day and future distributions of *S. alveolata* across the near-entirety of its range (from the Shetland isles in Scotland to Essaouira in Morocco - 29° in latitude) along the North-east Atlantic coastline. Using carefully selected modelling approaches (General Additive Models, Random Forests and an ensemble of both techniques, using the ‘sdm’ R package), based on the curated dataset of *S. alveolata* records and a combination of carefully selected oceanographic and terrestrial environmental variables, we predicted present day and future distributions in 2050 and 2100, under two different Representative Concentration Pathways (RCP 4.5 and 8.5). Contraction at the equatorial range limit is predicted to occur at a greater rate and extent than poleward-limit expansion. Future changes are predicted to occur not just at the species boundaries, but also in the centre range, where habitat suitability is consistently predicted to decrease.

The third section of this chapter presents the effects of scale (both environmental predictor grain size and spatial extent) on species distribution modelling, by comparing variable importance, response and model output at two different scales: 3km grain size across 25° extent in latitude (from the inner Hebrides in Scotland to Essaouira in Morocco), compared to 10-12km grain size across 29° latitude. Although the response to individual variables differs, both spatial scales have strikingly similar model outputs, thus validating the results from the second section of this chapter.

SECTION III-A

A BROAD-SCALE LONG-TERM DATASET OF *SABELLARIA ALVEOLATA* DISTRIBUTION AND ABUNDANCE CURATED THROUGH THE REEHAB (REEF HABITAT) PROJECT

Amelia Curd¹, Céline Cordier¹, Louise B. Firth², Laura Bush³, Michael T. Burrows⁴, Paul N Cunningham^{5,6}, Yves Gruet⁷, Patrick Le Mao⁸, Andrew J. Davies⁹, Julie A. Blaze¹⁰, François Bordeyne¹¹, Nicolas Desroy⁸, Hugh Edwards¹², Daniel R. Harris¹³, Francis Kerckhof¹⁴, Stephen J. Hawkins^{15,16}, Fernando P. Lima¹⁷, David McGrath¹⁸, Claudia Meneghesso^{17,19}, Nova Mieszkowska^{16,20}, Julia D. Nunn^{21,22}, Flavia Nunes¹, Nessa E. O'Connor²³, Ruth M. O'Riordan²⁴, Anne Marie Power²⁵, Christina Simkanin²⁶ and Stanislas F. Dubois¹

Dataset published in the SEANOE repository

- 1 IFREMER, Centre de Bretagne, ZI de la pointe du Diable, CS 10070, 29280 Plouzané, France
- 2 School of Biological and Marine Sciences, University of Plymouth, Drake Circus, PL4 8AA, Plymouth, UK
- 3 FUGRO GB Marine Limited, Gait 8, Research Park South, Heriot-Watt University, Edinburgh EH14 4AP, UK
- 4 Scottish Association for Marine Science, Dunbeg, Oban, Argyll PA37 1QA, UK
- 5 Manchester Institute of Innovation Research, University of Manchester, Manchester M13 9PL, UK
- 6 Former Department of Zoology, University of Manchester, Manchester M13 9PL, UK
- 7 University of Nantes, 58 rue Stendhal, 44300 Nantes, France

- 8 IFREMER, Laboratoire Environnement Ressources Bretagne Nord, 38 rue du Port Blanc, 35800 Dinard, France
- 9 University of Rhode Island, Department of Biological Sciences, Kingston, RI 02881, USA
- 10 Odum School of Ecology, University of Georgia, Athens, USA
- 11 Sorbonne Université, CNRS, UMR AD2M Adaptation et Diversité en Milieu Marin, Station Biologique de Roscoff, 29680 Roscoff, France
- 12 Department of Agriculture, Environment and Rural Affairs, Belfast, BT72JA, UK
- 13 Estuary & Ocean Science Center, San Francisco State University, 3150 Paradise Drive, Tiburon, CA 94920, USA
- 14 Royal Belgian Institute of Natural Sciences, Operational Directorate Natural Environment, Aquatic and Terrestrial Ecology, Marine Ecology and Management, 3de en 23ste Linierégimentsplein, 8400 Oostende, Belgium
- 15 Ocean and Earth Science, University of Southampton, National Oceanography Centre Southampton, Waterfront Campus, European Way, Southampton SO14 3ZH, UK
- 16 The Marine Biological Association of the UK, Citadel Hill, Plymouth, PL1 2PB, UK
- 17 CIBIO-InBIO, University of Porto, Campus de Vairão, Rua Padre Armando Quintas nº 7, 4485-661 Vairão, Portugal
- 18 Galway-Mayo Institute of Technology, Galway, Ireland
- 19 Departamento de Biologia, Faculdade de Ciências da Universidade do Porto, R. Campo Alegre, s/n, 4169-007 Porto, Portugal
- 20 Department of Earth, Ocean and Ecological Sciences, School of Environmental Sciences, University of Liverpool, Nicholson Building, Brownlow Street, Liverpool, L69 3GP, UK
- 21 National Museums Northern Ireland, 153 Bangor Rd, Holywood BT18 0EU, Northern Ireland
- 22 2 Windmill Lane, Portaferry, Co. Down BT22 1RW, Northern Ireland
- 23 School of Natural Sciences, Trinity College Dublin, Ireland
- 24 School of Biological, Earth and Environmental Sciences and Environmental Research Institute, University College Cork.
- 25 Zoology, National University of Ireland Galway, Galway, Ireland
- 26 Department of Biology, University of Victoria, Victoria, Canada

1. Introduction

Numerous important reef-forming species have declined dramatically in the last century, many of which have been insufficiently documented due to anecdotal or hard-to-access information. One such species, the honeycomb worm *Sabellaria alveolata* (L.), is a tube-building polychaete that can form large reefs, providing important ecosystem services such as coastal protection and habitat provision (Noernberg et al. 2010, Dubois et al. 2002). It currently ranges from Scotland to

Western Sahara (Lourenço et al., 2020), yet little is known about its distribution outside of the United Kingdom, where it is protected and where there is a strong heritage of natural history and sustained observations (Hawkins et al. 2016). As a result, online marine biodiversity information systems contain haphazardly distributed records of *S. alveolata* (Appendix 3). One of the objectives of the REEHAB project (www.honeycombworms.org) was to combine historical records with contemporary data to document changes in the distribution and abundance of *S. alveolata*. The result of the curation of 331 sources, gathered from literature, targeted surveys, local conservation reports, museum specimens, personal communications by authors and by their research teams, national biodiversity information systems (i.e. the UK National Biodiversity Network (NBN), www.nbn.org.uk) and validated citizen science observations (i.e. <https://www.inaturalist.org>) was published in March 2020. 88% of these records were not previously referenced in any online information system.

Additionally, historic field notebooks from Edouard Fischer-Piette and Gustave Gilson were scanned for *S. alveolata* information and manually entered. Each of the 21,512 records was checked for spatial and taxonomic accuracy (see Table 5), particularly in the English Channel and the North Sea where incorrectly identified observations of intertidal *Sabellaria spinulosa* had been previously recorded. A further 54 observations were recorded as '*Sabellaria* spp.' as the available information did not allow for an identification to species level. The result is a curated and comprehensive dataset spanning over two centuries on the past and present global distribution and abundance of *S. alveolata*. The data fields are compliant with existing database standards (e.g. the Darwin Core reference for biodiversity informatics) and are presented in Table 5 below.

Table 5. REEHAB dataset metadata

REEHAB dataset fields	Column Header	Notes
Record number	DB_ID	
Country	COUNTRY	
Site Name	SITE_NAME	In text format . e.g.: Auchenmalg Bay, Praia da Adraga
Latitude	LATITUDE	WGS84 in decimal degrees . e.g.: 43.269874
Longitude	LONGITUDE	WGS84 in decimal degrees . e.g.: -2.65874
Accuracy	POS_ACC	Drop-down menu, six categories: <10m (GPS positioning) <100m (precise location without GPS, e.g. digitization of a 1/100 000 map) <1km (beach, small bay) <10km (city, bay) <100km (record at county –UK or département FR level) >100km (marine / biogeographic region)
Start Date	START_DATE	YYYY-MM-DD format
End Date	END_DATE	Occasionally, records indicate the date at which <i>S. alveolata</i> is no longer observed in a location YYYY-MM-DD format
Tidal Zone	TIDAL_ZONE	Intertidal / Subtidal / Unknown
Latin Name	ORIG_LAT_NAME	The Latin name used in the publication, i.e. <i>Sabellaria alveolata</i> Linnaeus, 1767
Validated Species Name	VALID_SP_NAME	Either <i>Sabellaria alveolata</i> or <i>Sabellaria</i> spp.
Identification Change	NAME_MODIF	A YES/NO answer whether a species identification was changed, based on REEHAB project expert judgment. e.g.: based on their location and local

		expert knowledge, ‘ <i>Sabellaria</i> spp.’ Records from Edouard Fischer-Piette’s notebooks have been changed to ‘ <i>Sabellaria alveolata</i> ’.
Species Description Accuracy	SAB_ACC	Drop-down menu: Expert judgment , i.e. a citizen science observation without any photos, from an area known to have presence of <i>S. alveolata</i> Remote sensing Photo Reef structure Species morphology Genetics Unknown
Presence / Absence	PRES_ABS	P = Presence; A= Absence
SACFORNU	SACFORNU	Drop-down menu, eight categories: S = Super abundant Massive patches forming hummocks at least 60 cm thick, covering over a total 10 000 m ² surface; A = Abundant Numerous large patches almost always over 1 m ² in area forming hummocks over 30 cm thick, covering over 1000 m ² ; C = Common Numerous large patches or hummocks, protruding from the substrata less than 30 cm, covering more than 100 m ² in total; F = Frequent Many scattered small patches rarely extending over 1 m ² each exhibiting straight or perpendicular orientation to the substrata, covering less than a total of 100 m ² ; O = Occasional Scattered small patches of tubes, closely adhering to rocks or other hard

		<p>substrate (veneers), covering less than a total of 10 m²;</p> <p>R = Rare Scattered tubes closely attached to the substrate, often difficult to see, covering less than 1 m² surface area;</p> <p>N = None Absent. No honeycomb worms seen;</p> <p>U = Unknown No information on abundance.</p> <p>For old articles without a precise description, if there was some hesitation between two categories, the higher abundance category was always selected.</p>
Abundance	ABUNDANCE	Abundance information extracts from the source, in the language of origin.
Depth	DEPTH	Depth (in metres) for subtidal records. format: decimal number
Substrate	SUBSTRATE	Drop-down menu, seven categories: Mud Sand Shell fragments Gravel/Pebble Boulders Bedrock Unknown
Comments	COMMENTS	
Quotation	QUOTATION	Direct quote of the sentences with species information in the language of origin
Source type	DATA_TYPE	Drop-down menu, ten categories: Citizen Science Observation Database extraction Environmental Management Report Journal Article Mapping Study Museum Specimen Personal Observation Reef Structure (i.e. bioconstruction photo ID)

		<i>REEHAB opportunistic survey PhD Theses/ BSc dissertations</i>
Source	SOURCE	Reference in Elsevier Harvard format
URL web link	LINK	Web link to article, report, database...
Year	YEAR	Year of first observation (‘START_DATE’)
Information System	Database	When sources were accessed via a database, the name of the information system (i.e. GBIF, OBIS) is listed here.

2. Data sources

The vast majority of records stem from high-resolution mapping studies of the reefs in the Mont-Saint-Michel Bay (Guillaumont et al., 1987; Bonnot-Courtois et al., 2002; Noernberg et al., 2010; Fournier, unpublished data) and Cotentin peninsula (Basuyaux et Lecornu 2019) (Figure 23). The different source types are explained in Table 5, however the ‘personal observations’ category is worth expanding on, as it contains 3,085 previously unpublished records. For instance, this category holds 96 records from Yves Gruet’s field notes and epistolary exchanges with his peers across Europe between 1966-2014, 59 records from Edouard Fischer-Piette’s previously inaccessible field notebooks (1949-1971), 2,061 records from the MarClim project (1958-2017) and 290 records gathered across Ireland (1947-2019) by Louise Firth’s *S. alveolata* Irish task force (Firth et al., in prep).

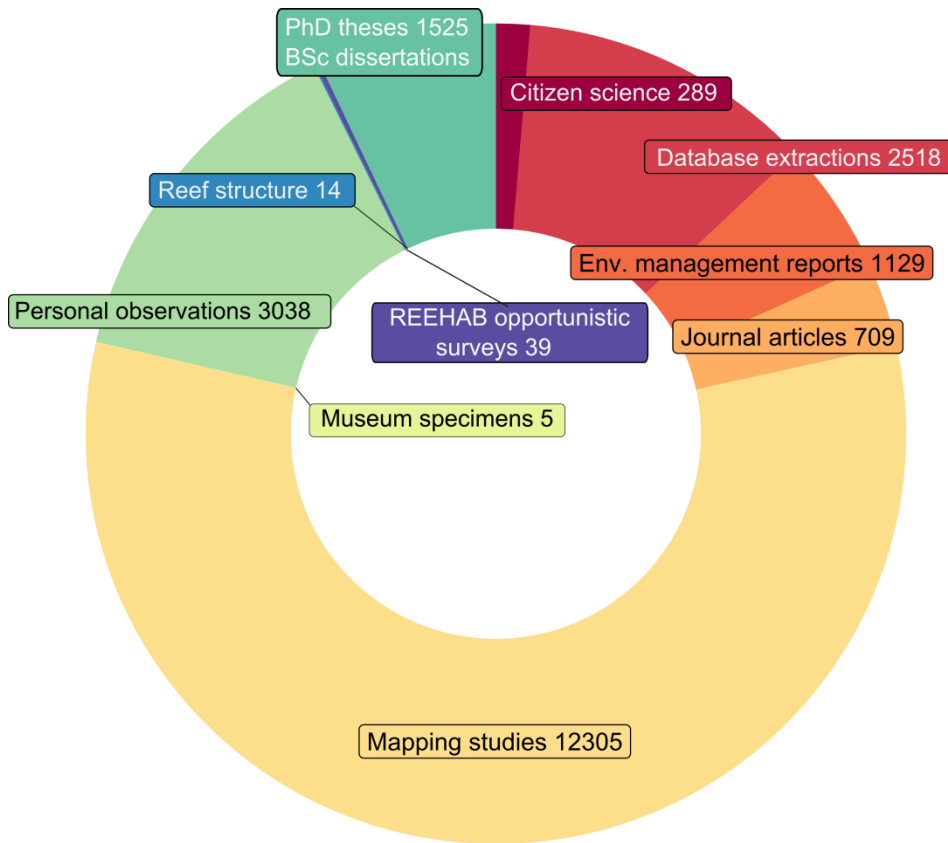


Figure 23. Donut plot illustrating the relative contribution of different types of sources to the 21,571 records collected, divided amongst 331 different sources.

3. Abundance

Out of 2,275 georeferenced occurrences stored in the Global Biodiversity Information System (GBIF - accessed on the 14-05-2020), 2,031 originated in the United Kingdom, 163 in Portugal, 47 in France, and the remaining 34 records were distributed between Ireland, Spain, Belgium and the Netherlands (both countries in which it is doubtful *S. alveolata* was ever present), Germany and one 'Unknown Country' record. Following the REEHAB project, 14,496 presence records were added, along with 4,800 absence records (currently not handled in the GBIF indexing processes), bringing the total number of records up to 21,571 – an 89.5% increase in records (Table 6). Furthermore, 90.6% of points in the REEHAB database either already had, or were assigned, an abundance score from the semi-quantitative SACFOR scale category (Table 6). The original ACFOR abundance scale was developed by Crisp and Southward (1958) and was adapted to *Sabellaria alveolata* by Cunningham et al. (1984).

Table 6. Number of occurrences per country and SACFOR scale category present in REEHAB dataset.

	S	A	C	F	O	R	N	U	Total
France	11472	900	529	155	62	29	1686	978	15811
UK	130	346	438	136	112	81	2380	453	4076
Ireland	2	67	64	30	17	10	487	108	784
Portugal	2	6	31	24	30	7	111	251	462
Spain		5	5	2	4	17	32	72	137
Italy		10	8	1	2		3	84	108
Morocco		3	2	6	4	3	11	59	88
Norway							41		41
Turkey							32	3	35
Cyprus							13		13
Mauritania						1	2	2	5
Tunisia					2			3	5
Germany							1	1	2
Belgium								1	1
Egypt								1	1
Senegal							1		1
Total	11606	1337	1077	354	233	148	4800	2016	21571

Data from the southern range boundary was also greatly increased, with 88 records collated for Morocco between 1921 (Charrier, 1921) and 2018, from 22 different sources, including field notebooks from Carla Lourenço, Fernando Lima, and Steve Hawkins (Figure 24). With two historical records found in Mauritania (Sourie, 1954) and a handful of recent observations recorded in Dakhla, western Sahara, a scattering of data has now been collected within the vicinity of the presumed equatorward limit of *S. alveolata*; Cap Blanc peninsula, which runs the border between Mauritania and Western Sahara and is a known biogeographic boundary between tropical and warm-temperate species (Lawson and John, 1977). Coupled with the fact it is situated within a rapidly changing upwelling system (Seabra et al., 2019), this understudied and not readily accessible stretch of coastline warrants a targeted ‘BioBlitz’ type survey of the intertidal zone.

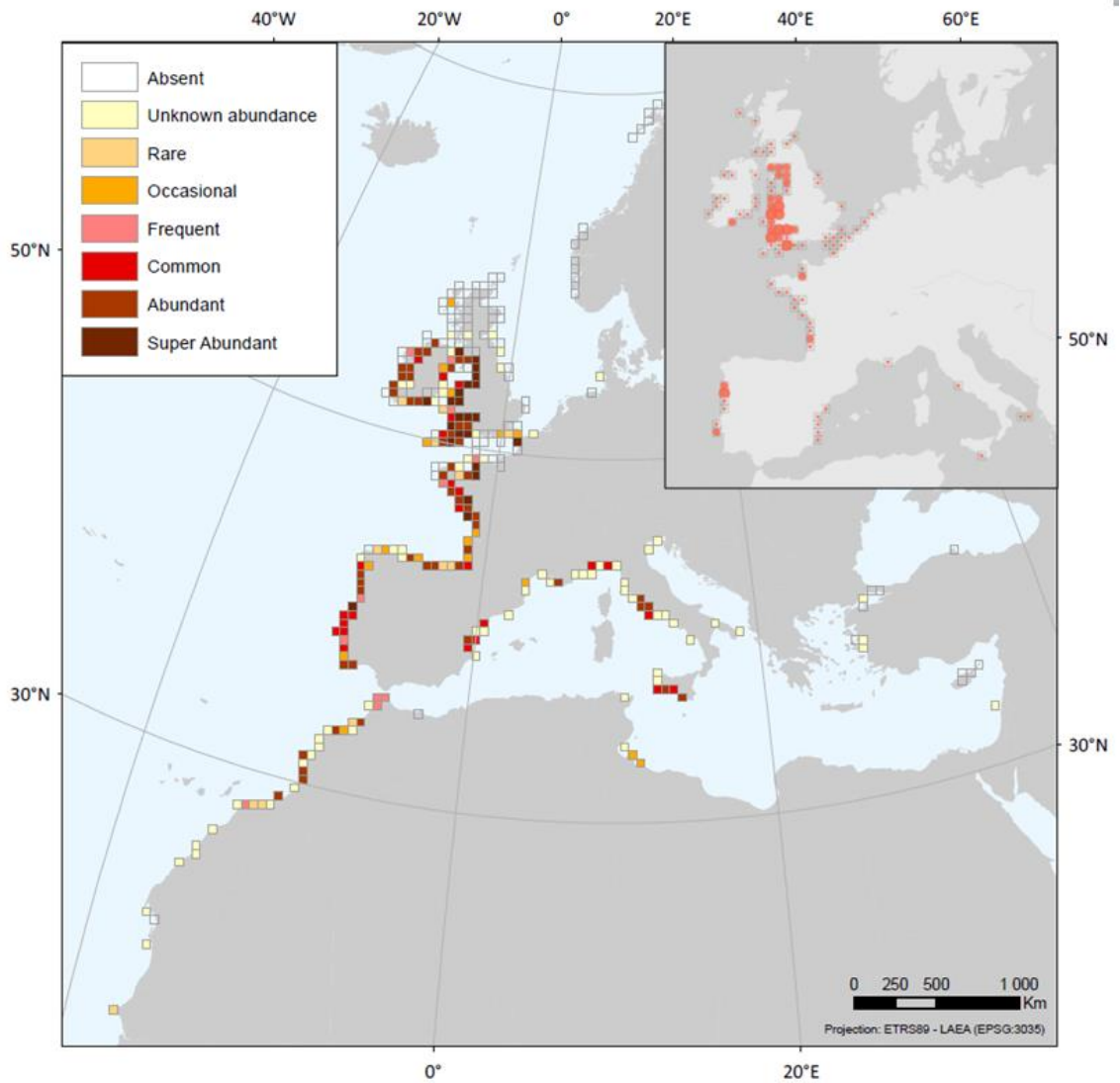


Figure 24. *Sabellaria alveolata* records in REEHAB dataset projected onto a 50km grid. When SACFOR scale abundance scores were given to occurrence records, the highest abundance value per grid cell was retained. The inset map in the top-right corner is a view of the georeferenced records held in GBIF (accessed on 28-05-2020).

4. Time series

The first georeferenced occurrence record in GBIF dates back to 1933, from the Ivor Rees North Wales marine fauna sightings (University of North Wales, 2018). Table 7 summarises the number of records per country and time period.

Table 7. Number of occurrence records per time period, ranked by country.

	1821-1900	1921-1925	1926-1950	1951-1975	1976-2000	2001-2019	Total
France	46	40	80	278	2148	13220	15812
UK	7	10	15	171	703	3170	4076
Ireland	3	5	1	197	131	447	784
Portugal				45	45	372	462
Spain		8	13	22	33	61	137
Italy	3	1		3	54	47	108
Morocco		4	4	12	15	53	88
Norway						41	41
Turkey					24	11	35
Cyprus					13		13
Mauritania				2	2	1	5
Tunisia			3			2	5
Germany				1	1		2
Belgium	1						1
Egypt	1						1
Senegal					1		1
Total	61	68	116	731	3170	17425	21571

In the REEHAB dataset, the earliest European¹ reference to *Sabellaria alveolata* with any sort of geographic precision refers to *Sabella alveolata* Linnaeus, 1767 and dates back to 1825. In the memoirs of a Linnean naturalist society in Normandy, the species is listed as forming dense aggregations atop of flat rocks along the west coast of the Cotentin peninsula (Figure 25; de Gerville, 1825).

¹The earliest mention of *Sabellaria alveolata* was found in 1821, published by Savigny in 1830, who listed the species as one of the polychaetes found in Syria and Egypt “during the French army expedition” (Savigny, 1830).

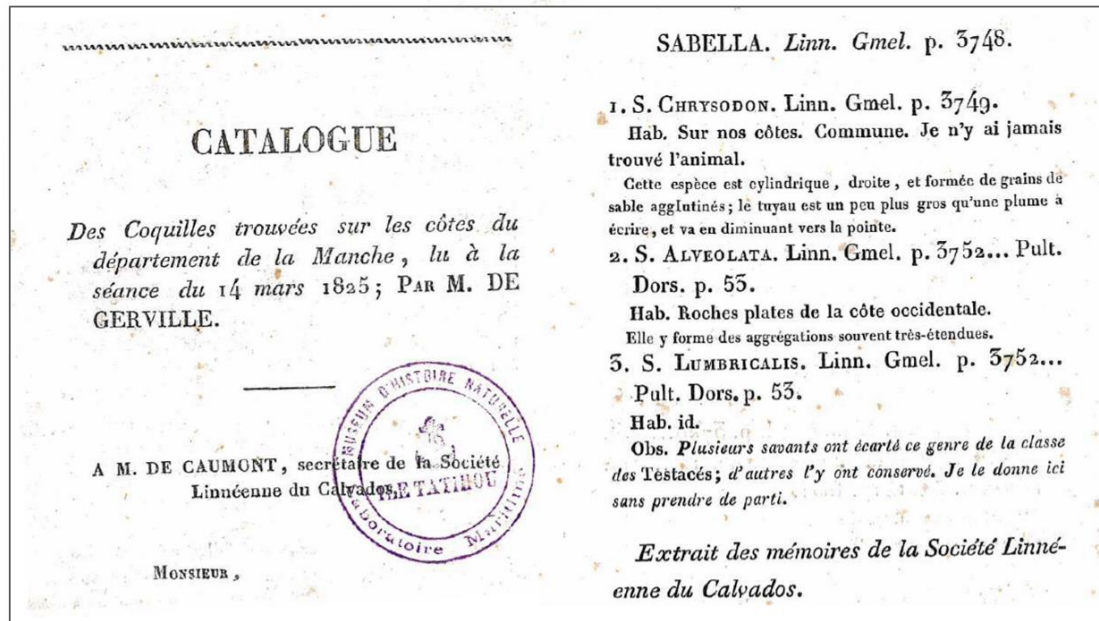


Figure 25. The oldest European record in the dataset - *Sabella alveolata* Linnaeus, 1767 (superseded original combination). From de Gerville, 1825.

Prior to this study, Cunningham et al. (1984) produced the most extensive review of the distribution of *S. alveolata*, in Britain or elsewhere. If we consider any data collected prior to 1984 as being historical (Firth et al., 2015), the REEHAB dataset contains 1,350 historical records, divided among 12 countries (Table 7).

5. Historical ecology

The primary objective of this data curation was to combine historical records and contemporary data to document changes in the distribution and abundance of *S. alveolata* bioconstructions, in order to elucidate which biotic and abiotic factors shape them. In parallel, the study of historical, local and grey literature also brought to light a shifting perception in the value of *S. alveolata* reefs. Past literature and local vernacular names reveal that these constructions have often been viewed as pests or parasites, particularly in areas with shellfish aquaculture (Dollfus, 1921), or even as an exploitable resource (Audouin and Milne-Edwards, 1832). There are scores of stories that could be told; as an example, how subtidal *S. alveolata* reefs were decimated within the space of a decade in the gulf of Marseilles is summarised in Box 1.

Box 1: The late 19th Century decimation of Marseilles' *S. alveolata* reefs

Paul Gourret (1859-1903) was a zoologist and the deputy director of Endoume marine biological station in Marseilles. Most of his work focused on Mediterranean fisheries. In 1893, he published “les appâts de pêche usités à Marseille” in the “Revue Maritime et Coloniale”, in which he documents which invertebrates were used to bait which fish by Sunday anglers. In this article, he lists *Hermella alveolata* (synonym for *Sabellaria alveolata*) (*Peiro abillo* or ‘bee stone’ in Provençal) as one of the popular fish baits, and refers to the species in mining terms, as a deposit that could be extracted at a rate of 1000kg a day (Gourret, 1893). In his 2007 article, the ecological historian Daniel Faget wrote that there was a nascent trend after the 1850s in weekend fishing excursions, so much so that an impromptu Saturday evening bait market arose on the old port in Marseille (Figure 26).



Figure 26. An engraving from the Musée d'Histoire de Marseille depicting the baits market that was held on the ‘Quai aux huiles’ in the old port in Marseille every Saturday evening circa 1870-1900 because of the recent fashion of Sunday angling. Photo courtesy of Daniel Faget.

The presence of *S. alveolata* on the market is described as having occurred in the ten years prior to Gourret’s publication (circa 1880), and of being a fishing bait that was made popular by Neapolitan immigrants, present in Marseilles as a result of the Italian diaspora. In his 1894 work on Mediterranean fisheries, Paul Gourret goes into some detail describing and drawing the *Sabellaria* species (Figure 27). He estimated the *Peiro abillo* extraction rate at 50 tonnes per year and goes on to say that “cette industrie, relativement récente [...] n’aura pas une bien longue durée” (“this relatively recent trade [...] will be short-lived”). His prediction proved to be correct: due to a combination of over-exploitation, pollution (from the “savon de Marseille’ soap factories) and the proximity of large mussel farms (Faget, 2007), *S. alveolata*

colonies in the gulf of Marseilles never returned to their former ‘super-abundance’, and only a few subtidal individuals can presently be found.

In a third publication from 1901 on the sedentary annelids of Marseilles, Paul Gourret compares the anatomy of the *Sabellaria* species found in Marseilles with the descriptions made by his peers, professors de Quatrefages and Grube. He states with some confidence that all the individuals found in the gulf of Marseilles are indeed *Sabellaria alveolata* (Gourret, 1901).

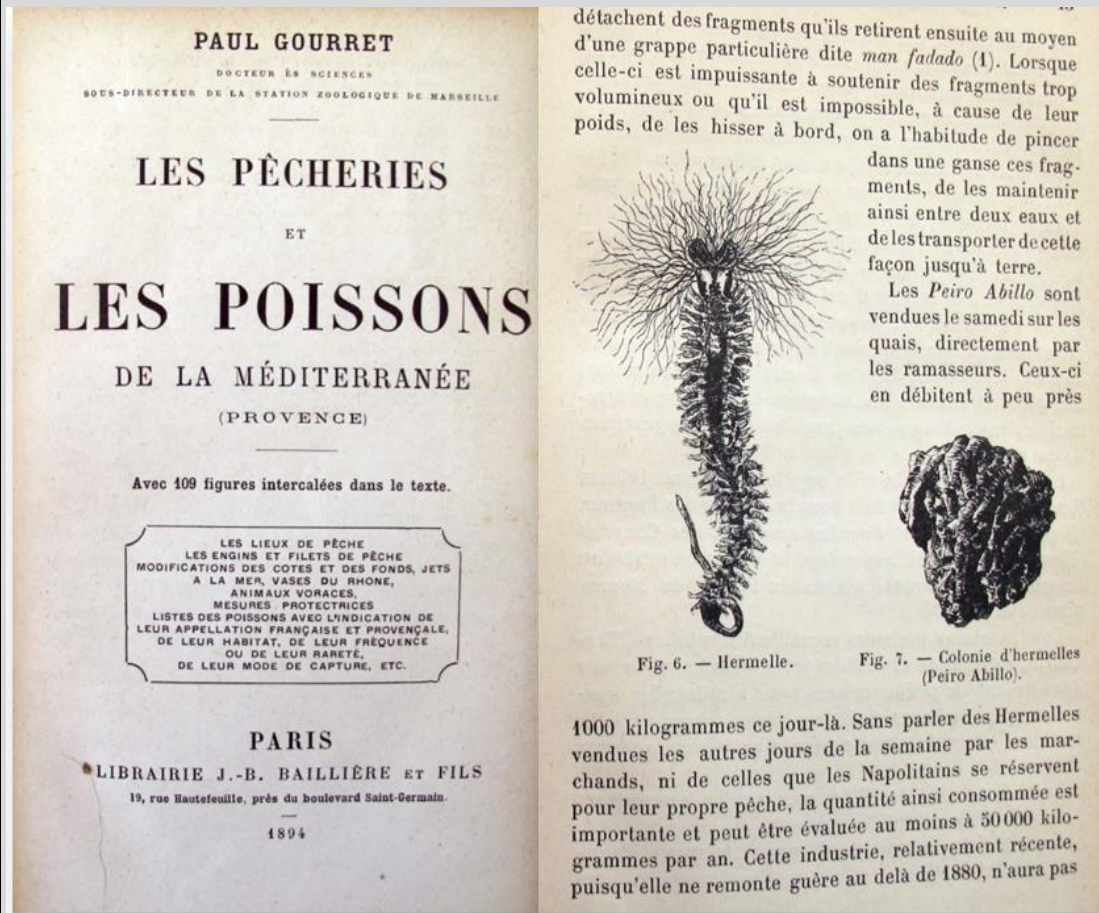


Figure 27. Extract from Gourret (1894) with drawings and quantification of the quantity of ‘hermelles’ extracted.

Given his detailed anatomical comparisons, coupled with many other references to *S. alveolata* in the Mediterranean (reviewed in Sanfilippo et al., 2019), Paul Gourret’s professional judgment of the species identification can be trusted.

6. Conclusion

There is evidence that the biodiversity of many marine habitats is being altered in response to a changing climate and human activity (Butchart et al., 2010). It has long been recognised that recycling old information can address a multitude of new policy concerns, and that broad-scale long-term observations are essential for disentangling climate-driven change from other regional and local-scale anthropogenic impacts and environmental fluctuations or cycles in natural systems (Hawkins et al., 2013). Despite being one of the most common phyla in the marine realm, polychaetes are under-represented in broad-scale studies as evidenced by their low numbers in georeferenced databases (Lenoir et al., 2020). Understanding changes, and forecasting where changes are likely to occur, requires as a bare minimum monitoring of organism diversity, distribution and abundance. However, existing global ocean observing infrastructure and programs often do not explicitly consider observations of marine biodiversity and associated processes and have focused instead on physical and biogeochemical measurements (Canonico et al., 2020). In chapter III-B, had *S. alveolata* occurrence data simply been downloaded from an online database – as is the case in the majority of SDM studies - our estimated distribution range and forecasts would have been grossly incorrect ('rubbish in, rubbish out'). The REEHAB dataset is now a part of the global biodiversity infrastructure and has provided a broader, longer-term view of *S. alveolata* distribution and abundance.

SECTION III-B

ARTICLE III – TO THE EDGES AND BEYOND: PROJECTING THE BIOGEOGRAPHIC DISTRIBUTION OF AN INTERTIDAL REEF-BUILDER UNDER CLIMATE CHANGE

Amelia Curd^{1*}, Mickaël Vasquez¹, Aurélien Boyé¹, Lucy M. Bricheno², Laura Bush³, Michael T. Burrows⁴, Céline Cordier¹, Andrew J. Davies⁵, Louise B. Firth⁶, Mattias Green⁷, Fernando Lima⁸, Martin Marzloff¹, Claudia Meneghesso^{8,9}, Rui Seabra⁸ and Stanislas F. Dubois¹

Article prepared for Nature Climate Change

- 1 IFREMER, Centre de Bretagne, DYNECO LEBCO, 29280 Plouzané, France.
- 2 National Oceanography Centre, Joseph Proudman Building, 6 Brownlow Street, Liverpool, L3 5DA, UK.
- 3 FUGRO GB Marine Limited, Gait 8, Research Park South, Heriot-Watt University, Edinburgh EH14 4AP, UK.
- 4 Scottish Association for Marine Science, Scottish Marine Institute, Oban, PA37 1QA, UK.
- 5 Department of Biological Sciences, University of Rhode Island, Kingston, RI 02881, USA.
- 6 School of Biological and Marine Sciences, University of Plymouth, Drake Circus, Plymouth, PL4 8AA, United Kingdom.
- 7 School of Ocean Sciences, Bangor University, 4 Askew Street, Menai Bridge, LL59 EG Bangor, United Kingdom.

8 CIBIO-InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto, Campus Agrário de Vairão, 4485-661, Vairão, Portugal.

9 Departamento de Biologia, Faculdade de Ciências da Universidade do Porto, R. Campo Alegre, s/n, 4169-007 Porto, Portugal

1. Introduction

Scientific evidence for warming of the climate system due to human activities is now irrefutable (IPCC, 2018). 2014-2019 were collectively the warmest five years on record, and ocean warming rate is accelerating (Cheng et al., 2020). Heatwaves, precipitation extremes and more frequent storm events are attributed to human influence on climate, although for the latter available evidence is less conclusive (IPCC, 2018). Temperature rises are accompanied by a multitude of altered environmental factors, such as ocean currents and wave action (Straub et al., 2019).

The key mechanism by which marine species respond to environmental change is to undergo distribution range shifts across broad spatial scales (Pinsky et al., 2020). While the directions in which species ranges have shifted (i.e. poleward in latitude or descent with depth) are often driven by increasing water temperature (Molinos, 2020), explanations for variation in range shifts across different distribution breaks within a given species' range remain elusive (Robinson et al., 2015). Successful reproduction and colonisation at leading edges drive range expansions; and reproduction failure and extirpations at trailing edges drive range contractions. Much variation is observed in range shifts among species, yet overall the proportion of leading range edges that are expanding is greater than the proportion of trailing edges that are contracting (Pinsky et al., 2020).

Due to concurrent development of similar applications with slightly different objectives, correlative models that quantify the relationship between environmental factors and known species occurrences have been described as 'bioclimatic envelope models' (Pearson and Dawson, 2003), 'habitat suitability models' (Hirzel and Le Lay, 2008), 'ecological niche models' (Harrison, 1997)

and ‘species distribution models’ (Elith and Leathwick, 2009) among other near-synonymous terms. The latter term is retained here and abbreviated as SDM, although some authors argue that SDM should include steps of niche estimation and assessment of dispersal ability or colonisation potential (Peterson and Soberón, 2012). Although the ecological niche concept is integral to SDM, the term ‘habitat’ more accurately describes what is most often modelled. A simple way of relating the ecological niche concept to SDM is that the niche describes species fitness in environmental space, a statistical method quantitatively describes that environmental profile, and the resulting predicted map translates the environmental profile into some measure of suitability in geographic space (Miller, 2010).

Intertidal species are exposed to environmental challenges posed by both the terrestrial and marine realms (Helmuth et al., 2006). Rising and fluctuating air and sea surface temperatures can have dramatic and lasting impacts on intertidal assemblages (Orton, 1933; Crisp, 1964; Sagarin et al., 1999, Firth et al., 2011). However, in temperate intertidal environments, fetch and salinity can exert as much influence on the distribution, abundance and diversity of intertidal species as temperature does (Zacharias and Roff, 2001). Temperature and precipitation are the two climatic variables that can reliably be projected under future climates, whilst wind and wave forecasts, and extreme wave projections in particular, carry more uncertainty (Morim et al. 2019). Whilst average wave height is overall projected to decrease across the North Atlantic Ocean under a warmer climate (Bricheno and Wolff, 2018), severe Autumn storms are predicted to increase both in frequency and in magnitude across Western Europe (Baatsen et al., 2015). Although SDM studies in the marine environment are on the rise and now number in the hundreds (Melo-Merino et al., 2020), to our knowledge, only eight intertidal studies overcame the challenge of compiling environmental data from both terrestrial and marine realms. Out of these eight studies, five of the model species were seaweeds (Martinez et al., 2012; Jueterbock et al., 2013; Neiva et al., 2014; Boo et al., 2019;

de la Hoz et al., 2019a), two were intertidal mollusks, echinoderms and crustaceans (Lima et al., 2007; Waltari and Hickerson, 2013) and one was reef-building worms (Faroni-Perez, 2017).

A paradox lies in the modelling of broadly-distributed intertidal species. One of the dogmas of macroecology states that coarse climatic data are what set species distribution, as environmental variables are more important than population processes or species interactions at the broader scale (Robinson et al., 2011). Yet, intertidal sessile organisms are known to respond to fine-scale variation in environmental variables such as substrate angle and aspect, which drives solar radiation and patterns of water and air flow (Wetthey, 1983, 1984, 2002; Helmuth and Hofmann, 2001; Harley, 2008). Although an increasing number of broad-scale high-resolution environmental and biological data are rapidly being generated and, importantly, are readily accessible, future climate conditions are all broad-brush predictions.

The honeycomb worm *Sabellaria alveolata* (Linnaeus, 1767) is an ecosystem engineer species capable of building tubes on low- to mid-shore hard substrates, in semi-exposed and exposed locations and can form biogenic structures ranging from veneers, hummocks to large reefs (Wilson, 1971; Curd et al., 2019). Its known equatorward range limit is in Morocco and its poleward range limit in southwest Scotland (Gruet, 1986). Outside of the United Kingdom where it is protected and where there is a strong heritage of natural history and sustained observations, little is known about its distribution. As a result, online marine biodiversity information systems (e.g. the Global Biodiversity Information Facility (GBIF); the Ocean Biodiversity Information System (OBIS)) currently contain scarce and haphazardly distributed records for *S. alveolata*. As a tube-building suspension-feeding species, it requires resuspended sand and therefore sufficient hydrodynamic energy for an abundant supply of sediment (Davies et al. 2009). Reef-forming *S. alveolata* has the potential to provide important coastal protection (Naylor and Viles, 2000) and biogenic habitat for a diverse range of other species (Dubois et al., 2002; Jones et al. 2018). Consequently, any changes in *S. alveolata* distribution will have

cascading effects on associated biodiversity, functions and services (Wetthey et al., 2011). Due to the ecological role of their engineered habitat, *S. alveolata* reefs are the target of European protection measures (Habitats Directive 92/42/EEC) and trigger management measures in coastal areas where they are present.

We predicted present-day and future distributions of *S. alveolata* across a broad latitudinal gradient (32-61° N) using carefully selected modelling techniques in order to answer the following questions: (1) can we generate an accurate broad-scale present distribution map of *S. alveolata*; (2) how will the biogeographical distribution of *S. alveolata*'s be altered in response to climate change? We used SDMs to forecast the intertidal distribution of *S. alveolata* under different climate change scenarios. We discuss the importance of environmental predictors, the relationship between the probability of occurrence and each predictor, before focusing on the future predictions and ecological consequences of *S. alveolata* tracking its climate niche into new areas.

2. Materials and Methods

2.1 Study area and Presence/Absence data

Our study was conducted across 29 degrees of latitude spanning a large gradient of coastal climatic conditions and almost the entire geographic distribution of *S. alveolata* along the north-east Atlantic coastline, from northern Scotland to Morocco (61°N to 32°N) and also along the English Channel. From the Iberian Peninsula southward, coastal waters are part of the Canary eastern boundary upwelling system linked to cooler sea surface temperatures (Seabra et al. 2019). Due to this strong upwelling, the shores and biota of northwest Spain have more in common with the shores and biota of northwest France than they do with the shores along the French Biscay coast (Wetthey and Woodin, 2008). Further north, around Britain and Ireland, the coast is heavily indented, with numerous sea lochs and large estuaries like the Shannon, Severn and Solway Firth (ICES, 2019).

S. alveolata is, and to the best of our knowledge always was, absent from the North Sea. Although it is occasionally cited as being present in the North Sea (e.g. Richter, 1927), expert consensus is that these were incorrectly identified intertidal observations *Sabellaria spinulosa* reefs (Reise, pers.comm.). This distribution limit is due to a combination of the long term hydrographic barrier to larval dispersal at the Cherbourg Peninsula in the English Channel (Salomon and Breton, 1993), and to niche occupancy by *S. spinulosa* in the Greater North Sea. Since both larval dispersal and niche occupancy are driven by processes which are not captured by SDM models, our study area does not extend to the North Sea.

2.1.2 Occurrence records

The majority of SDM terrestrial studies simply download occurrence data from GBIF. When it comes to *S. alveolata*, GBIF currently reflects the human observation effort, rather than the true distribution (Appendix 3; Figure 40). Presence and absence data were collated from numerous sources, including field observations, research articles, citizen science observations, management reports and online databases (see Appendix 4 and Curd et al., 2020). Presence records were considered between the years 2000-2019 (a time span compatible with the temporal coverage of the environmental variables), whilst absence records, of which there are fewer, were included from 1970-2019 for validation purposes. Subtidal observations, and observations without geographic accuracy down to shore level, were excluded. Overall, 109 literature sources were included in the analysis, resulting in 14,960 presence and 4,394 absence records. Only 12.2% of these records were previously accessible via online databases (Appendix 4).

S. alveolata is a sessile, non-cryptic species, therefore the dataset's observed absences could be considered 'true' absences (Peterson et al., 2011). Nevertheless, due to the compilation of multiple data sources, lack of a dedicated sampling design and uneven geographic spread in our absences, we chose to only use our presence data to build the models. Presence-only data are most appropriate for predicting potential distribution (Jiménez-Valverde et

al., 2008), such as with invasive species or climate change applications. Absence points, spanning the 1970-2019 time-step, were used instead for an independent evaluation of present-day model performance. Data were spatially thinned in the following manner: only one observation record was retained per raster cell; presence was selected over absence. The thinned occurrences (presence data) contained 363 observations.

2.2 Environmental variables

We chose to retain only ‘scenopoetic’ variables (*sensu* Hutchinson, 1978), on which the species has no impact, as predictors, as it has been argued that SDMs at coarse spatial resolutions will be more robust if they exclude variables that relate to population process or species interactions, that are manifest at the local scale (Peterson et al., 2011; Robinson et al., 2011). We did not include available seabed substrate maps because the best existing compilation layer on seabed substrate types (provided by the European Marine Observation and Data Network EMODnet) was not deemed fit-for-purpose due to low spatial accuracy in many areas.

2.2.1 Current conditions and model comparison

Environmental predictors available over the full latitudinal range of our study area come at a spatial resolution of 10-12km (while occurrence records are often located with a precision of ~100 m). To assess the sensitivity of SDMs to the spatial resolution of environmental variables, we also fitted statistical models of *S. alveolata* occurrence within a subset of our study domain (from 56°N (Glasgow, Scotland) to 32°N (Essaouira, Morocco)) , where higher-resolution (3-4 km) environmental predictors are available.

Comparisons of models performance using ~3km or 10-12km spatial resolution are presented and discussed, in terms of environmental predictors used, accuracy metrics, variable importance, response curves and ensemble modelling predictions in the third part of this chapter. Briefly, the two models yielded very similar present-day habitat suitability maps, thus validating our use of 10-12km spatial resolution environmental predictors, which also have

forecasts available for future predictions. Hereafter we only present and discuss results based on models fitted using environmental predictors at a 10-12 km spatial resolution across the whole study domain.

A set of 15 bioclimatic variables were chosen as climate-related candidate predictors (Appendix 5). This included 10-12km resolution metrics for air temperature from WorldClim version 1.4 (Hijmans et al., 2005), sea-surface temperature and salinity from Bio-ORACLE (Tyberghein et al. 2012; Assis et al. 2017) and significant wave height from Bricheno and Wolf (2018). Bricheno and Wolf (2018) developed present and future projections of coastal wave impacts in Atlantic Europe, running a WaveWatch IIITM spectral wave model (Tolman, 2009) at a regional scale. The regional projections were carried out at around 10km resolution from 1975-2100, using 1975-2005 as present climate. Wave fetch, the distance over which wind-driven waves can build given the orientation of the coastline, were re-projected and upscaled from Burrows (2012) to match our raster grid cells.

2.2.2 Future conditions

Two time horizons (2040-2050 and 2090-2100) and two Representative Concentration Pathway scenarios (RCP 4.5 and RCP 8.5) (Meinshausen et al. 2011 – Appendix 6) were considered to investigate potential distributional shifts of *S. alveolata* in response to greenhouse gas emission trajectories. Future air temperature, sea-surface temperature and significant wave height forecasts, issued from WorldClim, Bio-ORACLE and the NOC wave model respectively, were used as future predictors. Tidal amplitude, which stays relatively constant over such time scales, and fetch, for which we only have present-day data but which is a key predictor, were also included in the future predictor selection.

2.2.3 Variable processing

Since our study focuses on the coastal zone, all environmental predictors were masked at 0.1° (~10-12 km) distance to the European Environment Agency coastline for analysis (EEA, 2018). As our study covers the intertidal zone, one terrestrial and one marine variable had to be extrapolated in order to add values to those pixels with missing data which overlap with species observation data: 1) WorldClim air temperature values and 2) tidal amplitude.

2.2.4 Treatment of collinearity

Correlated variables can lead to very unstable estimates of their effects and greatly increase prediction uncertainty (Dormann et al. 2013). Collinearity was first checked by calculating the Pearson r coefficient for each pair of variables across the study area. For pairs with Pearson $|r| > 0.7$, we retained the variable known to be more ecologically relevant (Araújo et al., 2019). Because of the joint dependence of air and sea surface water temperature on solar radiation, metrics from these two temperature variables are highly correlated. Distributional boundaries are extremes, therefore it is reasonable to study them in terms of the coinciding extremes of environmental conditions (Hutchins, 1947). Since air temperatures are rising faster than those of upper ocean waters (Burrows et al., 2011), we chose to retain maximum air temperature and minimum sea surface temperature.

Following the pairwise correlation check, variance inflation factor (VIF) analyses were performed. Using the 'vif.step' function of the 'usdm' package (Naimi, 2015), variables with a VIF > 7 (Guisan et al., 2017) were excluded from the modelling framework. A final list of six variables was used in the rest of this chapter (Table 8).

Table 8. List of final predictors included in models after collinearity checks. Future projections are available for all ocean and atmospheric variables under alternative RCP scenarios 4.5 & 8.5. Variables fully described in Appendix 6.

Variable	Abbreviation	Time period
Sea Surface Temperature - Minimum	SST_MIN	Present/2040s/2090s
Sea Surface Salinity - Mean	SAL_MEAN	Present/2040s/2090s
Air Temperature - Maximum	AT_MAX	Present/2040s/2090s
Wave Fetch	FETCH	Present
Significant wave height - 90 th Percentile	HS_P90	Present/2040s/2090s
Tidal amplitude	TIDE	Present

2.3 Model building

Model building was performed in R (R Core Team, 2019) through the package ‘sdm’ (Naimi and Araújo, 2016). Two fundamentally different modelling approaches were selected to build the SDMs: generalized additive models (gam, Hastie 2017), a semi-parametric approach, and random forest (rf, Breiman 2001), a non-parametric one. The two approaches were shown to be efficient at modelling benthic species distributions (Bučas et al., 2013) and were selected in particular for their ability to model non-linear relationships without prior assumptions on the shape of the response: random forest through binary splits (regression trees) and GAMs using smoothing functions. Furthermore, as both approaches often makes contrasted predictions regarding species range shifts, RF projecting extreme range shifts and GAM being more conservative (Beaumont et al. 2016), an ensemble of both approaches was also constructed to take advantage of their respective strengths (de la Hoz et al., 2019b): the high predictive performance of RF and the transferability of GAM. Indeed, RF generally has amongst the highest predictive performance (Elith et al., 2006; Reiss et al. 2011). However, RF are prone to describe noise in the training data so that their high predictive performance based on current distributional data doesn’t ensure their effectiveness at extrapolating to future no-analog conditions (Wenger and Olden, 2012; Beaumont et al. 2016). GAM often show higher transferability

combined with good prediction accuracy (Wenger and Olden, 2012, Heikkinen et al. 2012). Modelling methods are described in Appendix 7.

Pseudo-absences (hereafter, PAs) were randomly generated within the masked area, outside of those pixels containing presence data. Ten sets of randomly-drawn PAs of the equivalent number of thinned presences (363 records) were generated, randomly sampling without replacement, as recommended by Barbet-Massin et al. (2012). Ten iterations of a random sub-sampling approach were performed on the ten datasets generated for SDM building, each time using 70% of the data to train the model and the remaining 30% as test data. 200 SDMs (i.e. 2 approaches * 10 sub-sample runs * 10 PA sets) were finally built. Since we used Pseudo-Absences, the models predict a habitat suitability index ranging from 0 to 1 rather than a probability of presence (Guisan et al., 2017).

2.4 Model evaluation and ensemble forecast

Each of the 200 SDMs was evaluated using two criteria 1) the threshold-independent area under the receiver operating characteristic curves (AUC – Delong et al. 1988) and 2) the the threshold-dependent true skill statistic TSS (Allouche et al., 2006). TSS (Sensitivity + Specificity -1) provides an alternative to Cohen’s kappa values and is prevalence (i.e. the ratio of ‘presence’ to ‘absence in the dataset) independent. The threshold used to determine TSS was the one that gives equal values to Sensitivity and Specificity. The SDMs whose predictions on the test data reached a $TSS \geq 0.61$ were retained for the ensemble modelling building process. This led to 116 model runs (38 gam + 78 rf) being retained for the ensemble model (Table 9).

Table 9. Mean accuracy metrics (\pm standard deviation) of models obtained for each approach, post-filtering model runs with a true skill statistic (TSS) >0.61 : generalized additive model (gam), Random Forest (rf). Numbers in brackets are the number of runs retained per approach. Area under the receiver operating characteristic curves scores are also given (AUC) .

Method	AUC	TSS	Sensitivity	Specificity
gam (38)	0.87 \pm 0.02	0.66 \pm 0.03	0.81 \pm 0.02	0.81 \pm 0.02
rf (78)	0.88 \pm 0.02	0.65 \pm 0.03	0.81 \pm 0.02	0.81 \pm 0.02

Environmental predictor importance scores were derived for each of the 116 individual models using the 'getVarImp' function in the 'sdm' package (Naimi and Araújo, 2016). Scores were derived from the AUC test metric. The median and variance in the predictor scores were ranked and plotted for each modelling technique (rf and gam) (Figure 28). Variable partial response curves for all retained variables were implemented using the 'rcurve' function also in the 'sdm' package. Responses to each variable were averaged per modelling technique across all input models, and confidence intervals were plotted (Figure 29).

In the ensemble modelling step, we combined predictions from the 116 contributing models using a weighted average, where the contribution of each single SDMs to the weighted average was based upon their respective TSS scores. Ensemble models were used to predict the current extent of *S. alveolata* (Figure 30a), and to plot mean habitat suitability scores against latitude (Figure 30b). Each ensemble predictive map was reclassified into a binary presence-absence surface, based on a threshold selection with an equal number of false positive and false negative errors (i.e. specificity equals sensitivity) (Phillips et al., 2006) (Appendix 8). Model performance was evaluated both using validation on left-out sub-samples (Table 9) and by using our true absence records to independently test the model. The models were run on these true absences, and for each model the percentage of absence points correctly

classified as being in unsuitable habitat ('true negative rates') was calculated (Appendix 9).

2.5 Calculating shifts in species core habitat

The weighted mean ensemble for each of the four future scenarios (2 time horizons * 2 RCPs) was computed by means of the 'predict' function from the SDM package. Predicted future distributions were also classified into binary presence-absence maps using the same threshold as for present distribution (specificity = sensitivity). The binary raster maps for the present-day scenario and the predicted habitat suitability shifts within the future scenarios were used to plot the areas of suitable habitat gain, loss or stability. The percentage gain or loss of suitable area in the future according to the different scenarios and time periods was calculated as:

$$\frac{n_F - n_p}{n_p} \times 100$$

where n_F is the number of suitable pixels in the future and n_p the number of suitable pixels in the present.

In addition to commenting on predicted climate-driven changes in the area of suitable habitat available, we also characterize latitudinal shifts in the core distribution of *S. alveolata* by tracking the latitudinal change between the 2040s and 2090s in the trailing edge (10th percentile), centroid (median) and leading edge (90th percentile) of the habitat suitability index (Figure 31). Present-day latitudes were subtracted from projected future latitudes for the range centroid, leading and trailing edge of *S. alveolata* habitat. All latitudinal shifts were converted to distance in kilometres, and projected distances shifted were converted to decadal rates of habitat shift using 2020 as a baseline (e.g. rates between 2020 and 2050; Table 10).

3. Results

3.1 Cross-validation and variable influence

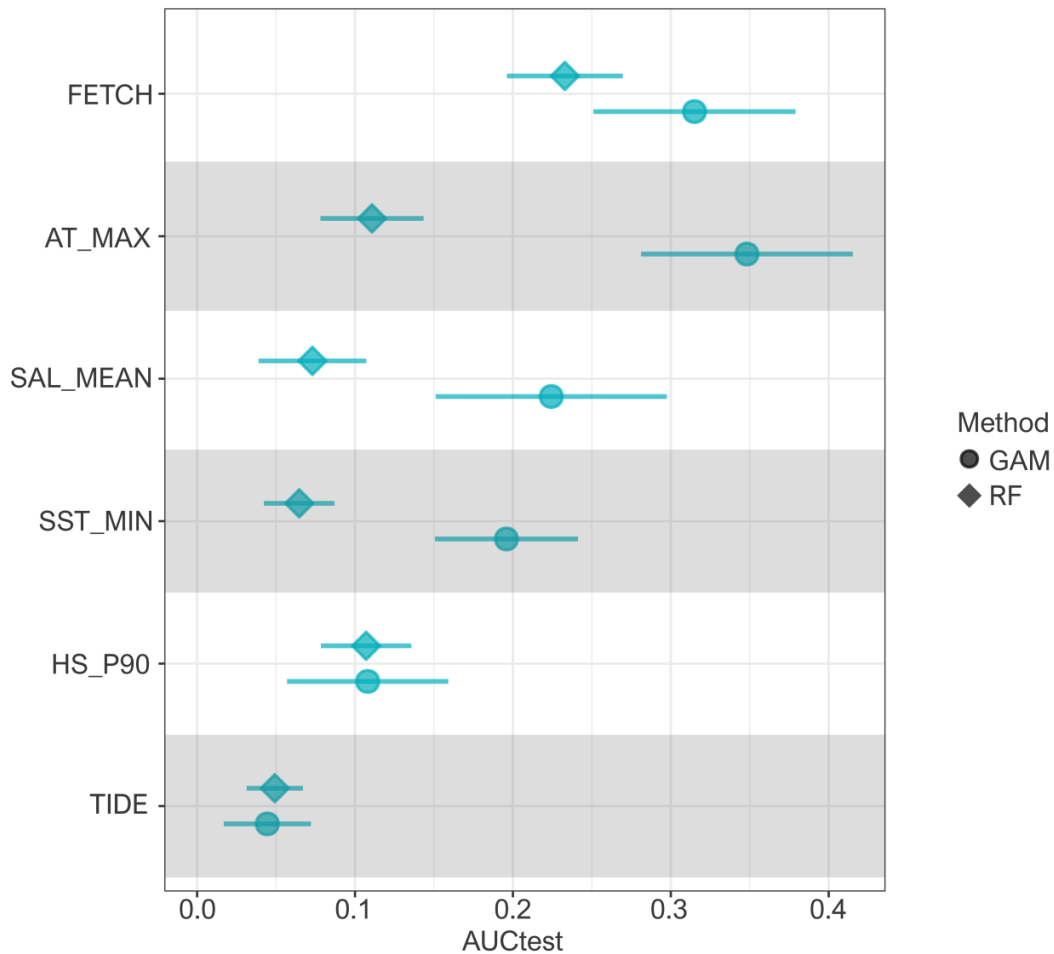


Figure 28. Variable importance scores for the model, for the two modelling approaches used (gam - generalized additive models and rf - random forests) ranked according to the improvement in AUC (area under the receiver operating characteristic curve) resulting from the inclusion of the variable in the models - a common metric for evaluating the discriminatory ability of a binary classification model. The dots (gam) and diamonds (rf) represent the mean scores, and the whiskers the standard deviation between different model runs with a TSS > 0.61. Abbreviations are as follows: FETCH = wave fetch; AT_MAX = maximum air temperature; SAL_MEAN = mean sea surface salinity; SST_MIN = minimum sea surface salinity; HS_P90 = significant wave height - 90th percentile; TIDE = tidal amplitude.

When averaging across all model runs, fetch, maximum air temperature and mean salinity were the three most important variables (Figure 28). Predicted habitat suitability is highest when fetch is between 500-1500km, when maximum air temperature is between 17-23°C and when minimum sea surface

temperature is above 11°C (Figure 29). Predicted habitat suitability decreases when the 90th percentile of significant wave height exceeds 2.25m, decreases when mean salinity exceeds 33.5 ppt. Optimal tidal amplitude (i.e. half the tidal range) is 2m, however habitat suitability values rise again after 5m (Figure 29).

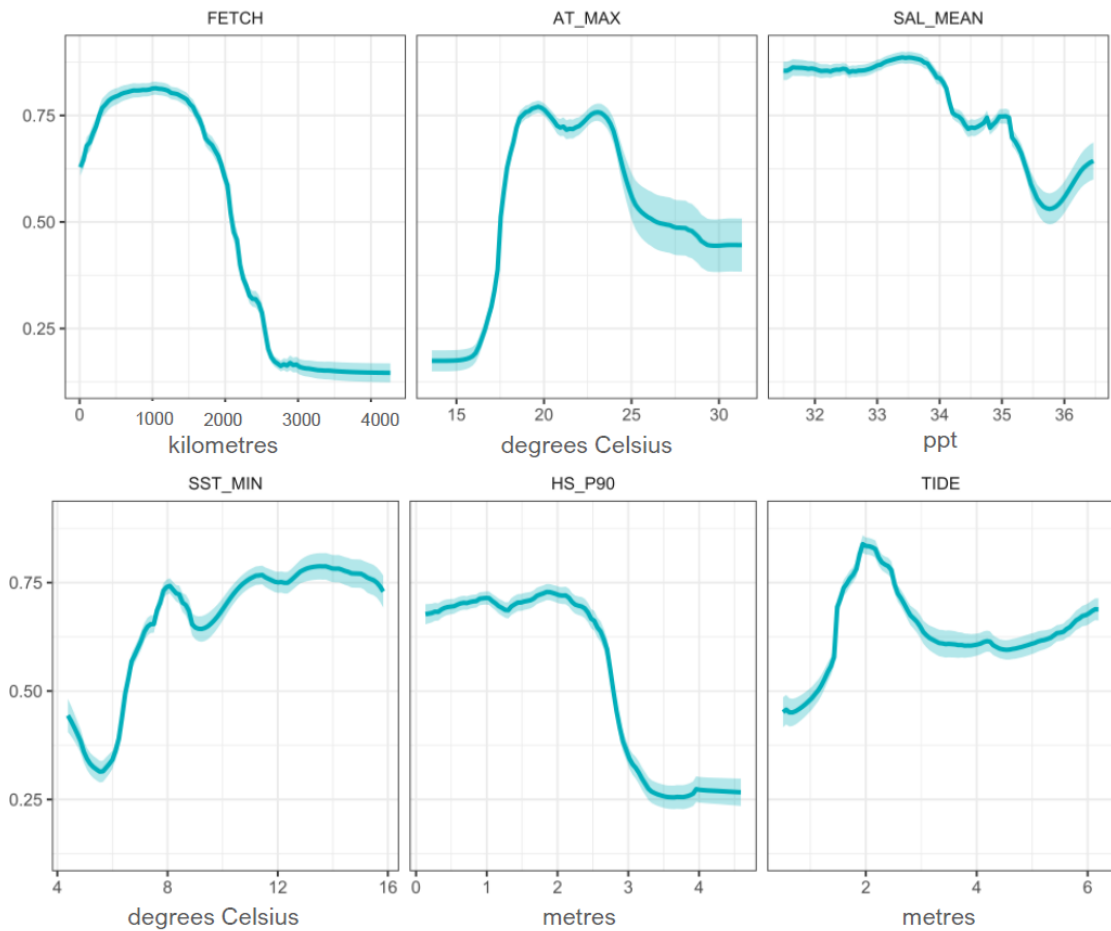


Figure 29. Variable response curves for the weighted mean ensemble models. Variables are arranged in order of importance (see Fig. 28). Abbreviations are as follows: FETCH = wave fetch; AT_MAX = maximum air temperature; SAL_MEAN = mean sea surface salinity; SST_MIN = minimum sea surface salinity; HS_P90 = significant wave height – 90th percentile; TIDE = tidal amplitude.

3.2 Predicted present-day (2000-2019) *S. alveolata* habitat

The map produced by the ensemble model output represents the most extensive and precise currently available broad-scale distribution map of *S. alveolata* (Figure 30a; Appendix 3, Figure 41). The areas of high habitat suitability are positioned where the major *S. alveolata* reefs are known to be found. The west coast of Britain, the south of Ireland and Mont-Saint-Michel Bay, France are just three location examples that demonstrate that high habitat suitability reflects *S. alveolata* abundance.

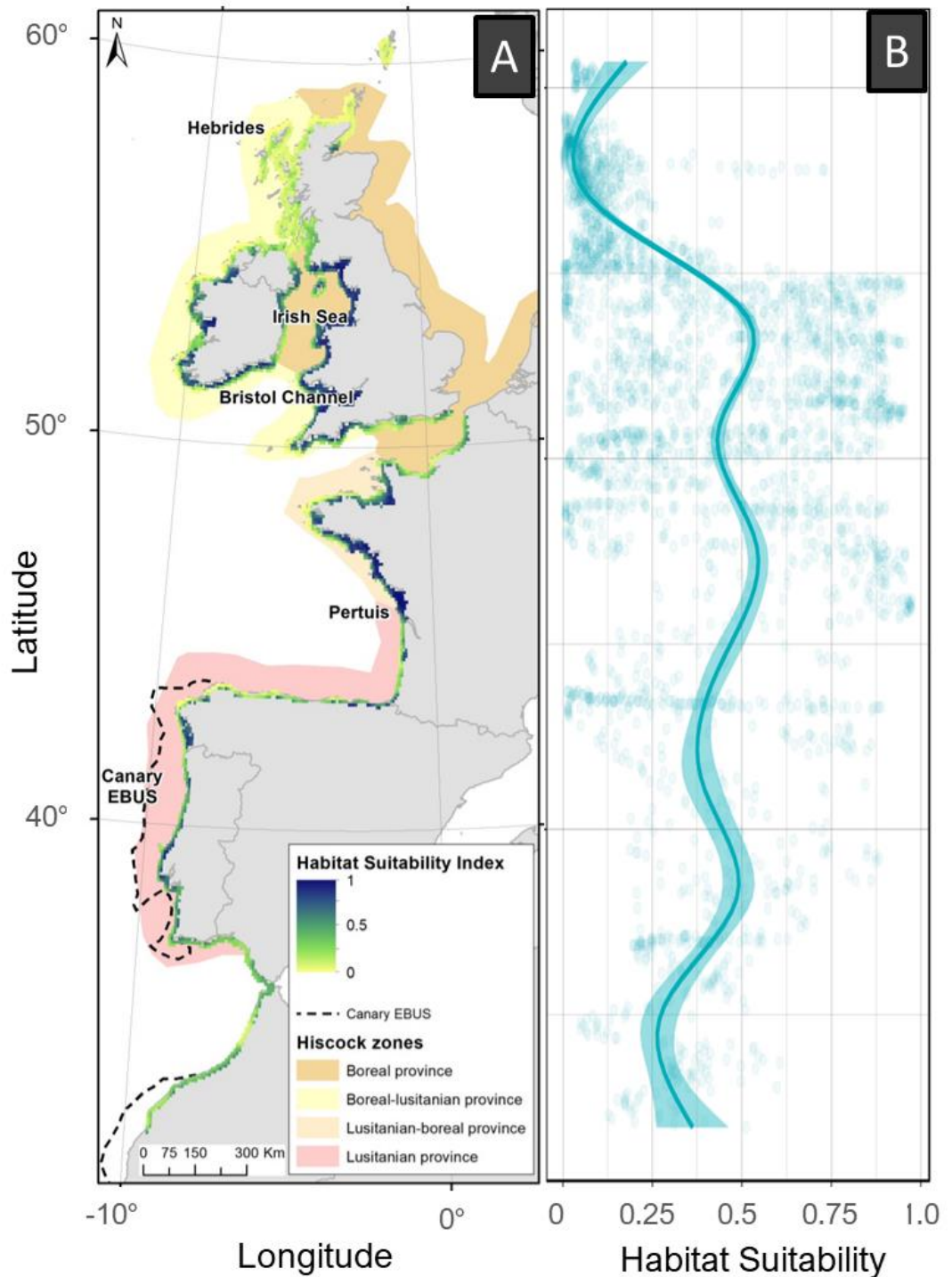


Figure 30. Weighted mean ensemble predictions for habitat suitability across our study area. A) Biogeographic provinces, based on abiotic factors, are redrawn from Hiscock (1998). Canary EBUS = Eastern Boundary Upwelling System, as described by Seabra et al. (2019). B) Longitudinally integrated latitudinal distributions (that is, predicted habitat suitability) are represented by smoothed conditional mean curves, calculated using a generalized additive model.

Our true absence record evaluation showed 71.2% of the 465 thinned absence observation records were correctly classified as absences (Appendix 9). The small areas with highly inaccurate false positives (i.e. with a habitat suitability index > 0.8) were all situated in embayments and/or intensively surveyed shorelines such as Galway Bay, Ireland, the Severn Estuary, Britain or the Pertuis Charentais, France (Appendix S7; Figure 44).

Predicted habitat suitability peaks at three latitudes: 40.2° N, 45.9°N and 52.9°N, with the central peak, situated at the latitude of Oléron Island in France, marking the highest habitat suitability (Figure 30b). The troughs between these habitat suitability peaks were situated at 43.1°N and 49.7°N, which correspond to the northern Spanish coastline and the middle of the English Channel respectively. These were used to divide the *S. alveolata* range into three regions (Figure 31), hereafter the poleward, central and equatorward regions.

3.3 Projected changes in area of suitable habitat

Loss of suitable habitat area in the equatorward region ranged from 34.5% under the RCP 4.5 'stabilisation' scenario in the 2040s, to 52.9 % under the RCP 8.5 'business as usual' scenario in the 2040s, with small areas of loss in habitat suitability throughout Spain, Portugal and Morocco (Figure 31). Loss of suitable habitat area in the central region ranged from 8.2% to 23%, for RCP 4.5 and RCP 8.5 respectively, both for the 2040s. Within the central region, the French Pertuis coast of the Bay of Biscay shows persistent loss in predicted habitat suitability, in contrast to the Brittany coastline, which displays either stable conditions or small areas of gain.

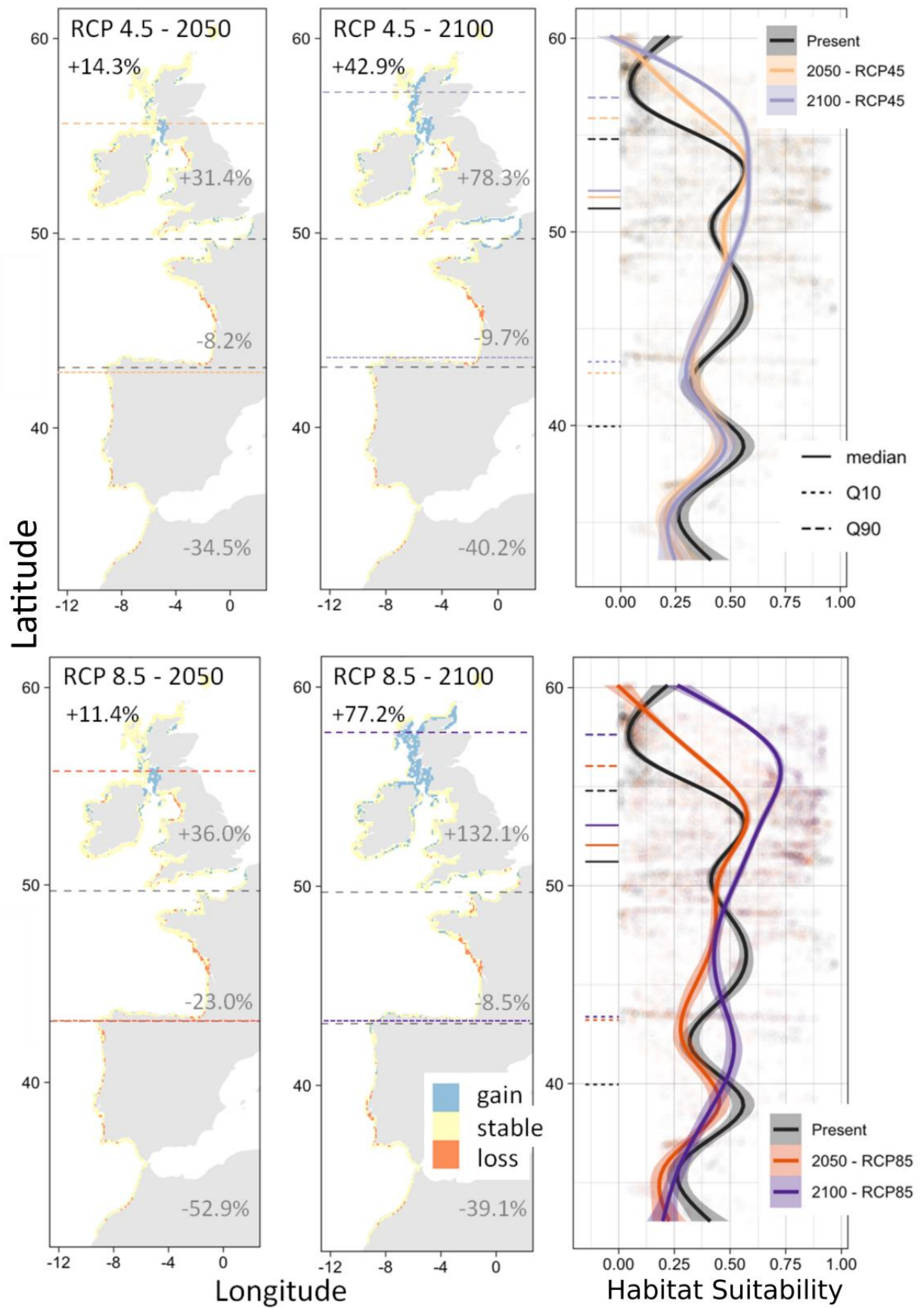


Figure 31 (previous page). Predicted shifts in habitat suitability, obtained from overlaying the binary presence-absence predictions of the weighted mean ensemble model for the present period with predicted binary distributions in the 2040s and 2090s under RCP 4.5 and 8.5. The longitudinally integrated latitudinal habitat suitability is represented by the smoothed conditional mean curves shown in the third column for the present-day (black solid line) compared to the 2040s and 2090s, for both RCP scenarios. Range leading edges (90th percentile) are represented by dashed lines, the range centroid (median) by solid lines, and range trailing edges (10th percentile) by dotted lines. Percentage loss or gain in suitable area is expressed for the poleward, central, and equatorward regions, the boundaries of which are the grey longdash lines on the four panels on the left. Numbers in the top left-hand corners of the four panels on the left are the overall percentage gain in suitable area.

The increase in suitable habitat area in the poleward region ranges from 31.4% to 132.1%, for RCP 4.5 in the 2040s and RCP 8.5 in the 2090s respectively. In Northern Ireland, the Isle of Man and the west coast of Scotland, *S. alveolata* habitat suitability is projected to increase under all future scenarios. In the 2090s, large swathes of the French and British coasts along the English Channel gain suitable habitat area under RCP 4.5, in contrast to the ‘business as usual’ RCP 8.5 scenario where only a scattering of small locations along the English Channel are predicted to gain in habitat suitability. Overall, under the RCP 8.5, by 2100 we expect 77.2% gain in *S. alveolata* distribution area, with important gains in the North of Britain and Ireland and heavy losses in the south. In contrast, under RCP4.5, overall habitat gain reaches only 42.9%, with areas of habitat gain predicted in the English Channel and western Scotland (Figure 31).

3.4 Projected shifts in *S. alveolata* range edges

Trailing edges of the *S. alveolata* range were consistently projected to shift further than leading edges and centres, both in 2050 and 2100 for both RCP scenarios (Table 10, Figure 31). Under both RCP 4.5 projections and the RCP 8.5 2050 scenario, the equatorward peak in habitat suitability is stable, the central peak disappears altogether, and the poleward peak shifts north (Figure 31). Under the 2100 RCP 8.5 scenario, the equatorward peak shifts north, the

central peak disappears altogether and the poleward peak shifts north and greatly increases in habitat suitability.

Table 10. Projected distances shifted, converted to decadal rates of habitat shift (from 2020-2050 and 2020-2100) and total difference in distance between the present-day ensemble model output and future RCP scenarios and time periods. Trailing edge = 10th percentile (Q10) of range, centre range = median and leading edge = 90th percentile (Q90).

Scenario	Range position	Decadal rate of shift (km.decade ⁻¹)	Difference (in km) to present position
2050 - RCP45	Leading	40.1	122.3
	Centre	21.6	66.7
	Trailing	102.0	300.1
2100 - RCP45	Leading	29.8	233.4
	Centre	12.8	100.0
	Trailing	46.3	366.8
2050 - RCP85	Leading	46.3	133.4
	Centre	30.9	88.91
	Trailing	121.1	355.6
2100 - RCP85	Leading	39.3	311.2
	Centre	25.6	200.1
	Trailing	47.5	377.9

Projected range edge and centroid distances shifted were converted to decadal rates of habitat shifts (Table 10). Predicted shift rates were on average twice as high from 2020 to 2050, than when computed over the whole century (2020 to 2100) for both RCP scenarios. Most of the difference in edge or centre positions is predicted to take place over the first half of the century, before levelling off in the second half of the century. In the first half of the century (2020-2050) rates of shifts are fairly similar between the two RCP scenarios, albeit with higher rates for trailing edges observed under RCP 8.5. Important differences between the two scenarios are however predicted by the end of the century, with the leading edge and centre being projected to shift much further under RCP 8.5, while trailing edge positions show little difference between scenarios. Overall, trailing edge rates of shift are higher than leading edges or centres, with little influence of the scenario on the magnitude of trailing edge shifts.

4. Discussion

As Earth's climate rapidly changes, species range shifts are considered key to species persistence. Here, we demonstrate that broad-scale SDM with carefully selected environmental predictors is an effective means of evaluating and predicting the suitable habitat of a widely distributed intertidal species. In addition to shifts in the locations of leading and trailing range edges, we discuss the significance of climate change in the centre range and the ecological consequences of a habitat-forming species tracking into new areas.

4.1 Future scenarios

Projected rates of habitat shift at the trailing edge of *S. alveolata*'s range were consistently greater than shifts at the leading edge under future climate change scenarios. Our results show the *S. alveolata* poleward range edge is estimated to expand at an average of 29.8 – 46.3 km decade⁻¹, compared to the trailing edge contracting at an estimated 46.3 – 121.1 km decade⁻¹. These results oppose those from a global synthesis of marine rates of change in distribution (Poloczanska et al. 2013), which found leading range edges of marine species to be significantly higher (72 km decade⁻¹) than at the trailing edge (15.4 km decade⁻¹). Another review focusing on intertidal species found poleward range edges to shift by as much as 50 km decade⁻¹, with an inferior rate and extent of contraction at the equatorial-range limit (Helmuth et al., 2006). As an intertidal species, *S. alveolata* experiences a combination of terrestrial and marine temperatures depending on the duration and timing of water emersion. Consequently, comparisons with existing meta-analyses of climate change focusing exclusively on marine species must be treated with caution, as these reviews either do not include any intertidal species (Poloczanska et al., 2013) or purposely exclude intertidal species from estimates of potential latitudinal ranges (Sunday et al., 2012). To our knowledge, the only study to have found consistently faster projected trailing edge shifts than leading edge concerns pelagic fish habitats in the southern

hemisphere (Robinson et al., 2015), which experienced faster shifts in the long-term (2070) than in the near-term, likely due to there being no poleward limit to the available habitat in their study area. Our results also diverge with the only other known climate change study on a sabellarid range. In South-America, the temperate reef-building *Phragmatopoma virgini* has a predicted increase in suitable habitat, however it demonstrated a multi-directional distribution shift under RCP 8.5, likely due to a broad-scale spatial homogenisation of the south-east Pacific biogeographic province, in opposition to the biogeographic provinces of the north-east Atlantic (Faroni-Perez 2017). Potential explanations for the asymmetry between leading and trailing edges found in our study include stronger regional climate change at lower latitudes and the coastline topography of the study area. In our study, although the area of suitable habitat is predicted to greatly increase in Britain and Ireland, and this is further discussed, the fact that the present-day northern range limit of *S. alveolata* is close to the northern tip of Scotland could signify that in the future it will have ‘nowhere to go’ (other than the Orkney and Shetland islands) at the poleward edge of its range. This highlights the importance of taking into account the geographical context and environmental specificities of each region before being able to make general conclusions.

Although climate change has occurred faster in temperate than tropical regions, the southern part of *S. alveolata*'s range between Portugal and its suspected equatorward range limit in Mauritania, is located within the Canary Eastern Boundary Upwelling System (EBUS - Seabra et al., 2019). This particular EBUS has been shown to be experiencing rapid warming rates at its equatorward limit (0.60°C. decade⁻¹ off Mauritania), leading to speculation that an upwelling shutdown or geographic shift has already begun (Seabra et al., 2019). This could potentially trigger a drastic regime shift in intertidal ecosystems by significantly decreasing algal cover (Bosman et al., 1987), with cascading effects through the intertidal community.

It is important to distinguish between the area of suitable habitat gained and the latitudinal distance distribution limits shift. The west coast of Scotland in particular has a very long stretch of coastline which explains why the leading edge, centroid and trailing edge of the range are all located further north than one might expect, and why there is a large increase in overall area gained. Caution must be exerted when focusing on range metric shifts. Rather than displaying a smooth north to south transition, our present-day models show three latitudinal peaks in habitat suitability. Our future projections show a small poleward shift in the range centroid (12.8 – 30.9 km decade⁻¹), yet all scenarios predict a disappearance in the centre-region habitat suitability peak in the Pertuis region of the French Atlantic coast. This increased geographic gap in suitable habitat could potentially lead to disjunct populations with multiple range edges or even, over time, speciation. Further work on broad-scale *S. alveolata* larval dispersal and recruitment, coupled genetic diversity studies, are needed to investigate whether these three peaks in habitat suitability are representative of separate metapopulations.

Range edges are characterized by variable and unstable conditions, relative to the centre range. It is likely that range edge populations evolve resistance to extreme conditions (Safriel, 1994). Therefore, those reefs in the centre-region may be subject to more environmental stability than at the edges, making individuals less adaptable, which in turn leads to greater climatic sensitivity (Robinson et al., 2015). High *S. alveolata* abundance creates large reefs such as those found on the centre-region peak on Oléron island, which further buffer and stabilise their environment (especially sediments and temperatures), possibly rendering individuals even less adaptable (Dubois, unpublished data). Range edge populations are expected to be genetically more variable since variable conditions induce fluctuating selection, which maintains high genetic diversity (Safriel, 1994). An ongoing phylogeographic study has revealed *S. alveolata* genetic diversity to be highest in the Irish Sea and the English Channel and relatively high in Morocco (Nunes, unpublished data) compared to the Bay of Biscay. Range edge populations rather than central ones may

therefore be more resistant to environmental extremes and changes, and should be treated as a biogenetic resource used for rehabilitation and restoration of damaged ecosystems.

4.2 Ecological consequences of *S. alveolata* tracking its climate niche into new areas

The potential gain of an extensive area of suitable *S. alveolata* suitable habitat, particularly in Britain and Ireland, could alter community structure and ecosystem processes, with ensuing positive and negative impacts (Wallingford et al., 2020). Whilst the unique high-biodiversity habitat *S. alveolata* fulfils an undeniable ecosystem service, it has also been qualified as ‘the dandelion of the sea’ (Hiscock, pers. comm.), as it uses force to win territory and outcompete other species such as anemones and limpet species (Wilson, 1971). It is also possible that Sabellaria reef-dwelling species will also experience range extensions by ‘hitchhiking’ along the new areas of reef presence. Climate change may therefore facilitate the dispersion of the associated fauna into new territories (Faroni-Perez 2017; Jones et al., 2018), although high species richness and diversity in resident ecological communities may slow its establishment by offering biotic resistance (i.e. Simkanin et al., 2013). As a habitat forming species, it could also promote in the new area the diversity and resilience of benthic fauna in the face of climate change (Bulleri et al., 2018). This dichotomy underscores the importance of considering the ecological impacts of range-shifting species, and habitat-forming species in particular, in terms of both the benefits and potential costs to recipient communities and ecosystem processes (Wallingford et al., 2020).

4.3 Predicted present-day distribution

Our present-day habitat suitability ensemble model outputs align well with known distribution, and shows high habitat suitability in areas with known high reef abundance (i.e. the Mont-Saint-Michel Bay and the Bristol Channel).

The fact that our model demonstrated a good performance in describing present-day distribution on the basis of six scenopoetic variables consolidates the macroecological law that coarse climatic data accurately models species distribution across their range (Robinson et al., 2015). Peterson et al. (2011) presented the Eltonian Noise Hypothesis, which is the idea that biotic interactions – not included in our models - seldom constitute a significant constraint on the distributional potential of species on large geographic extents and low resolutions. Despite all the complexity of the intertidal environment, *S. alveolata* is therefore one of those species where ecological interactions do not seem to play a dominant role at the mesoscale resolution typically used for modelling (Melo-Merino et al., 2020). This could partly be due to the fact that much of the heterogeneity in environmental stress that many intertidal sessile organisms are subject to is buffered by *S. alveolata*'s bioconstruction, which in turn acts as an environmental filter for associated fauna (Jones et al., 2018).

4.4 Variable importance

Many projections of future species distributions equate climate change with temperature increase. The median velocity at which marine isotherms shifted poleward between 1960-2009 was 37.3 km decade⁻¹ (Burrows et al., 2011). Although this rate is similar to the predicted poleward shift in *S. alveolata* (38.9 km decade⁻¹ on average), the fact that the equatorward retraction in habitat is predicted to occur at a greater rate (79.2 km decade⁻¹ on average) suggests either that climate velocity is accelerated towards the trailing edge of its range, or that *S. alveolata* is responding to other aspects of climate change than increasing temperature. The shape of temperature response curves will vary depending on whether a species is more tropical or temperate. Tropical species live closer to their physiological thermal limits, whereas temperate species may commonly experience temperatures closer to the centre between their maximum and minimum thermal limits (Tewksbury et al., 2008; Sunday et al., 2012; Pinsky et al., 2019). It is perhaps unsurprising that temperature is not the

variable of importance for an intertidal species, as they have a much broader range of temperature tolerance than fully marine species and can experience annual temperature ranges in excess of 40°C (Gandra et al., 2015).

Salinity, significant wave height and tidal amplitude also play a part in determining *S. alveolata* habitat suitability. While air and sea surface temperature are the second and fourth most important variables respectively, fetch is the most important variable, suggesting that coastal exposure to wind action is of utmost importance in defining *S. alveolata* habitat suitability. Sabellarid worm reefs are known to be tolerant to salinity fluctuations (Faroni-Perez, 2014; Aviz et al., 2016). However the fact that a slightly lowered salinity (~33.5 ppt) is an important variable for *S. alveolata* is perhaps indicative that salinity is a proxy of large meso- to macro tidal estuaries such as the Severn or Loire, which it favours not because of the lower salinity, but because of the vast amounts of suspended particulate food and sand for building its tubes. Our response curve clearly indicates a drop in habitat suitability above a 90th percentile value of 2.5 metres in offshore wave height. How this translates into wave breaks along the coast is uncertain, as due to the topographic complexity of rocky shores there is only a weak correlation with offshore wave height (Helmuth et al., 2005). A general prediction for most rocky shore organisms is that more severe wave conditions should result in increased dislodgment, shifting species distributions to more wave-protected habitats (Helmuth et al., 2005).

Tidal currents transport marine sediment, crucial for tube-building, as well as supplying food. Tidal amplitude could also be a proxy for the thermal environment and the potential for stress and desiccation (Finke, 2007). Our models show an optimal habitat suitability with a tidal amplitude of 2m (corresponding to a tidal range of 4m), with a rise in habitat suitability in the near-macrotidal range of 10m. This high amplitude inflexion is no doubt driven by the *S. alveolata* presence records in the macrotidal Severn Estuary and the Mont-Saint-Michel Bay, the latter of which is home to Europe's largest intertidal reefs (Desroy et al., 2011). Tide is intrinsically linked to temperature in

intertidal organisms, as the timing of the alternating exposure to terrestrial and marine environments is driven by the dynamics of the tidal cycle (Helmuth et al., 2002). Our model predicts and forecasts *S. alveolata* distribution at the adult life-history stage, which is expected to be influenced by both marine and terrestrial environmental variables (Raffaelli and Hawkins, 2012). By including air and sea surface temperature together with tidal amplitude in our scenopoetic variables, we indirectly capture the effect of the timing of high and low tides, which can for example make intertidal air temperatures plummet when spring low tides occur at night time (Mislán et al., 2009).

In light of our three most important environmental predictors, *S. alveolata*'s preferred habitat can be defined as large semi exposed meso- to macro tidal estuaries with varying salinity (<33.5 ppt). Highly exposed areas (fetch > 1500km) that are subject to high wave action (90th percentile >2.5 metres in offshore wave height) on the other hand are not suitable.

4.5 Realism and accuracy of model projection

We see four major factors that may affect the realism of our projections: 1) the dispersal ability of the species and how current dispersal boundaries may be modified in the future, 2) the growth of artificial structures, 3) the occurrence of extreme events and their effects on *S. alveolata*, and 4) the niche conservatism of *S. alveolata* and how its niche may be occupied in future suitable areas.

It is important to remember we modelled the existence, and not the accessibility, of suitable habitat for *S. alveolata* individuals. The net gain in suitable habitat rides on an important assumption: that larval dispersal will cross over existing biogeographic boundaries in the Irish Sea and the English Channel. There is a biogeographic boundary zone from the Cotentin Peninsula to the Isle of Wight in the English Channel (Crisp and Southward 1958), represented as the boundary between the Lusitanian-Boreal province and Boreal province on Figure 30. A similar biogeographic range edge exists between Northern Ireland and the Scottish isle of Islay, represented as the

boundary between the Boreal province and the Boreal-Lusitanian province on Figure 30. Both locations are situated where hydrographic features represent potential barriers to larval dispersal (Simpson et al., 1979; Salomon and Breton 1993). In response to recent warming temperatures some species have breached the English Channel boundary and are experiencing range extensions along both the French and British sides (Wetthey et al., 2011). This could also be the case for *S. alveolata* in the near future, in the English Channel and in western Scotland, providing it is not prevented by biogeographical barriers (Hiscock et al., 2001). If however, present-day larval dispersal boundaries are not breached, this will result in large areas of potentially suitable habitat, particularly along the extensive coastline of western Scotland, remaining unoccupied, leading to an overall net loss in suitable habitat area.

If and once larvae reach a new area of suitable habitat, they will need a suitable hard substrate on which to settle. Available hard substrate was not included in our model, as broad-scale intertidal rock data at a sufficiently high-resolution to depict potential larva substrate settlement does not yet exist. It is in fact exceedingly difficult to measure or model on a spatially explicit basis variability and heterogeneity at small scales over large geographic gradients (Helmuth, 2009). *S. alveolata* also settles well on artificial structures (Firth et al., 2015). Species range shifts should be evaluated based on an understanding of the interaction of environmental factors with non-climatic factors such as changes in land use (Wang et al., 2020). In a rapidly urbanising and warming world, artificial coastlines are proliferating (Firth et al. 2016) with artificial structures potentially functioning as stepping stones to dispersal for hard-bottom biota across stretches of unsuitable sedimentary habitat (Airoldi et al. 2015). The increase in artificial structures is expected to increase suitable area for *S. alveolata*, however this was impossible to quantitatively predict in our approaches.

Both spatial and temporal variability in temperature are greater in the intertidal zone than when compared with the ocean. All six environmental predictors used in our analyses are averaged over a decade or more, and may not represent the critical bottlenecks for long-term species persistence of terrestrial (or indeed intertidal) species (Sunday et al., 2012). As an example, there are predicted significant increases in marine heatwave intensity and count of annual marine heatwave days are projected to accelerate (Oliver et al., 2019). Interannual anomalies or short periods of extreme heat not captured by the monthly averages used here may be critical for limiting long-term occupancy at the trailing edge boundary, with cold waves exerting a similar influence on the poleward leading edge (Hutchins 1947).

A final critical underlying assumption in biogeographic modelling is that of stationarity or niche conservatism in space and time (Woodin et al., 2013), i.e. that predictions made on the basis of one location and time will be valid in other geographic regions at other times. Were local populations to become adapted in the future, with consequent shifts in the Grinnellian niche, SDM transferability would not be possible (Miller, 2010; Waltari and Hickerson, 2013).

5. Conclusion

Significant shifts in *S. alveolata*'s range are predicted to happen within the next 30 years, particularly at the equatorward range edge. Even if we allow for an overestimation of distributional limit shifts due to SDM not explicitly modelling the processes that drive population dynamics or organismal responses to the environment, the distance and rate of contraction of the southern distribution limit are of concern. This means we have no time to lose in focusing research efforts on the understudied trailing edge of *S. alveolata*'s range. The populations at both range edges should be conserved now as potentially resilient genetic repositories, to be used in the future for mitigating undesirable

effects of global climate change. Conservation efforts should also prioritise those high-abundance reefs that remain stable or are even set to gain suitability, i.e. Duncannon (Ireland), southern Brittany and Bourgneuf Bay (France). In those areas into which *S. alveolata* is predicted to shift, we suggest drawing inspiration from invasion ecology theory and risk assessment tools to quantify both its potential impacts and define specific conservation goals in response.

SECTION III-C

SPATIAL SCALE EFFECTS ON SPECIES DISTRIBUTION MODELLING: THE CASE OF THE HONEYCOMB WORM

1. Introduction

Spatial scale varies along two main dimensions – grain, the spatial size of individual samples, and extent, the total area under study. When investigating habitat and species distributions, complex effects, which vary by species and system, may result from changing spatial scale, yet empirical investigations of these effects are rare (Connor et al., 2019). In the marine realm, it has been argued that SDMs that only include climatic data are potentially more robust at a coarse than at a fine spatial scale, because environmental variables are more important than population process or species interactions at the larger scale (Pearson and Dawson, 2003; Montoya et al., 2009). Coarse-scale SDMs are known to be more suitable for widely distributed species in environments without fine-scale variation, such as some pelagic species (Robinson et al., 2011). Predictions relating to sessile organisms can be affected if resolution is reduced as fine-scale predictors can be more meaningful (Guisan and Thuiller, 2005). For a widespread intertidal engineer species the effect of spatial scale has yet to be tested.

It is important to understand the processes involved in order to choose the appropriate and ecologically relevant scale (Guisan and Thuiller, 2005). Despite the increased prominence of SDMs in scientific literature, studies that assess changing grain size, particularly in the marine realm, are few (but see Turner et al., 2019). Patterns observed at one scale may not be prevalent at another. While the effect of sample size on SDMs has been well explored (i.e. Hernandez et al., 2006), the effect of the extent of the study region has received considerable less attention (but see Anderson and Raza, 2010). At large total extents, a larger range of environmental predictor values allows the models to better differentiate between areas of low and high suitability at that given total extent. However large study extents do not always improve model accuracy. Depending on the geography of the study area and the dispersal ability of the model species, large total extents may include populations with different environmental responses within the same model, which can outweigh the positive effects of including an increased range of environmental variables (Connor et al., 2019).

The following chapter section presents the comparison between two models built to model the present distribution of the honeycomb worm *S. alveolata*, using two different grain sizes and total extents. We compared the effects of using environmental predictors available at a ~3km grain size, across a subset of our study area (56°N to 32°N), to using variables available at a 10-12km grain size across the entire study domain (61°N to 32°N) as used in section B of this chapter. Our results highlight the importance of modelling across the entire species distribution area and demonstrate that a parsimonious ‘mesoscale only’ approach can be effective for a very broad-scale SDM of a sessile organism.

2. Materials and Methods

2.1 Variable processing

A study area from 56°N to 32°N, was created as certain environmental variables with a ~3km grain size have a smaller geographic coverage. This finer scale set of bioclimatic variables included metrics for air and sea surface temperature, current velocity and sea surface salinity, air temperature and wind speed calculated by regional European models (Appendix 5). The two sets of bioclimatic variables used in the ~3km and 10-12km grain models shared tidal amplitude, fetch and significant wave height, giving a total of 18 predictors at ~3km grain size, and 15 predictors at 10-12km grain size. All environmental variables were masked based on a distance to the European Environment Agency coastline for analysis (EEA, 2018): 0.1° for the ~3km grain smaller extent models, and 0.25° for the 10-12km larger extent models. After collinearity checks, a final list of eight ~3km grain variables was used in the smaller extent model (Table 11) to validate our main 10-12km grain size larger extent model outputs.

Table 11. Final predictors used in models after collinearity checks for the two grain sizes and extents. Future variables were all available for two RCP scenarios (4.5 & 8.5). Variables fully described in Appendix 5.

Variable	Abbreviation	Grain and extent
Sea Surface Temperature - Minimum	SST_MIN	~3km smaller/ 10-12km larger
Sea Surface Salinity - Mean	SAL_MEAN	~3km smaller/ 10-12km larger
Air Temperature - Maximum	AT_MAX	~3km smaller/ 10-12km larger
Wave Fetch	FETCH	~3km smaller/ 10-12km larger
Wind Speed - 90 th Percentile	WIND_P90	~3km smaller
Surface Current Speed - Mean	CUR_MEAN	~3km smaller
Significant wave height - 90 th Percentile	HS_P90	~3km smaller/ 10-12km larger
Tidal amplitude	TIDE	~3km smaller/ 10-12km larger

2.2 Model building

After having spatially thinned the data so that only one observation record was retained per raster cell, 566 observations (presence records) were retained in the ~3km grain size dataset, compared to 363 observations in the 10-12km grain size dataset. Modelling methods are described in section III-B of this chapter. Ten sets of randomly-drawn PAs of the equivalent number of thinned presences (566 in the ~3km grain size models and 363 in the 10-12km grain size models) were generated, randomly sampling without replacement, as recommended by Barbet-Massin et al. (2012).

2.3 Model evaluation and ensemble forecast

After an exploratory analysis of different TSS thresholds, only the models whose TSS ≥ 0.61 were retained, as this score yielded the lowest number of false positives. This led to, out of the initial 200 model runs, 130 (36 gam + 94 rf) being retained for the ensemble ~3km grain size model, compared to 116 (38 gam + 78 rf) being retained for the ensemble 10-12km grain size model (Table 12).

Table 12. Mean accuracy metrics (\pm standard deviation) of models obtained for each approach, post-filtering model runs with a true skill statistic (TSS) >0.61 : generalized additive model (gam), Random Forest (rf). Numbers in brackets are the number of runs retained per approach. Area under the receiver operating characteristic curves scores are also given (AUC). The highest scores for each statistic are in bold.

Grain and extent	Method	AUC	TSS	Sensitivity	Specificity
~3 km	gam (n=36)	0.87 \pm 0.01	0.64 \pm 0.02	0.80 \pm 0.02	0.80 \pm 0.02
Smaller (24°)	rf (n=94)	0.90\pm0.01	0.67\pm0.03	0.82\pm0.02	0.82\pm0.02
10-12 km	gam (n=38)	0.87 \pm 0.02	0.66 \pm 0.03	0.81 \pm 0.02	0.81 \pm 0.02
Larger (29°)	rf (n=78)	0.88 \pm 0.02	0.65 \pm 0.03	0.81 \pm 0.02	0.81 \pm 0.02

Environmental predictor importance scores were derived for each of the 130 ~3km/116 10-12km grain individual models using the ‘getVarImp’ function in

the 'sdm' package. Scores were derived from the AUC test metric, which measures the importance of each variable based on the improvement of the model performance (AUC) when the variable is included in the model compared to when the variable is excluded through a cross-validation procedure (Naimi and Araújo 2016). The mean and variance in the predictor scores were ranked and plotted for each modelling technique (rf and gam) and bounding box (Figure 32).

Variable response curves were averaged per modelling technique across all input models for both the ~3km and 10-12km grain models, and confidence intervals were plotted (Figure 33). In the ensemble modelling step, we combined predictions from the 130 ~3km grain/116 10-12km grain contributing models using a weighted average, where the contribution of each single SDMs to the weighted average were based upon their respective TSS scores. Ensemble models were used to predict the current extent of *S. alveolata* within the two different study area extents (Figure 34). Where the two bounding boxes overlap, we compared the mean and standard deviation habitat suitability index scores between both scales (Figure 34c) and plotted the respective mean habitat suitability scores against latitude (Figure 34d).

Model performance was evaluated both with statistical indicators and by using our true absence records to independently test the model. The models were run on these true absences, and for each model the percentage of absence points correctly classified as being in unsuitable habitat (i.e. the 'true negative rate') was calculated (Appendix 9).

3. Results

Our true absence record evaluation showed that 63.5% of the 498 absence observation records used for the ~3km grain smaller extent model were correctly classified as true negatives in our binary presence-absence maps. For the 10-12km grain larger extent model, 71.2% of the 465 absence observation records were correctly classified as true negatives (Appendix 9).

For the ~3km grain smaller extent model, tidal amplitude (i.e. half the tidal range), mean surface current speed, and mean salinity were the three most important variables, whereas for the 10-12km grain larger extent model, fetch, maximum air temperature and mean salinity were the most important (Figure 32).

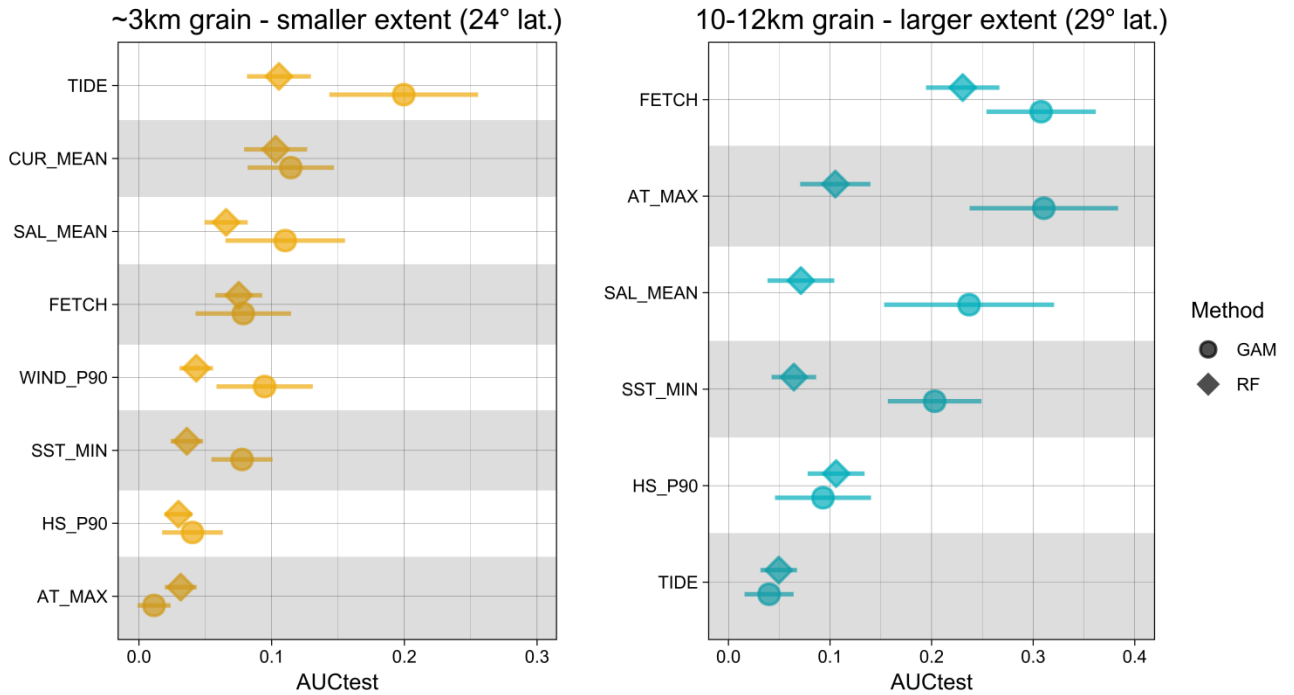


Figure 32. Variable importance scores for the two different grains and extents, for the two modelling approaches used (generalized additive models, GAM, and random forests, RF) ranked according to the improvement in AUC (area under the receiver operating characteristic curve) resulting from their inclusion in the models, a common metric for evaluating the discriminatory ability of a binary classification model. The dots (gam) and diamonds (rf) represent the mean scores \pm the standard deviation between different model runs with a TSS > 0.61 (represented by the whiskers). Abbreviations are as follows: FETCH = wave fetch; AT_MAX = maximum air temperature; SAL_MEAN = mean sea surface salinity; SST_MIN = minimum sea surface salinity; HS_P90 = significant wave height – 90th percentile; TIDE = tidal amplitude.

Both models displayed similar unimodal response curves for fetch, significant wave height, mean salinity and tidal amplitude. For both models, predicted habitat suitability is highest when fetch is between 500-1500km. Habitat suitability decreases for both models when the 90th percentile of significant wave height exceeds 2.25m, when mean salinity exceeds 32.5 ppt and when

tidal amplitude is inferior to 2.5 m (Figure 33). Both models displayed contrasting responses to temperature variables. For minimum sea surface temperature, the 10-12km grain model predicts decreased habitat suitability below 13° C, something which the ~3km grain model, truncated to the north, does not grasp. Likewise the ~3km grain model is not able to predict as accurately as the 10-12km grain model the unimodal response of *S. alveolata* to maximum air temperature, particularly its sensitivity to cold temperatures, due to its extent not geographically covering the whole range of temperatures the species is exposed to. The temperature response curves of the ~3km resolution model highlight the importance of using a broad geographic area in order to fully capture the species niche breadth. For the 10-12km resolution model, predicted habitat suitability is highest when maximum air temperature is between 17-23° C.

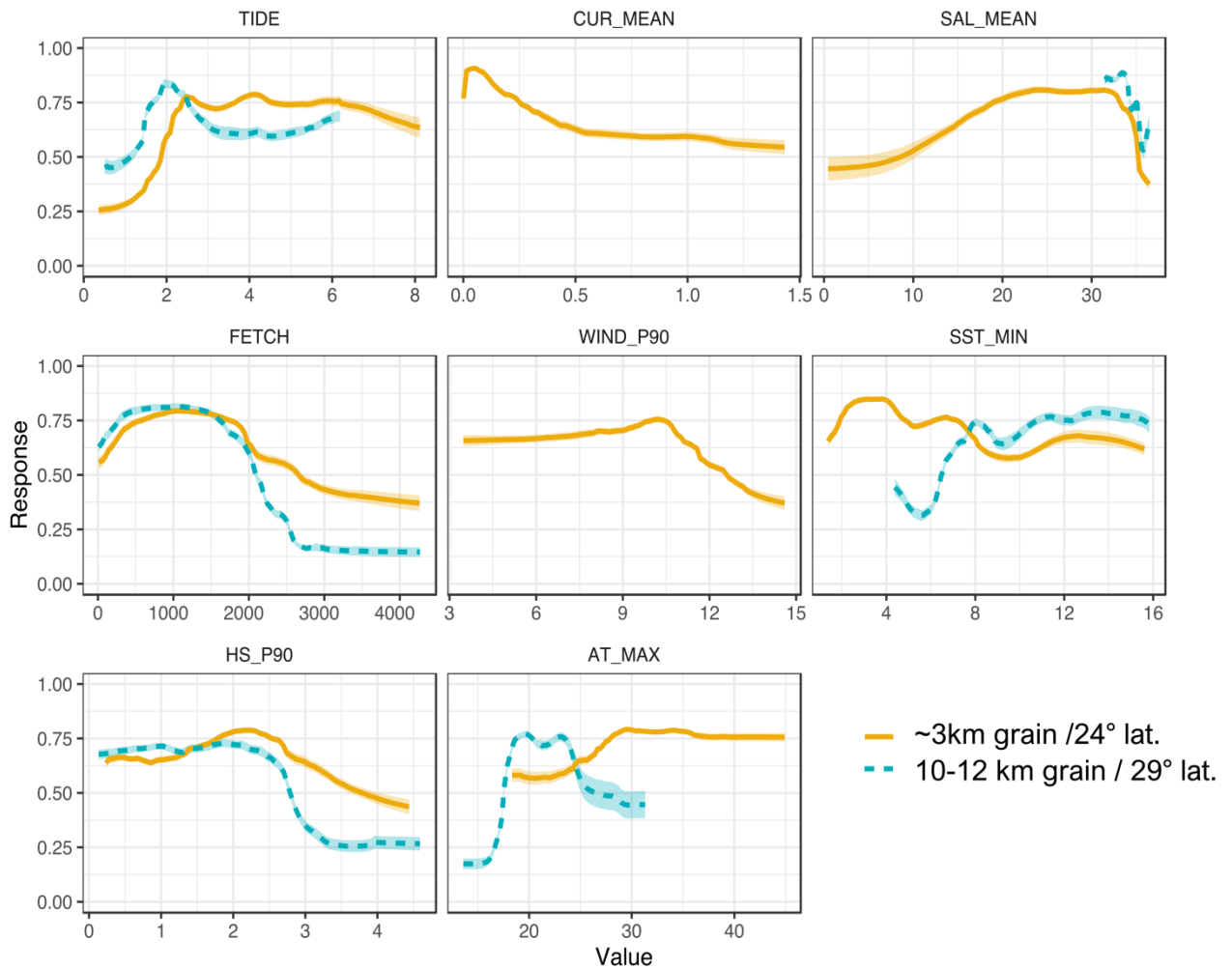


Figure 33. Variable response curves for the weighted mean ensemble models at ~3km and 10-12km grain size, ranked in order of importance of the ~3km grain size and 24° latitude extent model (Figure 32). Abbreviations and units are as follows: TIDE = tidal amplitude (metres); CUR_MEAN) mean surface current velocity (m/s); SAL_MEAN = mean sea surface salinity (ppt); FETCH = wave fetch (kilometres); WIND_P90 = wind speed – 90th percentile(m/s); SST_MIN = minimum sea surface salinity (degrees Celsius); HS_P90 = significant wave height – 90th percentile (metres); AT_MAX = maximum air temperature (degrees Celsius) .

The two models are in agreement with each other, as demonstrated by the concurrent predicted habitat suitability curves (Figure 34d). However, southern-facing coastlines do have divergent predictions: the 10-12km grain larger extent model tends to over-predict habitat suitability given the known distribution, as illustrated in Figure 34c.

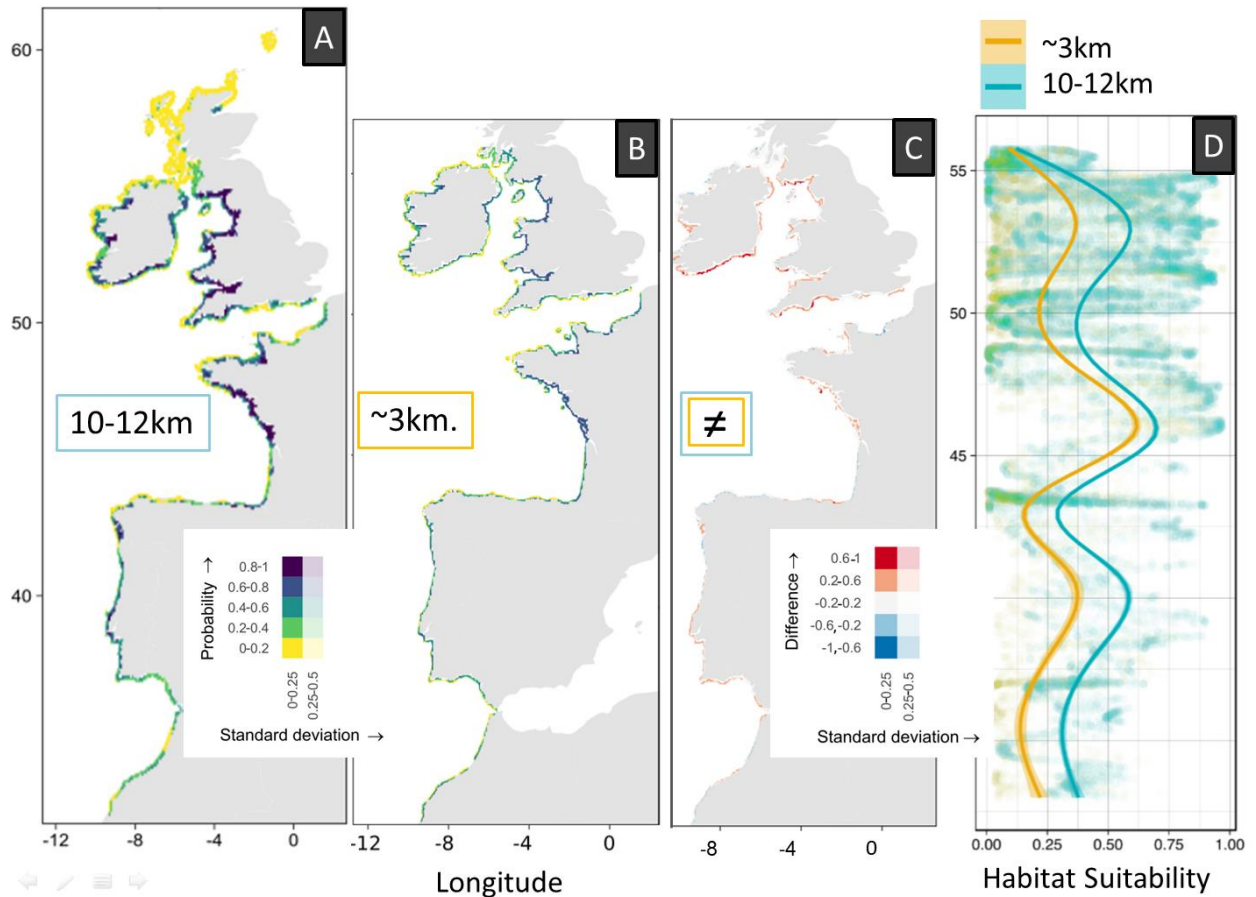


Figure 34. Weighted mean ensemble predictions for the A) 10-12km grain larger extent B) ~3km grain smaller extent and C) the difference in predicted habitat suitability between the two. Colour transparency indicates variation in the replicate model outputs. D) is the longitudinally integrated latitudinal distributions calculated for both the ~3km and 10-12km models (that is, predicted habitat suitability), represented by smoothed conditional mean curves, calculated using a generalized additive model.

4. Discussion

Despite the different selection of environmental predictors and different relationships the models display to these predictors, model outputs at both spatial scales are remarkably similar. Temperature response curves do differ between the two models, as the ~3km grain model and extent does not span the entire range of temperature conditions experienced across *S. alveolata*'s distribution area. Whilst this does make it more difficult to infer response to air and seawater surface temperature, it has little incidence on model outputs *per se*. The model outputs are divergent only along southern-facing shores in the northern part of the study area (i.e. southern Ireland or southwest England),

which have an inflated habitat suitability index in the 10-12km grain larger extent model. This is due to interactions between fetch, wind speed and surface current speed in the ~3km grain model that are not taken into account in the 10-12km grain model. The latter only takes into account the interaction between fetch and significant wave height, leading to inflated habitat suitability predictions along coastlines exposed to dominant south-westerly winds.

However, since all southern facing shores remain stable in all future habitat predictions, this does not affect the climate-change predictions discussed in section B of this chapter. For contemporary predictions of *S. alveolata* distribution, we found that 10-12km grain environmental predictors have a strong effect on SDM accuracy and spatial predictions, and found little evidence that additional finer grain predictors tested here are essential in SDMs.

Our results highlight the importance of modelling across a species distribution area in order to measure its response across the whole range of the drivers it is exposed to. They also demonstrate that a parsimonious ‘mesoscale only’ approach is effective for broad-scale modelling of *S. alveolata*.

CONCLUSIONS AND FUTURE WORK

KEY CONCLUSIONS: RETURNING TO ORIGINAL QUESTIONS

The ecological niche of a species reflects the sum of all environmental factors that enable it to complete its life cycle. Faced with the urgency of predicting ecological responses to rapid environmental change, the niche concept is as lively and important as ever. The majority of species responses to changing environments are linked through this concept (*sensu* Hutchinson 1957). This thesis focused on different aspects of *S. alveolata*'s niche, and different facets of its vulnerability to environmental change (see Box 1, modified from Dawson et al., 2011), through a hierarchical sequence of responses that involve, physiology, spatial variation of species-level traits and biogeography.

**Box 1. Species vulnerability in the context of environmental change.
Modified from Dawson et al., 2011.**

Vulnerability is the extent to which a population of a species is threatened with decline, reduced fitness, genetic loss, or extinction due to environmental change. Vulnerability has three components: sensitivity, adaptive capacity (both positively related to vulnerability) and exposure (negatively related).

Sensitivity is the degree to which the survival, persistence, fitness, performance or regeneration of a species or population is dependent on the prevailing environment. More sensitive species are more likely to show greater reductions in fecundity or survival with smaller changes to the environment. Sensitivity depends on a variety of factors, including ecophysiology and life history traits. ➔ **Chapter I**

Adaptive capacity refers to the capacity of a species or constituent populations to cope with environmental change by persisting *in situ*, by shifting to more suitable local micro habitats, or by migrating to more suitable regions. Adaptive capacity depends on a variety of intrinsic factors, including phenotypic plasticity, genetic diversity, evolutionary rates, life-history traits, and dispersal and colonisation ability. ➔ **Chapter II**

Exposure refers to the extent of environmental change likely to be experienced by a species or locale. Exposure depends on the rate and magnitude of environmental change in habitats and regions occupied by species. Most assessment of future exposure to environmental change are based on scenario projections from general circulation models, often downscaled with regional models and applied in niche models. ➔ **Chapter III**

In chapter I, *S. alveolata*'s functional niche was explored through a biochemical approach, using indicators of physiological condition at the individual level. Information on previously unstudied dimensions of the ecological niche was acquired. By exploring which biochemical macromolecules gave relevant information on the sensitivity of *S. alveolata*, and whether or not this was linked to their bioconstruction phase, we acquired new information on non-lethal physiological responses. The metabolic enzyme superoxide dismutase and citrate synthase, when analysed in conjunction with membrane (i.e. polar lipid) arachidonic acid, were found to serve as applicable *S. alveolata* physiological stress markers. Importantly, this article (Curd et al. 2019) also put forward a terminology which distinguishes between the bioconstruction types (veneers, hummocks and

platforms) and phase (retrograding and prograding). Citrate synthase was significantly higher in retrograding hummocks due to increased feeding, and membrane arachidonic acid was significantly lower in retrograding hummocks due to decreased physiological stress: both are presumed to be the result of less intra-specific competition in the less densely populated retrograding phase bioconstruction. Although mosaic patterns in marine benthos in general (Reise, 1991) and *S. alveolata* reefs in particular (Gruet, 1986) have been defined in the past, they have largely been described as being cyclical and have not separated bioconstruction height and surface area from the degree of erosion and surface micro-heterogeneity.

In chapter II, the niche breadth of *S. alveolata* was assessed through an analysis of the spatial variation of biochemical and reproductive traits. This macrophysiological study yielded information on trait-environment relationships along a latitudinal gradient. Despite the complex, non-linear coastline of the study area, all seven biochemical (citrate synthase, superoxide dismutase and polar lipid docosahexaenoic acid) and reproductive (total egg diameter, circle fit, symmetry and relative fecundity) traits examined did indeed display a significant linear or quadratic relationship with latitude, which could however be altered in its relationship or become non-significant depending on the sampling period. Our trait selection indicated the best physiological conditions as being in the southern range sites, whilst the individuals investing the most in reproduction are situated in the centre of *S. alveolata*'s range. Given the inauspicious habitat suitability predicted for centre-range sites in the near-future in chapter III, it will be interesting to observe if the *S. alveolata* populations in the Bay of Biscay increasingly invest in reproduction as their environment becomes progressively unsuitable, or vice-versa. By looking at the intra-specific trait variation (ITV) in total egg diameter and relative fecundity, this study quantified the proportion of ITV that was spatially structured. 59% of relative fecundity, and 79% of total egg diameter ITV occurred at the intra-site level and therefore could not be exposed by our site-scale predictors. Although functional ecology has advanced our understanding of the importance of ITV at local scales

(Albert et al., 2010), its importance at large scales has rarely been evaluated, with scarce empirical tests from the plant kingdom (Kazakou et al., 2014).

What both these chapters have unquestionably provided is more information on *S. alveolata*'s fitness and performance, which in turn informed us about its sensitivity and adaptive capacity in a changing environment. The response trait data collected through this work can subsequently be made available in trait databases (e.g. the Marine Species Traits portal), with a view to be used as input parameters for mechanistic modelling. As a pre-requisite to the statistical modelling in chapter III, an up-to-date broad-scale long-term dataset was curated, resulting in a ten-fold increase Europe-wide in the number of georeferenced *S. alveolata* records (2275 to 21571) and a far more accurate representation of its past and present distribution. Via the SEANOE repository where it has now been uploaded, the dataset will be 'harvested' by European and global biodiversity information systems such as EurOBIS and GBIF. The potential uses of this dataset are manifold, and range from analysing temporal trends in presence and abundance (i.e. separating short-term noise from climate signal) to informing the wider scientific community, general public and policy makers (Hawkins et al., 2013). It is worth noting here that 91% of the records in the *S. alveolata* dataset already had, or were attributed, an abundance score on the SACFOR scale. Although this abundance information was not included in the SDM due to technical difficulties associated with using semi-quantitative categorical data, it is invaluable information for assessing *S. alveolata* habitat distribution and abundance.

In chapter III, present-day and future *S. alveolata* habitat availability was modelled, by relying on the key assumption that species ranges are fundamentally determined by abiotic factors. This is a sensible supposition over a large geographic range, where in the well-connected marine environment species often do have closely matching fundamental and realised niches (Stuart-Smith et al., 2015). Global climate change studies have very much focused on thermal niches (e.g. Poloczanska et al., 2013; Beaugrand and Kirby 2018); this chapter analysed *S. alveolata*'s exposure to six carefully selected climatic variables. What it empirically showed was the importance of not only seawater but the unimodal response of the species to air temperature,

fetch, significant wave height and tide: too little hydrodynamic energy and it won't have enough food or resuspended building material, too much and the biogenic constructions will be physically impacted. The tri-modal distribution in habitat suitability clearly shows that within-range occupancy needs to be explored as well as range edges. In future scenarios, *S. alveolata* populations are predicted to be less connected, with an important geographic gap set to appear in the Bay of Biscay: exploring the evolutionary consequences of these greater gaps between populations is a stimulating perspective (see 'Phylogeographic studies' section below).

Research for Policy

In its 'reef' form, *S. alveolata* is protected under the EU Habitats Directive. However, there is no existing guidance setting out the qualifying characteristics required for a colony to be classified as a 'reef' in the context of these policies. Although several *S. alveolata* bioconstruction classifications already exist (e.g. Egerton, 2014), they are site-dependent and therefore not necessarily suitable for monitoring reef formation in all locations. Although discussions around defining pan-European characteristics of a *S. alveolata* 'reef' are still needed, defining different *S. alveolata* bioconstruction types (veneers, hummocks and platforms) and phases (retrograding and prograding) that are widely applicable is a first step. This shifting between different sub-habitat phases is regarded as key in relation to the ecosystem services that the reefs provide, which in turn underpins their conservation status. For instance, retrograding reefs are topographically complex, with features such as standing water, crevices and consolidated fine sediments providing microhabitats for other organisms and high levels of biodiversity (Jones et al., 2018), thus supporting increased food provisioning. However should they continue to retrograde, they could decay and disappear altogether.

We now know that some biochemical indicators such as membrane (i.e. polar lipid) arachidonic acid and citrate synthase activity can be used as an indicator of physiological condition at both intra- and inter-site scales (Muir et al., 2016; Curd et al., 2019). However, seasonal broad-scale studies are needed and to see whether

retrograding/prograding phases can be biochemically distinguished by the same macromolecules, between sites as well as within-sites. If this is achieved, it will be a step in the right direction towards less destructive monitoring, as only a few individual worms are needed for biochemical analyses. Ultimately, by furthering our understanding of the link between the engineer species and the engineered habitat it creates, the goal is non-destructive monitoring of *S. alveolata* reef health.

Marine population connectivity studies often focus on spatial patterns of larval dispersal (e.g., Cowen et al. 2006), and traditionally view and model larvae as having homogenous recruitment and post-settlement performances (Marshall and Keough, 2007). Chapter II of this thesis demonstrated that offspring size, shape and number, together with maternal physiological condition all fluctuate, both spatially and temporally, thus affecting both the quantity and quality of larvae entering different populations across a species range. Whilst our study does not yield information on *S. alveolata* recruitment success, the *in-situ* data collected on the geographical and temporal variation in reproductive traits will serve as valuable input to population connectivity models, which in turn can guide targeted marine spatial planning. Whether through direct physical impact or indirectly through conservation measures, human activity can drastically alter ITV by driving rapid trait change and could be shaping ecological dynamics (Palkovacs et al., 2011). Understanding geographic patterns in reproductive trait variability is therefore critical to applied problems, such as assessing the effectiveness of potential biodiversity offset schemes linked to coastal development (Stone et al., 2019) or optimal marine reserve design. The added benefits of an MPA network over a single MPA depend on some knowledge of the spatial patterns of population connectivity, which in turn depend in part on spatial patterns of reproduction (Gaylord et al. 2005; Lester, 2007). Macrophysiological studies such as this one support conservation efforts, enabling us to assess whether the positioning of an MPA tallies up with not only larval recruitment but also with the overall physiological condition of the adult individuals (Osovitz and Hofmann, 2007) crucial to a population's survival.

Assessing variability in habitat distribution and abundance is important at a time when the implementation of some marine policies (such as the establishment of marine reserves) assumes a degree of stability in the features being protected (Firth et al., 2015). For instance, due to the discovery of a subtidal reef-forming population of *S. alveolata* off Wicklow Head in Ireland in 1997 (De Grave and Whitaker 1997), the Wicklow Reef Special Area of Conservation (SAC) was designated *inter alia* because of its presence in 2001. In 2013, a subtidal reef survey of the site failed to detect any *S. alveolata* within the SAC (NPWS, 2013).

It is reasonable to state that SDM works well at very broad scales. Most management tools are spatial (e.g. MPA designation) therefore a broad-scale spatial approach is key. However it is unlikely that environmental management measures can be applied over large extents of coastline. A well-thought-out SDM is a pragmatic first-step that provides a means of pinpointing areas which should be investigated at the mesoscale, where both physical factors and biotic interactions affect the biotic landscape of intertidal rocky shores. Figure 35 illustrates the multiple sources and approaches needed for incorporating more biological realism into the biogeography of *S. alveolata*. Three approaches were undertaken within this thesis, namely the use of direct observations, habitat suitability models and broad-scale long-term datasets. The mechanistic approaches needed to complete the picture are discussed in the following section.

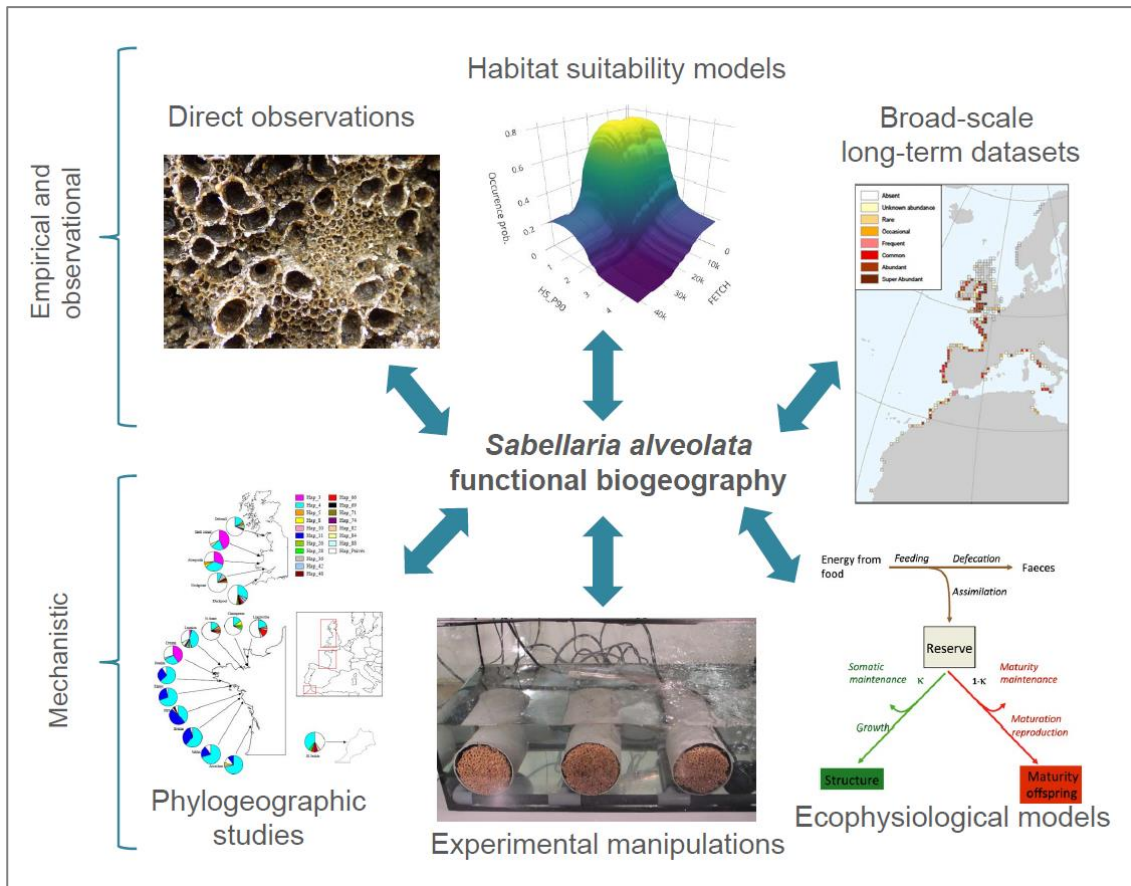


Figure 35. An integrated science of functional biogeography will draw from multiple sources and approaches. Each provides useful but incomplete information on exposure, sensitivity and adaptive capacity. Direct observations, including long-term monitoring, are applicable at a broad range of scales and can be used to assess all aspects of vulnerability. Habitat suitability (or niche) models are statistical models and are best suited for assessment of exposure. Broad-scale long-term data sets extend the observational foundation to encompass a broader range of rates, magnitudes and kinds of environmental change. Mechanistic models such as ecophysiological models are diverse and require taxon-specific parameters. They are particularly effective in assessing sensitivity and adaptive capacity. Experimental manipulations provide biochemical and morphological response traits which in turn provide information on sensitivity and adaptive capacity, and are valuable in parameterising mechanistic models. Phylogeographic studies look at the geographic distribution of population genetics and reveal adaptive capacity [Photo credits; direct observations, A. Curd ; habitat suitability model, A. Boyé, broad-scale data-set, C. Cordier, ecophysiological model, Sarà et al., 2013; experimental manipulations, F. Nunes, phylogeographic study, Rigal et al., unpublished]. Adapted from Dawson et al. (2011).

FUTURE PERSPECTIVES

More mechanism

Ecophysiological models

Dynamic Energy Budget Models (DEB) track energy flow and allocation to development, growth, maintenance and reproduction for any specified environmental conditions, allowing predictions of individual responses to climate change (Sarà et al., 2013). Thanks to the existing body of work *S. alveolata* physiology (summarised in Figure 11 in the introduction), together with the biochemical, reproductive and morphological data amassed throughout this thesis (where countless opercular crown diameters were measured), many input parameters for DEB models are now available. By fitting DEB models with what we know of *S. alveolata*'s physiology, model outputs could for example be maximum adult size and relative fecundity as a function of latitude. Once DEB models are successfully calibrated to predict reliable *in-situ* traits, they could then be tested under varying climate change scenarios.

Experimental manipulations

To ascertain non-lethal effects of, for example, air temperature at low tide, it would be desirable to conduct a series of controlled laboratory experiments that manipulated only this variable while environmental conditions were held constant. Whilst some experimental work has looked at varying seawater temperature and pH on adult worms (Faroni-Perez, unpublished data) and varying light exposure on larval behaviour (Bush, 2016), this thesis has highlighted the importance of hydrodynamic and air temperature variables in driving *S. alveolata* traits. Future work should consider manipulating these variables in tidal benthic mesocosm experiments that are able to simulate multi-factorial climate change scenarios, including the combination of warming, acidification, nutrient enrichment, sea level rise and increased storm events (e.g. Pansch et al., 2016).

Phylogeographic studies

Phylogeography considers the spatial distribution of alleles within a species in order to evaluate its recent evolutionary history (Avice et al., 1987). For *S. alveolata*, patterns of genetic diversity and differentiation allow us to make inferences about how past climate and habitat availability have influenced the distribution of the species, and about how current conditions affect connectivity. An ongoing study points to the Irish Sea and English Channel as two important reservoirs of genetic diversity for the species (Nunes, in prep), with the latter being poorly connected to the southern part of the range. Combining range-wide population genetics with range-wide SDM model outputs would yield a lot more information on the adaptation of *S. alveolata* both within its range and at the edges. There are many testable theoretical predictions about how and when range expansion should occur and there are a range of empirical systems with which to address these questions (reviewed in Bridle and Vines, 2007). As a pre-requisite, some genetic clarification of the European Sabellaria genus species is needed; there is a grey area between

subtidal *S. alveolata*, and intertidal *S. spinulosa* reefs. Although nowadays *S. spinulosa* is a mostly subtidal reef forming species, prior to heavy abrasion from the physical impacts of demersal fisheries, extensive intertidal reefs of *S. spinulosa* could be found in the German Wadden Sea (Reise 1982). Both species can co-occur (unpublished data; Arcachon subtidal reefs, Equihen intertidal reefs in northern France) due to temporal niche partitioning through distinct physiological and reproductive strategies. The Mediterranean is even more complex; three species are reported to co-occur, although *Sabellaria alcocki* occurrences are most likely juvenile *S. spinulosa* (Schimmenti et al., 2015). A fourth species, *S. taurica*, described as being present in the Black Sea, is suspected to be present along the North African coasts of the Mediterranean (Gruet, pers. comm.)

Hybrid models

The emergence of a new generation of distribution models, based on physiological mechanisms linking species performance and the environment (Morin and Lechowicz 2008), may offer a more accurate framework for predicting species distributions when taking into account species interactions (Kearney, 2006). Many diverse and entirely unrelated techniques, with varying degrees of complexity, are referred to as ‘hybrid models’. In their simplest form, constraining the range of predictor variables with a priori knowledge of the reproductive phenology of a species can be considered a hybrid model. As an example, Chefaoui et al. (2019) constrained sea surface temperature variables to the ‘reproductive window’ of the non-native alga *Sargassum muticum* species distribution model to refine habitat predictions in coastal areas of the northern hemisphere (Pacific and Atlantic oceans). Maps of functional traits could also be considered as new environmental layers for hybrid SDMs (e.g. Lamanna et al., 2014); for *S. alveolata*, larval dispersal ability could for example be one such trait layer.

DEB equations can also be associated to individual-based models (IBM) in order to explore properties of both individual life-history traits and population dynamics (e.g. Bacher and Gangnery, 2006). This population model, which provides predictions on

egg size and number, and the ensuing duration of the larval dispersal phase, can in turned be coupled with biophysical larval dispersal models (Nicolle et al., 2017). This form of hybrid model could further our understanding of *S. alveolata* population connectivity, and has already been tested on marine annelids at the local scale (De Cubber et al., 2019).

Adaptive capacity in response to novel environmental conditions is an important predictor of survival in a changing climate. Therefore the creation of evolutionary hybrid models that incorporate not only physiological but also evolutionary data are needed to provide new insights into the vulnerability of species of conservation concern (Waldvogel et al., 2019). For instance, through using biophysical models of energy and mass transfer combined with a method to predict potential climatic impacts on the evolutionary response of traits limiting distribution, it was shown that the range expansion in *Aedes aegypti*, the mosquito that transmits dengue fever, is far greater than would have been estimated using SDM (Kearney et al., 2009). Finally, at the top end of the complexity scale, novel techniques such as Bayesian hierarchical species distribution models, which as well as environmental variables can integrate data biological relationships and human activities at multiple scales (Banerjee et al., 2014; Talluto et al., 2016; Coll et al., 2019), are also referred to as hybrid models.

Fully mechanistic models are experimental-data intensive and generated at the level of the individual (Robinson et al., 2011). To our knowledge broad-scale mechanistic models for coastal benthic species have yet to become a part of the marine ecologists' toolkit. The combination of biophysical ecology and genetics, coupled with the detection of large-scale patterns of change, thus presents our best chance of predicting what to expect in the face of climate change in the coming decades.

Towards functional biogeography

Most of the 'process-included' hybrid models outlined above (eco-evolutionary models, coupled hydrodynamic larval dispersal models etc.) depend on large amounts of ecological, environmental and genomics (i.e. evolutionary), species-level data. *S. alveolata* could be one of a handful of species for which it may be possible to

deploy the whole works; not only is it an ecosystem engineer and therefore considered as a keystone species, but it is also amenable to common garden experiments and long-term monitoring. A pre-requisite is that fitness traits have to be identified and ideally experimentally confirmed (Shaw 2019). In most cases, a trait-based approach is the only solution. Biogeography is historically grounded in the species concept (Violle et al., 2014). Treating species as qualitative entities, where we need to understand each and every one, is logistically impossible. Trait-based biogeography can help model species interactions, dispersal ability, and physiological tolerance more simply and generically (Green et al., 2008).

Studying the geographic distribution of trait diversity across organisational levels has been a long-standing goal for ecologists (e.g. Whittaker, 1975) and calls for an interdisciplinary approach. This was formalised in 2014 in a special feature of the Proceedings of the National Academy of Sciences of the United States of America (PNAS), which described functional biogeography as an emergent discipline, defined as “the analysis of the patterns, causes and consequences of the geographic distribution of trait diversity – namely form and function” (Violle et al., 2014).

Functional traits are increasingly used in community ecology to detect and quantify the processes that shape ecological communities (Mouillot et al., 2013). Understanding the processes shaping the biological community hosted by *S. alveolata* reefs, under multiple disturbances, is the next core challenge; With a biogeography perspective, this approach can be applied to understand the spatial scaling of assembly processes across broad gradients (Violle et al., 2014).

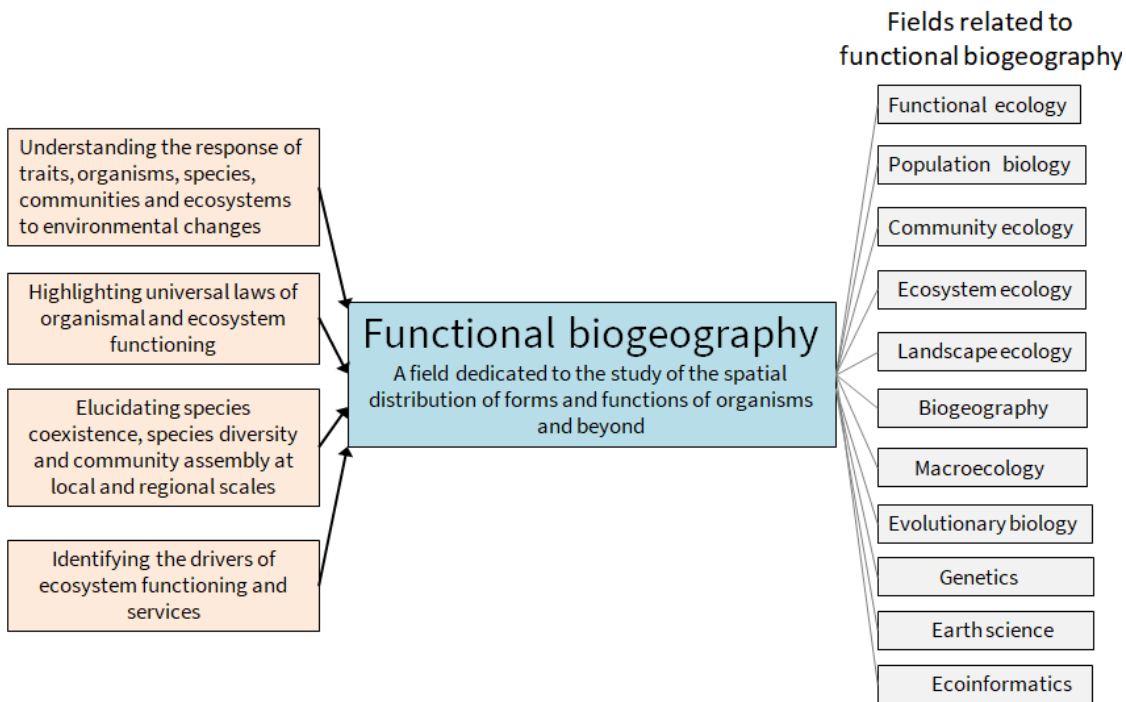


Figure 36. Functional biogeography: an emergent field at the crossroads of several science fields. Functional biogeography calls for knowledge from multiple fields to answer questions related to trait diversity across spatial scales. Modified from Violle et al. (2014).

Although measuring functional response traits may provide an accurate quantification of species niche parameters, a preliminary necessary step is to prioritise key environmental factors that significantly influence trait variations (McGill et al., 2006). This is necessary because the quantification of Hutchinson’s (1957) n-dimensional environmental space is logistically impossible when n becomes large. Consequently, the trait-based quantification of niche parameters requires the identification of a limited number of key environmental gradients (Violle and Jiang, 2009). Advocates of trait-based ecology recognise that we still lack knowledge on the response of organismal traits to environmental changes for most kingdoms (Violle et al., 2014). Before getting ‘carried away’, a necessary first step is to patiently characterise trait-environment relationships through experimental work in controlled conditions.

What this special feature in PNAS did not dwell upon is the fact that any advances in the area of functional biogeography require a great deal of interdisciplinary thinking and collaboration between a dozen different science fields

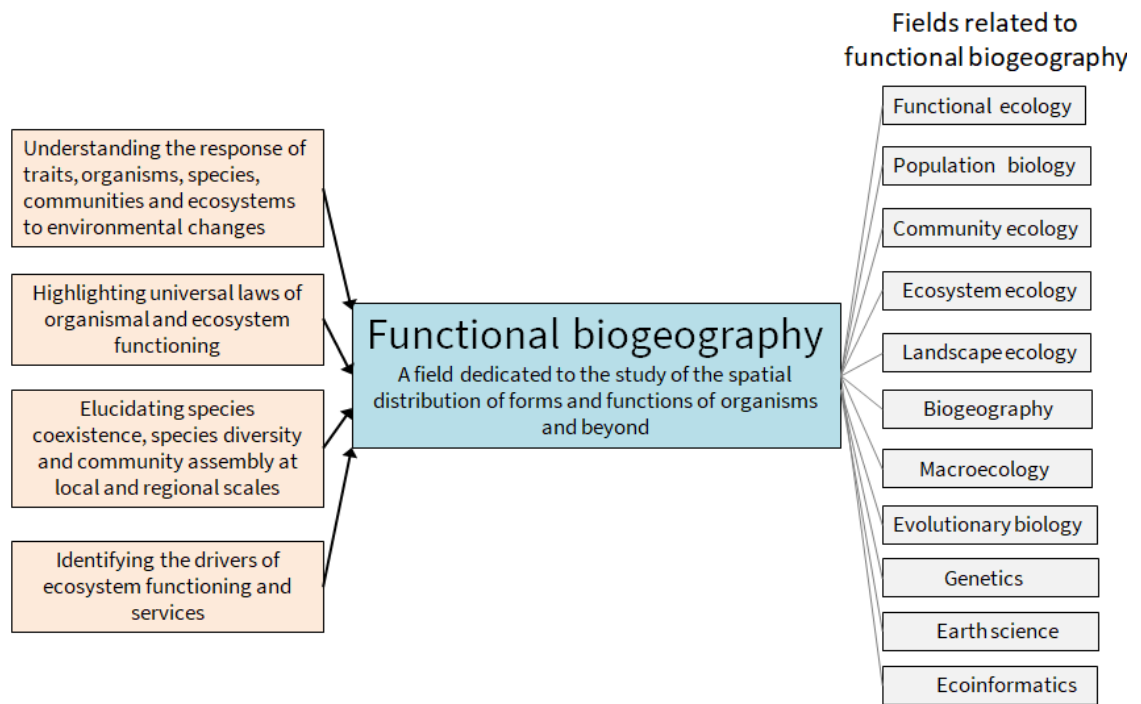


Figure 36). In order determine the physical, physiological and genetic factors that constrain, or promote, adjustment to changing environments over different time scales (e.g., behaviour, acclimation, plasticity and adaptation), large scientific consortia and inter-disciplinary education, synthetic thinkers, and scientists that can collaborate in mutualistic relationships are needed to see the possibilities revealed by a wider field of view (Schwenk et al., 2009).

Looking backwards to look forwards

Another discipline that could have been added to the long list on the right of

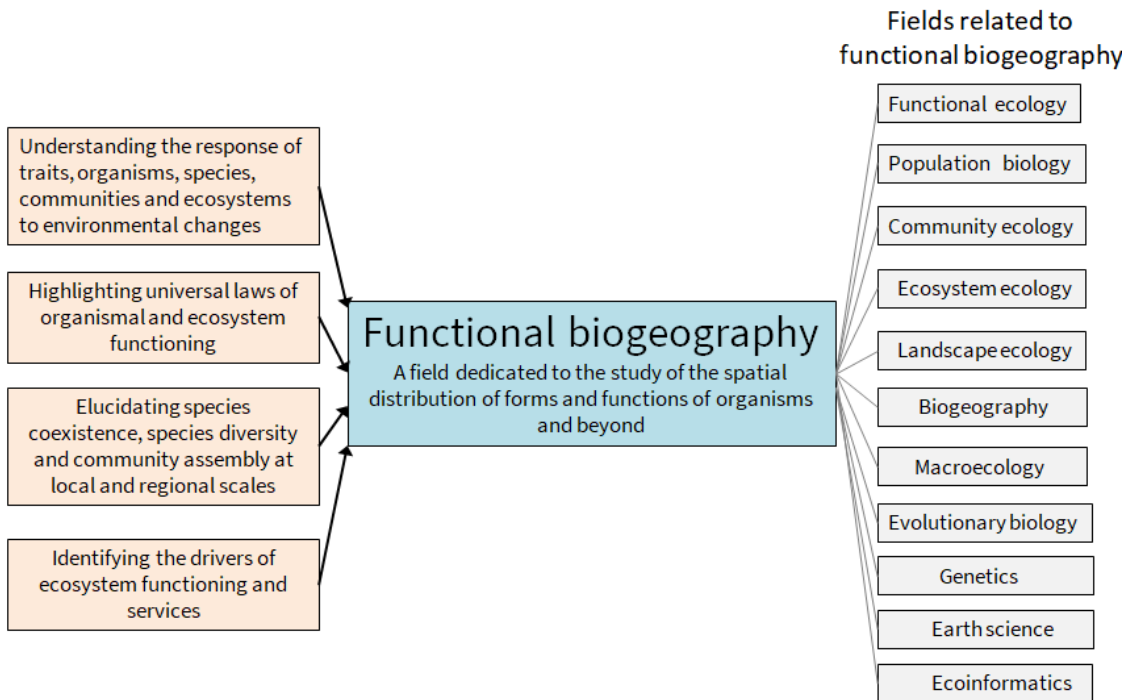


Figure 36 is that of historical ecology. Any perception of stable marine biogeography has fallen away amid observations of dramatic shifts in species geographic distributions over timescales from years to decades, centuries, and millennia (Pinsky et al., 2020). While climate change is projected to become equally or more important in the coming decades, habitat loss due to human land use remains the main driver of present-day species extinction (Hoffmann et al., 2010). Habitat loss is particularly severe in coastal marine ecosystems, where human activities have been historically concentrated (Airoldi and Beck, 2007).

In order to disentangle climate-driven change from other regional and local-scale anthropogenic impacts, information on past trends is essential (Hawkins et al., 2013). Historical perspectives increase our understanding of the dynamic nature of landscapes and provide a frame of reference for assessing modern patterns and processes (Swetnam et al., 1999). With the rise of a predictive era in ecology, there is an acceleration of societal demand regarding the evaluation and forecast of past, current and future ecosystem services (Violle et al., 2014). By nature, long-term datasets take time to build, and retroactively compiling datasets through data rescue and re-use from a multitude of diverse sources is a painstaking process.

Curating the *S. alveolata* dataset involved dozens of people and enlisted expertise not frequently part of the ecologists' palette of skills, ranging from document archiving in organising Yves Gruet's collection of samples, photographs and correspondences, to deciphering Edouard Fischer Piette's handwriting in his exhumated field notebooks in search of *S. alveolata* records. It also uncovered a wealth of nomenclature issues and taxonomic misidentifications associated with the *Sabellaria* genus (e.g. *Sabellaria alcocki* could be a misnomer; *S. alveolata* has probably never been present in the North Sea), and brought to light a fascinating shift in perception in the value of *S. alveolata* reefs. Past literature and local vernacular names (e.g. "crassier" or "teigne" in French, both unflattering terms) revealed how this nowadays priority habitat used to be viewed as a pest (Audouin and Milne-Edwards, 1832), a parasite (Dollfus, 1921), or even exploited as fishing bait (Gouret, 1893) or fertiliser (Audouin and Milne-Edwards, 1832).

The numerous past anecdotes, drawings, photographs and opinions on the honeycomb worm – the bulk of which are not searchable on electronic databases – are perhaps deserving of a freer and lengthier format than that of a traditional scientific article. It was not possible to bring this work to fruition within the time frame of a PhD. Many researchers who have studied *S. alveolata* are appreciative of the value of historical ecology: a "Nineteenth century narratives reveal shifts in the distribution and baseline in Europe's honeycomb worm reefs" type opus, with contributions from many authors covering different regional seas, genetic elucidation, role of artificial structures etc...would be a satisfying furtherance of this study.

Concluding remarks

With properly designed and executed studies, using traits as a common currency, understanding how environmental variation is conveyed through organismal physiology to ecological processes will allow us to predict the consequences of environmental change on natural systems. The understanding of keystone species and their niches is a relevant element in the assessment, conservation, and restoration of habitats across biomes (e.g. as developed in the EU Habitats Directive).

To achieve this goal, we need to deepen our mechanistic understanding of how the different levels of biological organisation, from the individual to the whole community, are intertwined and how that integration is perturbed at the edges of the niche.

S. alveolata creates an easily accessible biogenic habitat in a widely-surveyed part of the globe. Even with such a well-known model species, we are only just beginning to piece together all the knowledge required to understand how environmental variation is conveyed through organismal physiology to ecological processes, and to comprehend how much our habitat baseline has shifted. Every species has its own unique ecological niche; trait-based ecology seems like the only practical solution for scaling up to ecosystem alterations.

REFERENCES

-A-

- Abele, D., Puntarulo, S., 2004. Formation of reactive species and induction of antioxidant defence systems in polar and temperate marine invertebrates and fish. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 138, 405–415. <https://doi.org/10.1016/j.cbpb.2004.05.013>
- Abelson, A., Nelson, P.A., Edgar, G.J., Shashar, N., Reed, D.C., Belmaker, J., Krause, G., Beck, M.W., Brokovich, E., France, R. and Gaines, S.D., 2016. Expanding marine protected areas to include degraded coral reefs. *Conservation Biology*, 30: 1182–1191. doi:10.1111/cobi.12722
- Aebi, H., 1984. [13] Catalase in vitro, in: *Methods in Enzymology*. Elsevier, pp. 121–126. [https://doi.org/10.1016/S0076-6879\(84\)05016-3](https://doi.org/10.1016/S0076-6879(84)05016-3)
- Airoldi, L., Beck, M.W., 2007. Loss, status and trends for coastal marine habitats of Europe, in: *Oceanography and Marine Biology: An Annual Review*. CRC Press, pp. 357–417.
- Airoldi, L., Turon, X., Perkol-Finkel, S., Rius, M., 2015. Corridors for aliens but not for natives: effects of marine urban sprawl at a regional scale. *Diversity and Distributions* 21, 755–768. <https://doi.org/10.1111/ddi.12301>
- Albert, C.H., Thuiller, W., Yoccoz, N.G., Douzet, R., Aubert, S., Lavorel, S., 2010. A multi-trait approach reveals the structure and the relative importance of intra- vs. interspecific variability in plant traits: Intra- vs. interspecific variability in plant traits. *Functional Ecology* 24, 1192–1201. <https://doi.org/10.1111/j.1365-2435.2010.01727.x>
- Allouche, O., Tsoar, A., Kadmon, R., 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS): Assessing the accuracy of distribution models. *Journal of Applied Ecology* 43, 1223–1232. <https://doi.org/10.1111/j.1365-2664.2006.01214.x>

- Anadon, N., 1981. Contribucion al conocimiento de la fauna bentonica de la ria de Vigo. III. Estudio de los arrecifes de *Sabellaria alveolata* (L.) (Polychaeta, Sedentaria). Investigación Pesquera 45 (1), 105–122.
- Anderson, R.P., Raza, A., 2010. The effect of the extent of the study region on GIS models of species geographic distributions and estimates of niche evolution: preliminary tests with montane rodents (genus *Nephelomys*) in Venezuela: Effect of study region on models of distributions. Journal of Biogeography 37, 1378–1393. <https://doi.org/10.1111/j.1365-2699.2010.02290.x>
- Anthony, K., 2006. Enhanced energy status of corals on coastal, high-turbidity reefs. Marine Ecology Progress Series 319, 111–116. doi:10.3354/meps319111
- Araújo, M.B., Anderson, R.P., Márcia Barbosa, A., Beale, C.M., Dormann, C.F., Early, R., Garcia, R.A., Guisan, A., Maiorano, L., Naimi, B., O'Hara, R.B., Zimmermann, N.E., Rahbek, C., 2019. Standards for distribution models in biodiversity assessments. Science Advances 5, eaat4858. <https://doi.org/10.1126/sciadv.aat4858>
- Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E.A., De Clerck, O., 2018. Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modelling. Global Ecology and Biogeography 27, 277–284. <https://doi.org/10.1111/geb.12693>
- Audouin, J.V., Milne-Edwards, H., 1832. Voyage à Granville, aux îles Chausey et à Saint-Malo, Recherches pour servir à l'histoire naturelle du littoral de la France, ou Recueil de mémoires sur l'anatomie, la physiologie, la classification et les mœurs des animaux de nos côtes. Crochard, Libraire, Paris.
- Avisé, J.C., Arnold, J., Ball, R.M., Bermingham, E., Lamb, T., Neigel, J.E., Reeb, C.A., Saunders, N.C., 1987. Intraspecific phylogeography: the mitochondrial DNA bridge between population genetics and systematics. Annual review of ecology and systematics 18, 489–522.
- Avisé, J.C., 2009. Phylogeography: retrospect and prospect. Journal of biogeography 36, 3–15.
- Aviz, D., Pinto, A.J.A., Ferreira, M.A.P., Rocha, R.M., Rosa Filho, J.S., 2016. Reproductive biology of *Sabellaria wilsoni* (Sabellariidae: Polychaeta), an important ecosystem engineer on the Amazon coast. Journal of the Marine Biological Association of the United Kingdom 1–12. <https://doi.org/10.1017/S0025315416001776>
- Ayata, S.-D., Ellien, C., Dumas, F., Dubois, S., Thiébaud, É., 2009. Modelling larval dispersal and settlement of the reef-building polychaete *Sabellaria alveolata*: role of hydroclimatic processes on the sustainability of biogenic reefs. Continental Shelf Research 29, 1605–1623.

-B-

- Baatsen, M., Haarsma, R.J., Van Delden, A.J., de Vries, H., 2015. Severe Autumn storms in future Western Europe with a warmer Atlantic Ocean. *Climate Dynamics* 45, 949–964. <https://doi.org/10.1007/s00382-014-2329-8>
- Bacher, C., Gangnery, A., 2006. Use of dynamic energy budget and individual based models to simulate the dynamics of cultivated oyster populations. *Journal of Sea Research* 56, 140–155.
- Banerjee, S., Carlin, B.P., Gelfand, A.E., 2014. Hierarchical modeling and analysis for spatial data. CRC press.
- Barbet-Massin, M., Jiguet, F., Albert, C.H., Thuiller, W., 2012. Selecting pseudo-absences for species distribution models: how, where and how many? How to use pseudo-absences in niche modelling? *Methods in Ecology and Evolution* 3, 327–338. <https://doi.org/10.1111/j.2041-210X.2011.00172.x>
- Barboza, F.R., Kotta, J., Weinberger, F., Jormalainen, V., Kraufvelin, P., Molis, M., Schubert, H., Pavia, H., Nylund, G.M., Kautsky, L., Schagerström, E., Rickert, E., Saha, M., Fredriksen, S., Martin, G., Torn, K., Ruuskanen, A., Wahl, M., 2019. Geographic variation in fitness-related traits of the bladderwrack *Fucus vesiculosus* along the Baltic Sea-North Sea salinity gradient. *Ecology and Evolution* 9, 9225–9238. <https://doi.org/10.1002/ece3.5470>
- Bartol, I.K., Mann, R., Luckenbach, M., 1999. Growth and mortality of oysters (*Crassostrea virginica*) on constructed intertidal reefs: effects of tidal height and substrate level. *Journal of Experimental Marine Biology and Ecology* 237, 157–184. [https://doi.org/10.1016/S0022-0981\(98\)00175-0](https://doi.org/10.1016/S0022-0981(98)00175-0)
- Basuyaux, O., Lecornu, B., 2019. Cartographie des hermelles *Sabellaria alveolata* sur la façade ouest du département de la Manche 2009-2019, [SMEL. www.smel.fr](http://SMEL.www.smel.fr).
- Beaugrand, G., Kirby, R.R., 2018. How Do Marine Pelagic Species Respond to Climate Change? Theories and Observations. *Annual Review of Marine Science* 10, 169–197. <https://doi.org/10.1146/annurev-marine-121916-063304>
- Beaumont, L.J., Graham, E., Duursma, D.E., Wilson, P.D., Cabrelli, A., Baumgartner, J.B., Hallgren, W., Esperón-Rodríguez, M., Nipperess, D.A., Warren, D.L., 2016. Which species distribution models are more (or less) likely to project broad-scale, climate-induced shifts in species ranges? *Ecological Modelling* 342, 135–146.
- Bernardo, J., 1996. The Particular Maternal Effect of Propagule Size, Especially Egg Size: Patterns, Models, Quality of Evidence and Interpretations. *American Zoologist* 36, 216–236. <https://doi.org/10.1093/icb/36.2.216>
- Berthelin, C., Kellner, K., Mathieu, M., 2000. Storage metabolism in the Pacific oyster (*Crassostrea gigas*) in relation to summer mortalities and reproductive cycle (West Coast of France). *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology* 125, 359–369. [https://doi.org/10.1016/S0305-0491\(99\)00187-X](https://doi.org/10.1016/S0305-0491(99)00187-X)
- Bertocci, I., Araújo, R., Incera, M., Arenas, F., Pereira, R., Abreu, H., Larsen, K., Sousa-Pinto, I., 2012. Benthic assemblages of rock pools in northern Portugal: seasonal and between-pool variability. *Scientia Marina* 76, 781–789.

- Bertocci, I., Badalamenti, F., Lo Brutto, S., Mikac, B., Pipitone, C., Schimmenti, E., Vega Fernández, T., Musco, L., 2017. Reducing the data-deficiency of threatened European habitats: Spatial variation of sabellariid worm reefs and associated fauna in the Sicily Channel, Mediterranean Sea. *Marine Environmental Research* 130, 325–337. <https://doi.org/10.1016/j.marenvres.2017.08.008>
- Bertness, M.D., Leonard, G.H., Levine, J.M., Schmidt, P.R., Ingraham, A.O., 1999. Testing the relative contribution of positive and negative interactions in rocky intertidal communities. *Ecology* 80, 2711–2726. [https://doi.org/10.1890/0012-9658\(1999\)080\[2711:TTRCOP\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[2711:TTRCOP]2.0.CO;2)
- Blackburn, T.M., Gaston, K.J., 2002. Macroecology is distinct from biogeography. *Nature* 418, 723–723. <https://doi.org/10.1038/418723b>
- Bligh, E.G., Dyer, W.J., 1959. A Rapid Method of Total Lipid Extraction and Purification. *Canadian Journal of Biochemistry and Physiology* 37, 911–917. <https://doi.org/10.1139/o59-099>
- Bolnick, D.I., Svanbäck, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D., Forister, M.L., 2003. The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist* 161, 1–28.
- Bonifazi, A., Lezzi, M., Ventura, D., Lisco, S., Cardone, F., Gravina, M.F., 2019. Macrofaunal biodiversity associated with different developmental phases of a threatened Mediterranean *Sabellaria alveolata* (Linnaeus, 1767) reef. *Marine environmental research* 145, 97–111.
- Bonnot-Courtois, C., Guilpain, P., Legendre, V., Le Vot, M., Massé, M., Moré, F., Panizza, A., Prevost, C., Schoorens, J., Toupoint, N., 2007. Cartographie morpho-sédimentaire intertidale de la baie du Mont Saint-Michel. État 2002. CNRS, UMR 8586 PRODIG, Laboratoire de Géomorphologie et Environnement littoral. EPHE.
- Boo, G.H., Qiu, Y., Kim, J.Y., Ang, P.O., Bosch, S., De Clerck, O., He, P., Higa, A., Huang, B., Kogame, K., Liu, S., Nguyen, T., Suda, S., Terada, R., Miller, K.A., Boo, S.M., 2019. Contrasting patterns of genetic structure and phylogeography in the marine agarophytes *Gelidiophycus divaricatus* and *G. freshwateri* (Gelidiales, Rhodophyta) from East Asia. *Journal of Phycology* 55(6), 1319–1334. <https://doi.org/10.1111/jpy.12910>
- Bosman, A.L., Hockey, P.A.R., Siegfried, W.R., 1987. The influence of coastal upwelling on the functional structure of rocky intertidal communities. *Oecologia* 72, 226–232. <https://doi.org/10.1007/BF00379273>
- Box, G.E.P., Cox, D.R., 1964. An Analysis of Transformations. *Journal of the Royal Statistical Society. Series B (Methodological)* 26, 211–252.
- Bowman, R.S. and Lewis, J.R., 1977. Annual fluctuations in the recruitment of *Patella vulgata* L. *Journal of the Marine Biological Association of the United Kingdom*, 57(3), 793–815
- Breiman, L., 2001. Random forests. *Machine learning* 45, 5–32.

- Bricheno, L.M., Wolf, J., 2018. Future Wave Conditions of Europe, in Response to High-End Climate Change Scenarios. *Journal of Geophysical Research: Oceans* 123, 8762–8791. <https://doi.org/10.1029/2018JC013866>
- Brokordt, K.B., Himmelman, J.H., Nusetti, O.A., Guderley, H.E., 2000. Reproductive investment reduces recuperation from exhaustive escape activity in the tropical scallop *Euvola zizac*. *Marine Biology* 137, 857–865. <https://doi.org/10.1007/s002270000415>
- Brown, J.H., 1984. On the Relationship between Abundance and Distribution of Species. *The American Naturalist* 124, 255–279. <https://doi.org/10.1086/284267>
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a Metabolic Theory of Ecology. *Ecology* 85, 1771–1789. <https://doi.org/10.1890/03-9000>
- Bučas, M., Bergström, U., Downie, A., Sundblad, G., Gullström, M., Von Numers, M., Šiaulyš, A., Lindegarth, M., 2013. Empirical modelling of benthic species distribution, abundance, and diversity in the Baltic Sea: evaluating the scope for predictive mapping using different modelling approaches. *ICES Journal of Marine Science* 70, 1233–1243.
- Bulleri, F., Eriksson, B.K., Queirós, A., Airoidi, L., Arenas, F., Arvanitidis, C., Bouma, T.J., Crowe, T.P., Davoult, D., Guizien, K., Iveša, L., Jenkins, S.R., Michalet, R., Olabarria, C., Procaccini, G., Serrão, E.A., Wahl, M., Benedetti-Cecchi, L., 2018. Harnessing positive species interactions as a tool against climate-driven loss of coastal biodiversity. *PLoS Biology* 16, e2006852. <https://doi.org/10.1371/journal.pbio.2006852>
- Burrows, M., Harvey, R., Robb, L., 2008. Wave exposure indices from digital coastlines and the prediction of rocky shore community structure. *Marine Ecology Progress Series* 353, 1–12. <https://doi.org/10.3354/meps07284>
- Burrows, M.T., Schoeman, D.S., Buckley, L.B., Moore, P., Poloczanska, E.S., Brander, K.M., Brown, C., Bruno, J.F., Duarte, C.M., Halpern, B.S., Holding, J., Kappel, C.V., Kiessling, W., O'Connor, M.I., Pandolfi, J.M., Parmesan, C., Schwing, F.B., Sydeman, W.J., Richardson, A.J., 2011. The Pace of Shifting Climate in Marine and Terrestrial Ecosystems. *Science* 334, 652–655. <https://doi.org/10.1126/science.1210288>
- Burrows, M., 2012. Influences of wave fetch, tidal flow and ocean colour on subtidal rocky communities. *Marine Ecology Progress Series* 445, 193–207. <https://doi.org/10.3354/meps09422>
- Bush, L.E., 2016. Stability and variability of the ecosystem engineer *Sabellaria alveolata* on differing temporal and spatial scales. PhD Thesis, Bangor University. Available at : <https://ethos.bl.uk/OrderDetails.do?uin=uk.bl.ethos.690700> (Accessed: 16 April 2019)
- Butchart, S.H., Walpole, M., Collen, B., Van Strien, A., Scharlemann, J.P., Almond, R.E., Baillie, J.E., Bomhard, B., Brown, C., Bruno, J., 2010. Global biodiversity: indicators of recent declines. *Science* 328, 1164–1168.

-C-

- Canonico, G., Buttigieg, P.L., Montes, E., Muller-Karger, F.E., Stepien, C., Wright, D., Benson, A., Helmuth, B., Costello, M., Sousa-Pinto, I., Saeedi, H., Newton, J., Appeltans, W., Bednaršek, N., Bodrossy, L., Best, B.D., Brandt, A., Goodwin, K.D., Iken, K., Marques, A.C., Miloslavich, P., Ostrowski, M., Turner, W., Achterberg, E.P., Barry, T., Defeo, O., Bigatti, G., Henry, L.-A., Ramiro-Sánchez, B., Durán, P., Morato, T., Roberts, J.M., García-Alegre, A., Cuadrado, M.S., Murton, B., 2019. Global Observational Needs and Resources for Marine Biodiversity. *Frontiers in Marine Science* 6, 367. <https://doi.org/10.3389/fmars.2019.00367>
- Carson, R.L., 1955. *The Edge of the Sea*. The Riverside Press, Cambridge, Massachusetts.
- Cazaux, C., 1964. Développement larvaire de *Sabellaria alveolata* (Linné). *Bulletin de l'Institut Océanographique - Monaco* 62, 1–15.
- Chacón-Madrigal, E., Wanek, W., Hietz, P., Dullinger, S., 2018. Is local trait variation related to total range size of tropical trees? *PLoS ONE* 13, e0193268. <https://doi.org/10.1371/journal.pone.0193268>
- Charrier, H., 1921. Note sur les annélides polychètes de la région de Tanger. *Bulletin de la Société des sciences naturelles du Maroc* 1, 55–57.
- Chase, J.M., Leibold, M.A., 2003. *Ecological niches: linking classical and contemporary approaches*. University of Chicago Press.
- Chefaoui, R.M., Serebryakova, A., Engelen, A.H., Viard, F., Serrão, E.A., 2019. Integrating reproductive phenology in ecological niche models changed the predicted future ranges of a marine invader. *Diversity and Distributions* 25, 688–700. <https://doi.org/10.1111/ddi.12910>
- Cheng, L., Abraham, J., Zhu, J., Trenberth, K.E., Fasullo, J., Boyer, T., Locarnini, R., Zhang, B., Yu, F., Wan, L., Chen, X., Song, X., Liu, Y., Mann, M.E., 2020. Record-Setting Ocean Warmth Continued in 2019. *Advances in Atmospheric Sciences* 37, 137–142. <https://doi.org/10.1007/s00376-020-9283-7>
- Chenu, J.-C., 1842. *Illustration conchyliologiques, ou Description et figures de toutes les coquilles connues vivantes et fossiles, classées suivant le système de Lamarck modifié d'après les progrès de la science et comprenant les genres nouveaux et les espèces récemment découvertes.*, Fortin et Masson. ed. Paris.
- Childress, J.J., Somero, G.N., 1979. Depth-related enzymic activities in muscle, brain and heart of deep-living pelagic marine teleosts. *Marine Biology* 52, 273–283. <https://doi.org/10.1007/BF00398141>
- Chouikh, N., Gillet, P., Langston, W., Cheggour, M., Maarouf, A., Mouabad, A., 2020. Spatial distribution and structure of benthic polychaete communities of Essaouira intertidal rocky shores (Atlantic coast of Morocco). *Journal of Oceanology and Limnology* 38, 143–155.

- Clarke, A., 1992. Reproduction in the cold: Thorson revisited. *Invertebrate Reproduction and Development* 22, 175–183. <https://doi.org/10.1080/07924259.1992.9672270>
- Coll, M., Pennino, M.G., Steenbeek, J., Sole, J., Bellido, J.M., 2019. Predicting marine species distributions: Complementarity of food-web and Bayesian hierarchical modelling approaches. *Ecological Modelling* 405, 86–101. <https://doi.org/10.1016/j.ecolmodel.2019.05.005>
- Collin, A., Dubois, S., Ramambason, C., Etienne, S., 2018. Very high-resolution mapping of emerging biogenic reefs using airborne optical imagery and neural network: the honeycomb worm (*Sabellaria alveolata*) case study. *International Journal of Remote Sensing* 39, 5660–5675.
- Connallon, T., Sgrò, C.M., 2018. In search of a general theory of species' range evolution. *PLoS Biology* 16, e2006735. <https://doi.org/10.1371/journal.pbio.2006735>
- Connell, J.H., 1961. The Influence of Interspecific Competition and Other Factors on the Distribution of the Barnacle *Chthamalus stellatus*. *Ecology* 42, 710–723. <https://doi.org/10.2307/1933500>
- Connell, J.H., 1983. On the Prevalence and Relative Importance of Interspecific Competition: Evidence from Field Experiments. *The American Naturalist* 122, 661–696. <https://doi.org/10.1086/284165>
- Connor, T., Viña, A., Winkler, J.A., Hull, V., Tang, Y., Shortridge, A., Yang, H., Zhao, Z., Wang, F., Zhang, J., Zhang, Z., Zhou, C., Bai, W., Liu, J., 2019. Interactive spatial scale effects on species distribution modeling: The case of the giant panda. *Scientific Reports* 9, 14563. <https://doi.org/10.1038/s41598-019-50953-z>
- Costanza, R., 1992. Towards an operational definition of ecosystem health, in: *Ecosystem Health: New Goals for Environmental Management*. Island Press, pp. 239–256.
- Costello, D.P., Henley, C., Marine Biological Laboratory (Woods Hole, Mass.), 1971. Methods for obtaining and handling marine eggs and embryos. [s.n.], Woods Hole, Massachusetts. <https://doi.org/10.5962/bhl.title.1020>
- Crean, A.J., Marshall, D.J., 2008. Gamete plasticity in a broadcast spawning marine invertebrate. *Proceedings of the National Academy of Sciences* 105, 13508–13513. <https://doi.org/10.1073/pnas.0806590105>
- Crisp, D., Southward, A.J., 1958. The distribution of intertidal organisms along the coasts of the English Channel. *Journal of the Marine Biological Association of the United Kingdom* 37, 157–203.
- Crisp, D.J., 1964. The effects of the severe winter of 1962-63 on marine life in Britain. *Journal of Animal Ecology*, 33(1), pp.165-210.
- Crisp, M.D., Arroyo, M.T., Cook, L.G., Gandolfo, M.A., Jordan, G.J., McGlone, M.S., Weston, P.H., Westoby, M., Wilf, P., Linder, H.P., 2009. Phylogenetic biome conservatism on a global scale. *Nature* 458, 754–756.

- Culloty, S.C., Favier, E., Ní Riada, M., Ramsay, N.F., O’Riordan, R.M., 2010. Reproduction of the biogenic reef-forming honeycomb worm *Sabellaria alveolata* in Ireland. *Journal of the Marine Biological Association of the United Kingdom* 90, 503. <https://doi.org/10.1017/S0025315409990932>
- Cunningham, P.N., 1984. The geographical distribution of *Sabellaria alveolata* (L.) in England, Wales and Scotland, with investigations into the community structure of, and the effects of trampling on *Sabellaria alveolata* colonies. (N.C.C. Contract No. HF3/11/22.).
- Curd, A., Pernet, F., Corporeau, C., Delisle, L., Firth, L.B., Nunes, F.L.D., Dubois, S.F., 2019. Connecting organic to mineral: How the physiological state of an ecosystem-engineer is linked to its habitat structure. *Ecological Indicators* 98, 49–60. <https://doi.org/10.1016/j.ecolind.2018.10.044>
- Curd, A., Cordier, C., Firth, L.B., Bush, L., Gruet, Y., Le Mao, P., Blaze, J.A., Board, C., Bordeyne, F., Burrows, M.T., Cunningham, P.N., Davies, A.J., Desroy N., Edwards H., Harris D.R., Hawkins, S.J., Kerckhof, F., Lima, F.P., McGrath, D., Meneghesso, C., Mieszkowska, N., Nunn, J.D., Nunes, F.L.D., O’ Connor, N.E., O’ Riordan, R.M., Power, A.M., Seabra, R., Simkanin, C., Dubois, S.F., 2020. A broad-scale long-term dataset of *Sabellaria alveolata* distribution and abundance curated through the REEHAB (REEf HABitat) Project. SEANO. <https://doi.org/10.17882/72164>
- Cuvier, G., 1836. Le règne animal distribué d’après son organisation, pour servir de base à l’histoire naturelle des animaux et d’introduction à l’anatomie comparée. Volume 10: les annélides, avec un atlas par M. Milne Edwards. Fortin, Masson. ed. Paris.

-D-

- Dahlhoff, E.A., Somero, G.N., 1993. Effects of temperature on mitochondria from abalone (genus *Haliotis*): adaptive plasticity and its limits. *Journal of Experimental Biology* 185, 151.
- Dahlhoff, E.P., Stillman, J.H., Menge, B.A., 2002. Physiological community ecology: variation in metabolic activity of ecologically important rocky intertidal invertebrates along environmental gradients. *Integrative and comparative biology* 42, 862–871.
- Dahlhoff, E.P., 2004. Biochemical Indicators of Stress and Metabolism: Applications for Marine Ecological Studies. *Annual Review of Physiology* 66, 183–207. <https://doi.org/10.1146/annurev.physiol.66.032102.114509>
- Dalsgaard J., St. John, M., Kattner, G., Muller-Navarra, D., Hagen, W., 2003. Fatty acid trophic markers in the pelagic marine environment. *Advances in Marine Biology* 46:225-340. doi: 10.1016/S0065-2881(03)46005-7
- Darwin, C., 1859. *On the Origin of Species by Means of Natural Selection* (J. Murray, London).

- Davies, A.J., Last, K.S., Attard, K., Hendrick, V.J., 2009. Maintaining turbidity and current flow in laboratory aquarium studies, a case study using *Sabellaria spinulosa*. *Journal of Experimental Marine Biology and Ecology* 370, 35–40.
- Davis, M.B., 2001. Range Shifts and Adaptive Responses to Quaternary Climate Change. *Science* 292, 673–679. <https://doi.org/10.1126/science.292.5517.673>
- Dawson, T.P., Jackson, S.T., House, J.I., Prentice, I.C., Mace, G.M., 2011. Beyond Predictions: Biodiversity Conservation in a Changing Climate. *Science* 332, 53–58. <https://doi.org/10.1126/science.1200303>
- de Cubber, L., Lefebvre, S., Lancelot, T., Denis, L., Gaudron, S.M., 2019. Annelid polychaetes experience metabolic acceleration as other Lophotrochozoans: Inferences on the life cycle of *Arenicola marina* with a Dynamic Energy Budget model. *Ecological Modelling* 411, 108773. <https://doi.org/10.1016/j.ecolmodel.2019.108773>
- de Gerville, 1825. Catalogue des coquilles trouvées sur les côtes du département de la Manche, lu à la séance du 14 mars 1825. *Mémoires de la Société linnéenne du Calvados* 169–224.
- de Grave, S., Whitaker, A., 1997. The Occurrence of a subtidal *Sabellaria alveolata* (L.) Reef off Wicklow Head, Irish Sea. *The Irish Naturalists' Journal* 25, 416–418.
- de la Hoz, C.F., Ramos, E., Puente, A., Juanes, J.A., 2019a. Climate change induced range shifts in seaweeds distributions in Europe. *Marine Environmental Research* 148, 1–11. <https://doi.org/10.1016/j.marenvres.2019.04.012>
- de la Hoz, C.F., Ramos, E., Puente, A., Juanes, J.A., 2019b. Temporal transferability of marine distribution models: The role of algorithm selection. *Ecological Indicators* 106, 105499. <https://doi.org/10.1016/j.ecolind.2019.105499>
- Delaporte, M., 2003. Effect of a mono-specific algal diet on immune functions in two bivalve species - *Crassostrea gigas* and *Ruditapes philippinarum*. *Journal of Experimental Biology* 206, 3053–3064. <https://doi.org/10.1242/jeb.00518>
- DeLong, E.R., DeLong, D.M., Clarke-Pearson, D.L., 1988. Comparing the areas under two or more correlated receiver operating characteristic curves: a nonparametric approach. *Biometrics* 837–845.
- Déqué, M., Drevet, C., Braun, A., Cariolle, D., 1994. The ARPEGE/IFS atmosphere model: a contribution to the French community climate modelling. *Climate Dynamics* 10, 249–266. <https://doi.org/10.1007/BF00208992>
- Des Roches, S., Post, D.M., Turley, N.E., Bailey, J.K., Hendry, A.P., Kinnison, M.T., Schweitzer, J.A., Palkovacs, E.P., 2018. The ecological importance of intraspecific variation. *Nature Ecology and Evolution* 2, 57–64. doi:10.1038/s41559-017-0402-5
- Desroy, N., Dubois, S.F., Fournier, J., Ricquiers, L., Le Mao, P., Guerin, L., Gerla, D., Rougerie, M., Legendre, A., 2011. The conservation status of *Sabellaria alveolata* (L.) (Polychaeta: Sabellariidae) reefs in the Bay of Mont-Saint-Michel. *Aquatic Conservation: Marine and Freshwater Ecosystems* 21, 462–471. doi:10.1002/aqc.1206

- Dias, A.S., Paula, J., 2001. Associated fauna of *Sabellaria alveolata* colonies on the central coast of Portugal. *Journal of the Marine Biological Association of the United Kingdom* 81, 169–170.
- Doledec, S., Chessel, D., 1994. Co-inertia analysis: an alternative method for studying species-environment relationships. *Freshwater Biology* 31, 277–294. <https://doi.org/10.1111/j.1365-2427.1994.tb01741.x>
- Dollfus, R.P., 1921. Résumé de nos principales connaissances pratiques sur les maladies et les ennemis de l'huître. *Notes et mémoires* 7, 51.
- Dong, Y., Miller, L.P., Sanders, J.G., Somero, G.N., 2008. Heat-shock protein 70 (Hsp70) expression in four limpets of the genus *Lottia*: interspecific variation in constitutive and inducible synthesis correlates with *in situ* exposure to heat stress. *The Biological Bulletin* 215, 173–181.
- Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36, 27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>
- Dowd, W.W., Felton, C.A., Heymann, H.M., Kost, L.E., Somero, G.N., 2013. Food availability, more than body temperature, drives correlated shifts in ATP-generating and antioxidant enzyme capacities in a population of intertidal mussels (*Mytilus californianus*). *Journal of Experimental Marine Biology and Ecology* 449, 171–185.
- Dubois, S., Retière, C., Olivier, F., 2002. Biodiversity associated with *Sabellaria alveolata* (Polychaeta: Sabellariidae) reefs: effects of human disturbances. *Journal of the Marine Biological Association of the UK* 82, 817–826. doi:10.1017/S0025315402006185
- Dubois, S., Barillé, L., Retière, C., 2003. Efficiency of particle retention and clearance rate in the polychaete *Sabellaria alveolata* L. *Comptes Rendus Biologies* 326, 413–421. [https://doi.org/10.1016/S1631-0691\(03\)00124-0](https://doi.org/10.1016/S1631-0691(03)00124-0)
- Dubois, S., Barillé, L., Cognie, B., Beninger, P., 2005. Particle capture and processing mechanisms in *Sabellaria alveolata* (Polychaeta: Sabellariidae). *Marine Ecology Progress Series* 301, 159–171. <https://doi.org/10.3354/meps301159>
- Dubois, S., Commito, J.A., Olivier, F., Retière, C., 2006. Effects of epibionts on *Sabellaria alveolata* (L.) biogenic reefs and their associated fauna in the Bay of Mont Saint-Michel. *Estuarine, Coastal and Shelf Science* 68, 635–646. <https://doi.org/10.1016/j.ecss.2006.03.010>
- Dubois, S., Orvain, F., Marin-Léal, J., Ropert, M., Lefebvre, S., 2007a. Small-scale spatial variability of food partitioning between cultivated oysters and

- associated suspension-feeding species, as revealed by stable isotopes. *Marine Ecology Progress Series* 336, 151–160. <https://doi.org/10.3354/meps336151>
- Dubois, S., Comtet, T., Retière, C., Thiébaud, E., 2007b. Distribution and retention of *Sabellaria alveolata* larvae (Polychaeta: Sabellariidae) in the Bay of Mont-Saint-Michel, France. *Marine Ecology Progress Series* 346, 243–254.
- Dubois, S., Barillé, L., Cognie, B., 2009. Feeding response of the polychaete *Sabellaria alveolata* (Sabellariidae) to changes in seston concentration. *Journal of Experimental Marine Biology and Ecology* 376, 94–101. <https://doi.org/10.1016/j.jembe.2009.06.017>
- Dubois, S.F., Colombo, F., 2014. How picky can you be? Temporal variations in trophic niches of co-occurring suspension-feeding species. *Food Webs* 1, 1–9. <https://doi.org/10.1016/j.fooweb.2014.07.001>
- DuBois, M., Gilles, K.A., Hamilton, J.K., Rebers, P.A., Smith, F., 1956. Colorimetric Method for Determination of Sugars and Related Substances. *Analytical Chemistry* 28, 350–356. <https://doi.org/10.1021/ac60111a017>
- D’Urban Jackson, T., Williams, G.J., Walker-Springett, G., Davies, A.J., 2020. Three-dimensional digital mapping of ecosystems: a new era in spatial ecology. *Proceedings of the Royal Society B* 287, 20192383.

-E-

- Ebling, F.J., 1945. Memoirs: Formation and Nature of the Opercular Chaetae of *Sabellaria alveolata*. *Journal of Cell Science* s2-85, 153.
- Egerton, S., 2014. Distribution mapping and health assessment of honeycomb worm, *Sabellaria alveolata*, reefs on Heysham Flat, Lancashire 2013. <https://doi.org/10.13140/RG.2.2.33283.91683>
- Ellis, R.P., Parry, H., Spicer, J.I., Hutchinson, T.H., Pipe, R.K., Widdicombe, S., 2011. Immunological function in marine invertebrates: Responses to environmental perturbation. *Fish & Shellfish Immunology* 30, 1209–1222. <https://doi.org/10.1016/j.fsi.2011.03.017>
- Elith*, J., H. Graham*, C., P. Anderson, R., Dudík, M., Ferrier, S., Guisan, A., J. Hijmans, R., Huettmann, F., R. Leathwick, J., Lehmann, A., 2006. Novel methods improve prediction of species’ distributions from occurrence data. *Ecography* 29, 129–151.
- Elith, J., Leathwick, J.R., 2009. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annual Review of Ecology, Evolution and Systematics* 40, 677–697. <https://doi.org/10.1146/annurev.ecolsys.110308.120159>
- Elton, C., 1927. *Animal Ecology*. Sedgwick and Jackson, London.

- Egbert, G.D., Erofeeva, S.Y., 2002. Efficient Inverse Modeling of Barotropic Ocean Tides. *Journal of Atmospheric and Oceanic Technology* 19, 183–204. [https://doi.org/10.1175/1520-0426\(2002\)019<0183:EIMOBO>2.0.CO;2](https://doi.org/10.1175/1520-0426(2002)019<0183:EIMOBO>2.0.CO;2)
- Egbert, G.D., Erofeeva, S.Y., Ray, R.D., 2010. Assimilation of altimetry data for nonlinear shallow-water tides: Quarter-diurnal tides of the Northwest European Shelf. *Continental Shelf Research* 30, 668–679. <https://doi.org/10.1016/j.csr.2009.10.011>
- Estrada, A., Morales-Castilla, I., Caplat, P., Early, R., 2016. Usefulness of Species Traits in Predicting Range Shifts. *Trends in Ecology & Evolution* 31, 190–203. <https://doi.org/10.1016/j.tree.2015.12.014>
- European Environment Agency, 2018. EEA coastline for analysis <https://www.eea.europa.eu/data-and-maps/data/eea-coastline-for-analysis-2#tab-metadata> , Accessed 16th January 2019.

-F-

- Faget, D., 2007. Pour une approche transdisciplinaire de l'histoire maritime: l'étude des colonies d'hermelles *Sabellaria alveolata* (Linné 767) à Marseille (France) à la fin du XIXe siècle. *Mésogée* 63, 27–35.
- Faroni-Perez, L., 2014. Variação sazonal no recrutamento de *Phragmatopoma caudata* (Polychaeta, Sabellariidae) na costa sudeste do Brasil: biometria e validação de metodologia para categorização de classes etárias. *Iheringia, Sér. Zool.* 104, 05–13. <https://doi.org/10.1590/1678-476620141041513>
- Faroni-Perez, L., 2017. Climate and environmental changes driving idiosyncratic shifts in the distribution of tropical and temperate worm reefs. *Journal of the Marine Biological Association of the United Kingdom* 97, 1023–1035. <https://doi.org/10.1017/S002531541700087X>
- Ferron, A., Leggett, W.C., 1994. An Appraisal of Condition Measures for Marine Fish Larvae, in: *Advances in Marine Biology*. Elsevier, pp. 217–303. [https://doi.org/10.1016/S0065-2881\(08\)60064-4](https://doi.org/10.1016/S0065-2881(08)60064-4)
- Finke, G., Navarrete, S., Bozinovic, F., 2007. Tidal regimes of temperate coasts and their influences on aerial exposure for intertidal organisms. *Marine Ecology Progress Series* 343, 57–62. <https://doi.org/10.3354/meps06918>
- Firth, L.B., Williams, G.A., 2009. The influence of multiple environmental stressors on the limpet *Cellana toreuma* during the summer monsoon season in Hong Kong. *Journal of Experimental Marine Biology and Ecology* 375, 70–75. <https://doi.org/10.1016/j.jembe.2009.05.011>
- Firth, L.B., Knights, A.M., Bell, S.S., 2011. Air temperature and winter mortality: Implications for the persistence of the invasive mussel, *Perna viridis* in the intertidal zone of the south-eastern United States. *Journal of Experimental*

- Marine Biology and Ecology 400, 250–256.
<https://doi.org/10.1016/j.jembe.2011.02.007>
- Firth, L.B., Mieszkowska, N., Grant, L.M., Bush, L.E., Davies, A.J., Frost, M.T., Moschella, P.S., Burrows, M.T., Cunningham, P.N., Dye, S.R., Hawkins, S.J., 2015. Historical comparisons reveal multiple drivers of decadal change of an ecosystem engineer at the range edge. *Ecology and Evolution* 5, 3210–3222.
<https://doi.org/10.1002/ece3.1556>
- Firth, L.B., Knights, A.M., Bridger, D., Evans, A., Mieszkowska, N., Moore, P.J., O'Connor, N.E., Sheehan, E.V., Thompson, R.C., Hawkins, S.J., 2016. Ocean sprawl: challenges and opportunities for biodiversity management in a changing world. *Oceanography and Marine Biology: an annual review* 54, 189–262. 10.1201/9781315368597
- Flammang, P., Lambert, A., Bailly, P., Hennebert, E., 2009. Polyphosphoprotein-Containing Marine Adhesives. *The Journal of Adhesion* 85, 447–464.
<https://doi.org/10.1080/00218460902996358>
- Foo, S.A., Byrne, M., 2017. Marine gametes in a changing ocean: Impacts of climate change stressors on fecundity and the egg. *Marine Environmental Research* 128, 12–24. <https://doi.org/10.1016/j.marenvres.2017.02.004>
- Fournier, J., Etienne, S., Le Cam, J.-B., 2010. Inter- and intraspecific variability in the chemical composition of the mineral phase of cements from several tube-building polychaetes. *Geobios* 43, 191–200.
<https://doi.org/10.1016/j.geobios.2009.10.004>
- Fraser, A.J., 1989. Triacylglycerol Content as a Condition Index for Fish, Bivalve, and Crustacean Larvae. *Canadian Journal of Fisheries and Aquatic Sciences* 46, 1868–1873. <https://doi.org/10.1139/f89-235>
- Frost, M. T., Leaper, R., Mieszkowska, N., Moschella, P., Murua, J., Smyth, C. and Hawkins, S.J., 2004. Recovery of a Biodiversity Action Plan Species in Northwest England: possible role of climate change, artificial habitat and water quality amelioration. *Sabellaria alveolata*: Report to English Nature.
- Fuhrmann, M., Delisle, L., Petton, B., Corporeau, C., Pernet, F., 2018. Metabolism of the Pacific oyster, *Crassostrea gigas*, is influenced by salinity and modulates survival to the Ostreid herpesvirus OsHV-1. *Biology Open* 7, bio028134.
<https://doi.org/10.1242/bio.028134>
- Fung, T., Seymour, R.M., Johnson, C.R., 2011. Alternative stable states and phase shifts in coral reefs under anthropogenic stress. *Ecology* 92, 967–982.
<https://doi.org/10.1890/10-0378.1>

-G-

- Gabbott, P.A., 1975. Storage cycles in marine bivalve molluscs: a hypothesis concerning the relationship between glycogen metabolism and

gametogenesis. Presented at the Ninth European Marine Biology Symposium, Aberdeen University Press, Oban, pp. 191–211.

- Gallager, S.M., Mann, R., Sasaki, G.C., 1986. Lipid as an index of growth and viability in three species of bivalve larvae. *Aquaculture* 56, 81–103. [https://doi.org/10.1016/0044-8486\(86\)90020-7](https://doi.org/10.1016/0044-8486(86)90020-7)
- Gandra, M., Seabra, R., Lima, F.P., 2015. A low-cost, versatile data logging system for ecological applications. *Limnology and Oceanography: Methods* 13, 115–126.
- Garcia-Esquivel, Z., Bricelj, V.M., Felbeck, H., 2002. Metabolic depression and whole-body response to enforced starvation by *Crassostrea gigas* postlarvae. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 133, 63–77.
- Gause, G.F., 1934. *The Struggle for Existence: A Classic of Mathematical Biology and Ecology*. Courier Dover Publications.
- Gaylord, B., Gaines, S.D., Siegel, D.A., Carr, M.H., 2005. Marine Reserves Exploit Population Structure and Life History in Potentially Improving Fisheries Yields. *Ecological Applications* 15, 2180–2191. <https://doi.org/10.1890/04-1810>
- Gohin, F., 2011. Annual cycles of chlorophyll-a, non-algal suspended particulate matter, and turbidity observed from space and in-situ in coastal waters. *Ocean Science* 7, 705–732. <https://doi.org/10.5194/os-7-705-2011>
- Goldberg, W.M., 2013. *The biology of reefs and reef organisms*. University of Chicago Press, Chicago.
- Gourret, P., 1893. Les appâts de pêche usités à Marseille. *Revue maritime et coloniale* 117, 427–443.
- Gourret, P., 1894. *Les pêcheries et les poissons de la Méditerranée (Provence)*. Librairie J.-B. Baillière et Fils, Paris.
- Gourret, P., 1901. Sur quelques Annélides sédentaires (Gen. Hydroides, Pomatoceros et Hermella) du Golfe de Marseille, in: *Comptes Rendus de l'association Française Pour l'avancement Des Sciences*. Ajaccio, pp. 685–691.
- Green, J.L., Bohannon, B.J., Whitaker, R.J., 2008. Microbial biogeography: from taxonomy to traits. *Science* 320, 1039–1043.
- Grinnell, J., 1917. The niche-relationships of the California Thrasher. *Auk*, 34, 427–433.
- Gruet, Y., 1982. *Recherches sur l'écologie des "récifs" d'hermelles édifiés par l'Annélide Polychète Sabellaria alveolata (Linné)*. (Thèse Doctorat d'Etat). Nantes.
- Gruet, Y., Lassus, P., 1983. Contribution à l'étude de la biologie reproductive d'une population naturelle de l'Annelide Polychete, *Sabellaria alveolata* (Linnaeus). *Annals of the Institute of Oceanography, Monaco* 59, 127–140.

- Gruet, Y., 1984. Granulometric evolution of the sand tube in relation to growth of the Polychaete Annelid *Sabellaria alveolata* (Linné)(Sabellariidae). *Ophelia* 23, 181–193.
- Gruet, Y., 1986. Spatio-temporal Changes of Sabellarian Reefs Built by the Sedentary Polychaete *Sabellaria alveolata* (Linné). *Marine Ecology* 7, 303–319. doi:10.1111/j.1439-0485.1986.tb00166.x
- Gruet, Y., Vovelle, J., Grasset, M., 1987. Composante biominérale du ciment du tube chez *Sabellaria alveolata* (L.), Annélide Polychète. *Canadian journal of zoology* 65, 837–842.
- Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. *Ecology letters* 8, 993–1009.
- Guisan, A., Thuiller, W., Zimmermann, N.E., 2017. *Habitat suitability and distribution models with applications in R, Ecology, biodiversity and conservation.* Cambridge University Press, Cambridge, United Kingdom ; New York, NY.

-H-

- Haas, A.F., Guibert, M., Foerschner, A., Co, T., Calhoun, S., George, E., Hatay, M., Dinsdale, E., Sandin, S.A., Smith, J.E., Vermeij, M.J.A., Felts, B., Dustan, P., Salamon, P., Rohwer, F., 2015. Can we measure beauty? Computational evaluation of coral reef aesthetics. *PeerJ* 3, e1390. <https://doi.org/10.7717/peerj.1390>
- Harley, C.D.G., Randall Hughes, A., Hultgren, K.M., Miner, B.G., Sorte, C.J.B., Thornber, C.S., Rodriguez, L.F., Tomanek, L., Williams, S.L., 2006. The impacts of climate change in coastal marine systems: Climate change in coastal marine systems. *Ecology Letters* 9, 228–241. <https://doi.org/10.1111/j.1461-0248.2005.00871.x>
- Harley, C., 2008. Tidal dynamics, topographic orientation, and temperature-mediated mass mortalities on rocky shores. *Marine Ecology Progress Series* 371, 37–46. <https://doi.org/10.3354/meps07711>
- Harrison, S., 1997. How Natural Habitat Patchiness Affects the Distribution of Diversity in Californian Serpentine Chaparral. *Ecology* 78, 1898–1906. [https://doi.org/10.1890/0012-9658\(1997\)078\[1898:HNHPAT\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[1898:HNHPAT]2.0.CO;2)
- Hastie, T.J., 2017. Generalized additive models, in: *Statistical Models in S.* Routledge, pp. 249–307.
- Hattam, C., Atkins, J.P., Beaumont, N., Börger, T., Böhnke-Henrichs, A., Burdon, D., Groot, R. de, Hoefnagel, E., Nunes, P.A.L.D., Piwowarczyk, J., Sastre, S., Austen, M.C., 2015. Marine ecosystem services: Linking indicators to their classification. *Ecological Indicators* 49, 61–75. <https://doi.org/10.1016/j.ecolind.2014.09.026>
- Hawkins, S., Moore, P., Burrows, M., Poloczanska, E., Mieszkowska, N., Herbert, R., Jenkins, S., Thompson, R., Genner, M., Southward, A., 2008. Complex

interactions in a rapidly changing world: responses of rocky shore communities to recent climate change. *Climate Research* 37, 123–133. <https://doi.org/10.3354/cr00768>

- Hawkins, S., Sugden, H., Mieszkowska, N., Moore, P., Poloczanska, E., Leaper, R., Herbert, R., Genner, M., Moschella, P., Thompson, R., Jenkins, S., Southward, A., Burrows, M., 2009. Consequences of climate-driven biodiversity changes for ecosystem functioning of North European rocky shores. *Marine Ecology Progress Series* 396, 245–259. <https://doi.org/10.3354/meps08378>
- Hawkins, S.J., Firth, L.B., McHugh, M., Poloczanska, E.S., Herbert, R.J.H., Burrows, M.T., Kendall, M.A., Moore, P.J., Thompson, R.C., Jenkins, S.R., Sims, D.W., Genner, M.J., Mieszkowska, N., 2013. Data rescue and re-use: Recycling old information to address new policy concerns. *Marine Policy* 42, 91–98. <https://doi.org/10.1016/j.marpol.2013.02.001>
- Hawkins, S.J., Mieszkowska, N., Firth, L.B., Bohn, K., Burrows, M.T., MacLean, M.A., Thompson, R.C., Chan, B.K.K., Little, C., Williams, G.A., 2016. Looking backwards to look forwards: the role of natural history in temperate reef ecology. *Marine and Freshwater Research* 67, 1. <https://doi.org/10.1071/MF14413>
- Hawkins, S.J., Evans, A.J., Mieszkowska, N., Adams, L.C., Bray, S., Burrows, M.T., Firth, L.B., Genner, M.J., Leung, K.M.Y., Moore, P.J., Pack, K., Schuster, H., Sims, D.W., Whittington, M., Southward, E.C., 2017. Distinguishing globally-driven changes from regional- and local-scale impacts: The case for long-term and broad-scale studies of recovery from pollution. *Marine Pollution Bulletin* 124, 573–586. <https://doi.org/10.1016/j.marpolbul.2017.01.068>
- Hawkins, S.J., Pack, K., Firth, L., Mieszkowska, N., Evans, A., Martins, G., Aberg, P., Adams, L., Arenas, F., Boaventura, D., 2019. The intertidal zone of the North-East Atlantic region: pattern and process, in: *Interactions in the Marine Benthos: Global Patterns and Processes*. Cambridge University Press, Cambridge, United Kingdom.
- Hazel, J.R., Williams, E.E., 1990. The role of alterations in membrane lipid composition in enabling physiological adaptation of organisms to their physical environment. *Progress in Lipid Research* 29, 167–227. [https://doi.org/10.1016/0163-7827\(90\)90002-3](https://doi.org/10.1016/0163-7827(90)90002-3)
- Hazel, J.R., 1995. Thermal Adaptation in Biological Membranes: Is Homeoviscous Adaptation the Explanation? *Annual Review of Physiology* 57, 19–42. <https://doi.org/10.1146/annurev.ph.57.030195.000315>
- Heikkinen, R.K., Marmion, M., Luoto, M., 2012. Does the interpolation accuracy of species distribution models come at the expense of transferability? *Ecography* 35, 276–288.
- Helmuth, B.S., Hofmann, G.E., 2001. Microhabitats, thermal heterogeneity, and patterns of physiological stress in the rocky intertidal zone. *The Biological Bulletin* 201, 374–384.

- Helmuth, B., Harley, C.D.G., Halpin, P.M., O'Donnell, M., Hofmann, G.E., Blanchette, C.A., 2002. Climate Change and Latitudinal Patterns of Intertidal Thermal Stress. *Science* 298, 1015–1017. <https://doi.org/10.1126/science.1076814>
- Helmuth, B., Kingsolver, J.G., Carrington, E., 2005. Biophysics, physiological ecology, and climate change: does mechanism matter? *Annual Review of Physiology* 67, 177–201. <https://doi.org/10.1146/annurev.physiol.67.040403.105027>
- Helmuth, B., Mieszkowska, N., Moore, P., Hawkins, S.J., 2006. Living on the Edge of Two Changing Worlds: Forecasting the Responses of Rocky Intertidal Ecosystems to Climate Change. *Annual Review of Ecology, Evolution and Systematics* 37, 373–404. <https://doi.org/10.1146/annurev.ecolsys.37.091305.110149>
- Hendrick, V.J., Foster-Smith, R.L., 2006. *Sabellaria spinulosa* reef: a scoring system for evaluating 'reefiness' in the context of the Habitats Directive. *Journal of the Marine Biological Association of the UK* 86, 665. doi:10.1017/S0025315406013555
- Henson, S., Cole, H., Beaulieu, C., Yool, A., 2013. The impact of global warming on seasonality of ocean primary production. *Biogeosciences* 10, 4357–4369. <https://doi.org/10.5194/bg-10-4357-2013>
- Hentschel, B.T., 1998. Spectrofluorometric quantification of neutral and polar lipids suggests a food-related recruitment bottleneck for juveniles of a deposit-feeding polychaete population. *Limnology and Oceanography* 43, 543–549. <https://doi.org/10.4319/lo.1998.43.3.0543>
- Herbert, R., Hawkins, S., Shearer, M., Southward, A., 2003. Range extension and reproduction of the barnacle *Balanus perforatus* in the eastern English Channel. *Journal of the Marine Biological Association of the United Kingdom* 83, 73–82.
- Hernandez, P.A., Graham, C.H., Master, L.L., Albert, D.L., 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* 29, 773–785.
- Heuner, M., Silinski, A., Schoelynck, J., Bouma, T.J., Puijalon, S., Troch, P., Fuchs, E., Schröder, B., Schröder, U., Meire, P., Temmerman, S., 2015. Ecosystem Engineering by Plants on Wave-Exposed Intertidal Flats Is Governed by Relationships between Effect and Response Traits. *PLoS ONE* 10, e0138086. <https://doi.org/10.1371/journal.pone.0138086>
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25, 1965–1978. <https://doi.org/10.1002/joc.1276>
- Hirzel, A.H., Le Lay, G., 2008. Habitat suitability modelling and niche theory. *Journal of Applied Ecology* 45, 1372–1381. <https://doi.org/10.1111/j.1365-2664.2008.01524.x>

- Hiscock, K., Southward, A., Tittley, I., Jory, A., Hawkins, S., 2001. The impact of climate change on subtidal and intertidal benthic species in Scotland. SNH Research Survey and Monitoring Report.
- Hiscock, K., Southward, A., Tittley, I., Hawkins, S., 2004. Effects of changing temperature on benthic marine life in Britain and Ireland. *Aquatic Conservation: Marine and Freshwater Ecosystems* 14, 333–362. <https://doi.org/10.1002/aqc.628>
- Hochachka, P.W., Somero, G.N., 2002. Biochemical adaptation: mechanism and process in physiological evolution. Oxford University Press, New York.
- Hoffmann, M., Hilton-Taylor, C., Angulo, A., Böhm, M., Brooks, T.M., Butchart, S.H., Carpenter, K.E., Chanson, J., Collen, B., Cox, N.A., 2010. The impact of conservation on the status of the world's vertebrates. *Science* 330, 1503–1509.
- Hofmann, G., Somero, G., 1996. Interspecific variation in thermal denaturation of proteins in the congeneric mussels *Mytilus trossulus* and *M. galloprovincialis*: evidence from the heat-shock response and protein ubiquitination. *Marine Biology* 126, 65–75.
- Hofmann, P., Chatzinotas, A., Harpole, W.S., Dunker, S., 2019. Temperature and stoichiometric dependence of phytoplankton traits. *Ecology* ecy.2875. <https://doi.org/10.1002/ecy.2875>
- Holt, T.J., Rees, E.I., Hawkins, S.J., Seed, R., 1998. Biogenic Reefs. An overview of dynamic and sensitivity characteristics for conservation management of marine SACs. (No. volume IX). Scottish Association for Marine Science (UK Marine SACs Project).
- Holt, R.D., 2009. Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences* 106, 19659–19665. <https://doi.org/10.1073/pnas.0905137106>
- Hulbert, A., Else, P.L., 1999. Membranes as possible pacemakers of metabolism. *Journal of theoretical biology* 199, 257–274.
- Hulbert, A.J., Turner, N., Storlien, L.H., Else, P.L., 2005. Dietary fats and membrane function: implications for metabolism and disease. *Biological Reviews* 80, 155–169. <https://doi.org/10.1017/S1464793104006578>
- Hutchins, L.W., 1947. The Bases for Temperature Zonation in Geographical Distribution. *Ecological Monographs* 17, 325–335. <https://doi.org/10.2307/1948663>
- Hutchinson, G.E., 1957. Concluding remarks. *Population Studies: Animal Ecology and Demography*. Cold Spring Harbor Symposium on Quantitative Biology, 22, 415–457.
- Hutchinson, G.E., 1978. An introduction to population ecology. (No. 504: 51 HUT)

- ICES Advice 2019. Ecosystem Overviews: Celtic Seas Ecoregion. Published 12 December 2019. <https://doi.org/10.17895/ices.advice.5749>
- Ingrosso, G., Abbiati, M., Badalamenti, F., Bavestrello, G., Belmonte, G., Cannas, R., Benedetti-Cecchi, L., Bertolino, M., Bevilacqua, S., Bianchi, C.N., 2018. Mediterranean bioconstructions along the Italian coast, in: *Advances in Marine Biology*. Elsevier, pp. 61–136.
- IPCC, 2018: Global warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty [V. Masson-Delmotte, P. Zhai, H. O. Pörtner, D. Roberts, J. Skea, P.R. Shukla, A. Pirani, W. Moufouma-Okia, C. Péan, R. Pidcock, S. Connors, J. B. R. Matthews, Y. Chen, X. Zhou, M. I. Gomis, E. Lonnoy, T. Maycock, M. Tignor, T. Waterfield (eds.)]. In Press.

-J-

- Jiménez-Valverde, A., Lobo, J.M., Hortal, J., 2008. Not as good as they seem: the importance of concepts in species distribution modelling. *Diversity and distributions* 14, 885–890.
- Johnson, C.R., 2009. Natural Length Scales of Ecological Systems: Applications at Community and Ecosystem Levels. *Ecology and Society* 14. doi:10.5751/ES-02749-140107
- Jones, A.G., Dubois, S.F., Desroy, N., Fournier, J., 2018. Interplay between abiotic factors and species assemblages mediated by the ecosystem engineer *Sabellaria alveolata* (Annelida: Polychaeta). *Estuarine, Coastal and Shelf Science* 200, 1–18. doi:10.1016/j.ecss.2017.10.001
- Jueterbock, A., Tyberghein, L., Verbruggen, H., Coyer, J.A., Olsen, J.L., Hoarau, G., 2013. Climate change impact on seaweed meadow distribution in the North Atlantic rocky intertidal. *Ecology and evolution* 3, 1356–1373.

-K-

- Kazakou, E., Violle, C., Roumet, C., Navas, M., Vile, D., Kattge, J., Garnier, E., 2014. Are trait-based species rankings consistent across data sets and spatial scales? *Journal of Vegetation Science* 25, 235–247.
- Kearney, M., 2006. Habitat, environment and niche: what are we modelling? *Oikos* 115, 186–191. <https://doi.org/10.1111/j.2006.0030-1299.14908.x>

Kearney, M., Porter, W.P., Williams, C., Ritchie, S., Hoffmann, A.A., 2009. Integrating biophysical models and evolutionary theory to predict climatic impacts on species' ranges: the dengue mosquito *Aedes aegypti* in Australia. *Functional Ecology* 23, 528–538. <https://doi.org/10.1111/j.1365-2435.2008.01538.x>

-L-

Lamanna, C., Blonder, B., Violle, C., Kraft, N.J., Sandel, B., Šímová, I., Donoghue, J.C., Svenning, J.-C., McGill, B.J., Boyle, B., 2014. Functional trait space and the latitudinal diversity gradient. *Proceedings of the National Academy of Sciences* 111, 13745–13750.

Lane, D.E., Clarke, C.M., Clarke, J.D., Mycoo, M., Gobin, J., 2015. Managing adaptation to changing climate in Coastal Zones. Baztan, J; Chouinard, O.; Jorgensen, B.; Tett, P 141–160.

Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional ecology* 16, 545–556.

Lawson, G.W., John, D.M., 1977. The marine flora of the Cap Blanc peninsula: its distribution and affinities. *Botanical Journal of the Linnean Society* 75, 99–118. <https://doi.org/10.1111/j.1095-8339.1977.tb01480.x>

Lawton, J.H., 1999. Are There General Laws in Ecology? *Oikos* 84, 177. <https://doi.org/10.2307/3546712>

Leander, B.S., Lloyd, S.A., Marshall, W., Landers, S.C., 2006. Phylogeny of marine gregarines (Apicomplexa)—Pterospira, Lithocystis and Lankesteria—and the origin (s) of coelomic parasitism. *Protist* 157, 45–60.

Leander, B.S., 2008. Marine gregarines: evolutionary prelude to the apicomplexan radiation? *Trends in Parasitology* 24, 60–67.

Le Cam, J.-B., Fournier, J., Etienne, S., Couden, J., 2011. The strength of biogenic sand reefs: Visco-elastic behaviour of cement secreted by the tube building polychaete *Sabellaria alveolata*, Linnaeus, 1767. *Estuarine, Coastal and Shelf Science* 91, 333–339. <https://doi.org/10.1016/j.ecss.2010.10.036>

Lecornu, B., Schlund, E., Basuyaux, O., Cantat, O., Dauvin, J.-C., 2016. Dynamics (from 2010–2011 to 2014) of *Sabellaria alveolata* reefs on the western coast of Cotentin (English Channel, France). *Regional studies in marine science* 8, 157–169.

Lefebvre, S., Leal, J.C.M., Dubois, S., Orvain, F., Blin, J.-L., Bataillé, M.-P., Ourry, A., Galois, R., 2009. Seasonal dynamics of trophic relationships among co-occurring suspension-feeders in two shellfish culture dominated ecosystems. *Estuarine, Coastal and Shelf Science* 82, 415–425.

Le Foll, C., Corporeau, C., Le Guen, V., Gouygou, J.-P., Berge, J.-P., Delarue, J., 2006. Long-chain n-3 polyunsaturated fatty acids dissociate phosphorylation of Akt

- from phosphatidylinositol 3'-kinase activity in rats. *AJP: Endocrinology and Metabolism* 292, E1223–E1230. <https://doi.org/10.1152/ajpendo.00446.2006>
- Lê, S., Josse, J., Husson, F., 2008. FactoMineR: An R Package for Multivariate Analysis. *Journal of Statistical Software* 25(1), 1-18. <https://doi.org/10.18637/jss.v025.i01>
- Lefebvre, S., Marín Leal, J.C., Dubois, S., Orvain, F., Blin, J.-L., Bataillé, M.-P., Ourry, A., Galois, R., 2009. Seasonal dynamics of trophic relationships among co-occurring suspension-feeders in two shellfish culture dominated ecosystems. *Estuarine, Coastal and Shelf Science* 82, 415–425. <https://doi.org/10.1016/j.ecss.2009.02.002>
- Legendre, P., Legendre, L., 2012. Numerical ecology. 3rd English ed. Developments in environmental modelling, 24. 1006 pp.
- Lenoir, J., Bertrand, R., Comte, L., Bourgeaud, L., Hattab, T., Murienne, J., Grenouillet, G., 2020. Species better track climate warming in the oceans than on land. *Nature Ecology and Evolution*. <https://doi.org/10.1038/s41559-020-1198-2>
- Lesser, M.P., 2006. Oxidative Stress in Marine Environments: Biochemistry and Physiological Ecology. *Annual Review of Physiology* 68, 253–278. <https://doi.org/10.1146/annurev.physiol.68.040104.110001>
- Lester, S.E., Gaines, S.D., Kinlan, B.P., 2007. Reproduction on the Edge: Large-scale Patterns of Individual Performance in a Marine Invertebrate. *Ecology* 88, 2229–2239. <https://doi.org/10.1890/06-1784.1>
- Levoy, F., Anthony, E.J., Monfort, O., Larssonneur, C., 2000. The morphodynamics of megatidal beaches in Normandy, France. *Marine Geology* 171, 39–59. [https://doi.org/10.1016/S0025-3227\(00\)00110-9](https://doi.org/10.1016/S0025-3227(00)00110-9)
- Lewis, J.R., 1986. Latitudinal trends in reproduction, recruitment and population characteristics of some rocky littoral molluscs and cirripedes. *Hydrobiologia* 142, 1-13.
- Lima, F.P., Queiroz, N., Ribeiro, P.A., Hawkins, S.J., Santos, A.M., 2006. Recent changes in the distribution of a marine gastropod, *Patella rustica* Linnaeus, 1758, and their relationship to unusual climatic events. *Journal of Biogeography* 33, 812–822.
- Lima, F.P., Ribeiro, P.A., Queiroz, N., Xavier, R., Tarroso, P., Hawkins, S.J., Santos, A.M., 2007. Modelling past and present geographical distribution of the marine gastropod *Patella rustica* as a tool for exploring responses to environmental change. *Global Change Biology* 13, 2065–2077. <https://doi.org/10.1111/j.1365-2486.2007.01424.x>
- Lima, F.P., Gomes, F., Seabra, R., Wethey, D.S., Seabra, M.I., Cruz, T., Santos, A.M., Hilbish, T.J., 2016. Loss of thermal refugia near equatorial range limits. *Global Change Biology* 22, 254–263. <https://doi.org/10.1111/gcb.13115>
- Lochmiller, R.L., Deerenberg, C., 2000. Trade-offs in evolutionary immunology: just what is the cost of immunity? *Oikos* 88, 87–98. <https://doi.org/10.1034/j.1600-0706.2000.880110.x>

- Lourenço, S., Roura, Á., Fernández-Reiriz, M.-J., Narciso, L., González, Á.F., 2017. Feeding Relationship between *Octopus vulgaris* (Cuvier, 1797) Early Life-Cycle Stages and Their Prey in the Western Iberian Upwelling System: Correlation of Reciprocal Lipid and Fatty Acid Contents. *Frontiers in Physiology* 8. <https://doi.org/10.3389/fphys.2017.00467>
- Lourenço, C.R., Nicastro, K.R., McQuaid, C.D., Krug, L.A., Zardi, G.I., 2020. Strong upwelling conditions drive differences in species abundance and community composition along the Atlantic coasts of Morocco and Western Sahara. *Marine Biodiversity* 50, 15. <https://doi.org/10.1007/s12526-019-01032-z>
- Lowry, O. H., Rosebrough, N. J., Farr, A. L. and Randall, R. J., 1951. Protein measurement with the Folin phenol reagent. *The Journal of Biological Chemistry* 193, 265-75.
- Lucas, A., Beninger, P.G., 1985. The use of physiological condition indices in marine bivalve aquaculture. *Aquaculture* 44, 187–200. [https://doi.org/10.1016/0044-8486\(85\)90243-1](https://doi.org/10.1016/0044-8486(85)90243-1)

-M-

- Martínez, B., Viejo, R.M., Carreño, F., Aranda, S.C., 2012. Habitat distribution models for intertidal seaweeds: responses to climatic and non-climatic drivers. *Journal of biogeography* 39, 1877–1890.
- Marty, Y., Delaunay, F., Moal, J., Samain, J.-F., 1992. Changes in the fatty acid composition of *Pecten maximus* (L.) during larval development. *Journal of Experimental Marine Biology and Ecology* 163, 221–234. [https://doi.org/10.1016/0022-0981\(92\)90051-B](https://doi.org/10.1016/0022-0981(92)90051-B)
- Marshall, D.J., Keough, M.J., 2007. The Evolutionary Ecology of Offspring Size in Marine Invertebrates, in: *Advances in Marine Biology*. Elsevier, pp. 1–60. [https://doi.org/10.1016/S0065-2881\(07\)53001-4](https://doi.org/10.1016/S0065-2881(07)53001-4)
- Masuda, R., 2003. The critical role of docosahexaenoic acid in marine and terrestrial ecosystems: from bacteria to human behavior, in: *The Big Fish Bang. Proceedings of the 26th Annual Larval Fish Conference*. Howard I. Browman & Anne Berit Skiftesvik, Os, Norway, pp. 249–256.
- McCarthy, D., Young, C., Emson, R., 2003. Influence of wave-induced disturbance on seasonal spawning patterns in the sabellariid polychaete *Phragmatopoma lapidosa*. *Marine Ecology Progress Series* 256, 123–133. <https://doi.org/10.3354/meps256123>
- McGill, B.J., Enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution* 21, 178–185.
- McGill, B.J., 2019. The what, how and why of doing macroecology. *Global Ecology and Biogeography* 28, 6–17. <https://doi.org/10.1111/geb.12855>

- Meinshausen, M., Smith, S.J., Calvin, K., Daniel, J.S., Kainuma, M., Lamarque, J.-F., Matsumoto, K., Montzka, S., Raper, S., Riahi, K., 2011. The RCP greenhouse gas concentrations and their extensions from 1765 to 2300. *Climatic change* 109, 213.
- Melo-Merino, S.M., Reyes-Bonilla, H., Lira-Noriega, A., 2020. Ecological niche models and species distribution models in marine environments: A literature review and spatial analysis of evidence. *Ecological Modelling* 415, 108837. <https://doi.org/10.1016/j.ecolmodel.2019.108837>
- Menge, B. A. and A. M. Olson. 1990. Role of scale and environmental factors in regulation of community structure. *Trends in Ecology and Evolution* 5:52–57.
- MERC, 2013. Survey of Wicklow Reef SAC (Site code 0002274). Produced by MERC on behalf of the Marine Institute in partnership with National Parks & Wildlife Service.
- Merder, J., Freund, J.A., Meysick, L., Simkanin, C., O’Riordan, R.M., Power, A.M., 2018. East-west spatial groupings in intertidal communities, environmental drivers and key species. *Journal of the Marine Biological Association of the UK* 98, 423–435. <https://doi.org/10.1017/S0025315416001442>
- Messier, J., McGill, B.J., Lechowicz, M.J., 2010. How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters* 13, 838–848. <https://doi.org/10.1111/j.1461-0248.2010.01476.x>
- Metcalfe, L.D., Schmitz, A.A., 1961. The Rapid Preparation of Fatty Acid Esters for Gas Chromatographic Analysis. *Analytical Chemistry* 33, 363–364. <https://doi.org/10.1021/ac60171a016>
- Mieszkowska, N., Leaper, R., Moore, P., Kendall, MA., Burrows, MT., Lear, D., Poloczanska, ES., Hiscock, K., Moschella, P., Thompson, RC., Herbert, RJH., Laffoley, D., Baxter, J., Southward, AJ., Hawkins, SJ., 2006 Marine biodiversity and climate change: assessing and predicting the influence of climatic change using intertidal rocky shore biota. Occasional Publication of the Marine Biological Association 20. Plymouth (UK), Marine Biological Association of the United Kingdom, 202pp.
- Mieszkowska, N., Hawkins, S., Burrows, M., Kendall, M., 2007. Long-term changes in the geographic distribution and population structures of *Osilinus lineatus* (Gastropoda: Trochidae) in Britain and Ireland. *Journal of the Marine Biological Association of the United Kingdom* 87, 537–545.
- Mieszkowska, N., Sugden, H., Firth, L., Hawkins, S., 2014. The role of sustained observations in tracking impacts of environmental change on marine biodiversity and ecosystems. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* 372, 20130339.
- Miller, D.C., Geider, R.J. and MacIntyre, H.L., 1996. Microphytobenthos: the ecological role of the “secret garden” of unvegetated, shallow-water marine habitats. II. Role in sediment stability and shallow-water food webs. *Estuaries*, 19(2), 202–212.

- Miller, J., 2010. Species Distribution Modeling: Species distribution modeling. *Geography Compass* 4, 490–509. <https://doi.org/10.1111/j.1749-8198.2010.00351.x>
- Mislan, K.A.S., Wethey, D.S., Helmuth, B., 2009. When to worry about the weather: role of tidal cycle in determining patterns of risk in intertidal ecosystems. *Global Change Biology* 15, 3056–3065. <https://doi.org/10.1111/j.1365-2486.2009.01936.x>
- Molinos, J.G., 2020. Global marine warming in a new dimension. *Nature Ecology & Evolution* 4, 16–17.
- Montoya, D., Purves, D.W., Urbieto, I.R., Zavala, M.A., 2009. Do species distribution models explain spatial structure within tree species ranges? *Global Ecology and Biogeography* 18, 662–673.
- Moran, A.L., McAlister, J.S., 2009. Egg Size as a Life History Character of Marine Invertebrates: Is It All It's Cracked Up to Be? *The Biological Bulletin* 216, 226–242. <https://doi.org/10.1086/BBLv216n3p226>
- Moran, E.V., Hartig, F., Bell, D.M., 2016. Intraspecific trait variation across scales: implications for understanding global change responses. *Global Change Biology* 22, 137–150. <https://doi.org/10.1111/gcb.13000>
- Morim, J., Hemer, M., Wang, X.L., Cartwright, N., Trenham, C., Semedo, A., Young, I., Bricheno, L., Camus, P., Casas-Prat, M., Erikson, L., Mentaschi, L., Mori, N., Shimura, T., Timmermans, B., Aarnes, O., Breivik, Ø., Behrens, A., Dobrynin, M., Menendez, M., Staneva, J., Wehner, M., Wolf, J., Kamranzad, B., Webb, A., Stopa, J., Andutta, F., 2019. Robustness and uncertainties in global multivariate wind-wave climate projections. *Nature Climate Change* 9, 711–718. <https://doi.org/10.1038/s41558-019-0542-5>
- Morin, X., Lechowicz, M.J., 2008. Contemporary perspectives on the niche that can improve models of species range shifts under climate change. *Biology Letters* 4, 573–576. <https://doi.org/10.1098/rsbl.2008.0181>
- Morley, S.A., Hirse, T., Pörtner, H.-O., Peck, L.S., 2009. Geographical variation in thermal tolerance within Southern Ocean marine ectotherms. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 153, 154–161. <https://doi.org/10.1016/j.cbpa.2009.02.001>
- Morrison, W. R. and Smith, L. M., 1964. Preparation of fatty acid methyl esters and dimethylacetals from lipids with boron fluoride-methanol. *Journal of Lipid Research* 5, 600-8.
- Mouillot, D., Graham, N.A., Villéger, S., Mason, N.W., Bellwood, D.R., 2013. A functional approach reveals community responses to disturbances. *Trends in Ecology and Evolution* 28, 167–177.

- Moyes, C.D., 2003. Controlling muscle mitochondrial content. *Journal of Experimental Biology* 206, 4385–4391. <https://doi.org/10.1242/jeb.00699>
- Muir, A.P., Nunes, F.L.D., Dubois, S.F., Pernet, F., 2016. Lipid remodelling in the reef-building honeycomb worm, *Sabellaria alveolata*, reflects acclimation and local adaptation to temperature. *Scientific Reports* 6, 35669. doi:10.1038/srep35669
- Muir, A.P., Dubois, S.F., Ross, R.E., Firth, L.B., Knights, A.M., Lima, F.P., Seabra, R., Corre, E., Corguillé, G.L., Nunes, F.L.D., 2020. Seascape genomics reveals population isolation in the reef-building honeycomb worm, *Sabellaria alveolata* (L.) (preprint). In Review. <https://doi.org/10.21203/rs.2.11848/v2>

-N-

- Naimi, B., 2015. usdm: Uncertainty analysis for species distribution models. R package version 1, 1–12.
- Naimi, B., Araújo, M.B., 2016. sdm: a reproducible and extensible R platform for species distribution modelling. *Ecography* 39, 368–375. <https://doi.org/10.1111/ecog.01881>
- Naylor, L.A., Viles, H.A., 2000. A temperate reef builder: an evaluation of the growth, morphology and composition of *Sabellaria alveolata* (L.) colonies on carbonate platforms in South Wales. Geological Society, London, Special Publications 178, 9–19.
- Neiva, J., Assis, J., Fernandes, F., Pearson, G.A., Serrão, E.A., 2014. Species distribution models and mitochondrial DNA phylogeography suggest an extensive biogeographical shift in the high-intertidal seaweed *Pelvetia canaliculata*. *Journal of Biogeography* 41, 1137–1148. <https://doi.org/10.1111/jbi.12278>
- Nicolle, A., Moitié, R., Ogor, J., Dumas, F., Foveau, A., Foucher, E., Thiébaud, E., 2017. Modelling larval dispersal of *Pecten maximus* in the English Channel: a tool for the spatial management of the stocks. *ICES Journal of Marine Science* 74, 1812–1825. <https://doi.org/10.1093/icesjms/fsw207>
- Noernberg, M.A., Fournier, J., Dubois, S., Populus, J., 2010. Using airborne laser altimetry to estimate *Sabellaria alveolata* (Polychaeta: Sabellariidae) reefs volume in tidal flat environments. *Estuarine, Coastal and Shelf Science* 90, 93–102. <https://doi.org/10.1016/j.ecss.2010.07.014>
- Novikoff, A. B., 1939. Surface changes in unfertilized and fertilized eggs of *Sabellaria vulgaris*. *Journal of Experimental Zoology*, 82(2), 217-237.
- NPWS, 2013. Wicklow Reef SAC (Site code 0002274): Conservation objectives supporting document – 9p. <https://www.npws.ie/protected-sites/sac/002274>

-O-

- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2018. vegan: Community Ecology Package. R package version 2.5-3. <https://CRAN.R-project.org/package=vegan>
- Oliver, E.C.J., Burrows, M.T., Donat, M.G., Sen Gupta, A., Alexander, L.V., Perkins-Kirkpatrick, S.E., Benthuyesen, J.A., Hobday, A.J., Holbrook, N.J., Moore, P.J., Thomsen, M.S., Wernberg, T., Smale, D.A., 2019. Projected Marine Heatwaves in the 21st Century and the Potential for Ecological Impact. *Frontiers in Marine Science* 6, 734. <https://doi.org/10.3389/fmars.2019.00734>
- Olofsson, H., Ripa, J., Jonzén, N., 2009. Bet-hedging as an evolutionary game: the trade-off between egg size and number. *Proceedings of the Royal Society B: Biological Sciences* 276, 2963–2969. <https://doi.org/10.1098/rspb.2009.0500>
- Orton, J.H., 1933. Summer Mortality of Cockles on some Lancashire and Cheshire Dee Beds in 1933. *Nature* 132, 314–315. <https://doi.org/10.1038/132314a0>
- Osada, M., Nishikawa, M., Nomura, T., 1989. Involvement of prostaglandins in the spawning of the scallop, *Patinopecten yessoensis*. *Comparative Biochemistry and Physiology. C: Comparative Pharmacology* 94, 595–601.
- Osovitz, C.J., Hofmann, G.E., 2007. Marine macrophysiology: Studying physiological variation across large spatial scales in marine systems. *Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology* 147, 821–827. <https://doi.org/10.1016/j.cbpa.2007.02.012>

-P-

- Paine, R.T., 1974. Intertidal community structure. *Oecologia* 15, 93–120. <https://doi.org/10.1007/BF00345739>
- Palkovacs, E.P., Kinnison, M.T., Correa, C., Dalton, C.M., Hendry, A.P., 2012. Fates beyond traits: ecological consequences of human-induced trait change: Fates beyond traits. *Evolutionary Applications* 5, 183–191. <https://doi.org/10.1111/j.1752-4571.2011.00212.x>
- Palmer, M.A., Zedler, J.B., Falk, D.A., Holl, K., 2016. *Foundations of Restoration Ecology*.
- Pansch, A., Winde, V., Asmus, R., Asmus, H., 2016. Tidal benthic mesocosms simulating future climate change scenarios in the field of marine ecology: Marine benthic mesocosm facility sylt. *Limnology and Oceanography: Methods* 14, 257–267. <https://doi.org/10.1002/lom3.10086>

- Pasteels, J.J., 1965. Etude au microscope électronique de la réaction corticale. II. La réaction corticale de l'oeuf vierge de *Sabellaria alveolata*. *Journal of Embryology and Experimental Morphology* 13, 327–339.
- Pawlik, J.R., 1986. Chemical induction of larval settlement and metamorphosis in the reef-building tube worm *Phragmatopoma californica* (Sabellariidae: Polychaeta). *Marine Biology* 91, 59–68. <https://doi.org/10.1007/BF00397571>
- Pawlik, J.R., 1988. Larval settlement and metamorphosis of two gregarious sabellariid polychaetes: *Sabellaria alveolata* compared with *Phragmatopoma californica*. *Journal of the Marine Biological Association of the United Kingdom* 68, 101–124.
- Peaucellier, G., Dorée, M., Picard, A., 1984. Rise and fall of protein phosphorylation during meiotic maturation in oocytes of *Sabellaria alveolata* (polychaete annelid). *Developmental biology* 106, 267–274.
- Pearson, R.G., Dawson, T.P., 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* 12, 361–371. <https://doi.org/10.1046/j.1466-822X.2003.00042.x>
- Peres-Neto, P.R., Legendre, P., Dray, S., Borcard, D., 2006. Variation Partitioning of Species Data Matrices: Estimation and Comparison of Fractions. *Ecology* 87, 2614–2625. [https://doi.org/10.1890/0012-9658\(2006\)87\[2614:VPOSDM\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[2614:VPOSDM]2.0.CO;2)
- Pernet, B., Jaekle, W.B., 2004. Size and Organic Content of Eggs of Marine Annelids, and the Underestimation of Egg Energy Content by Dichromate Oxidation. *The Biological Bulletin* 207, 67–71. <https://doi.org/10.2307/1543629>
- Pernet, F., Tremblay, R., Comeau, L., Guderley, H., 2007. Temperature adaptation in two bivalve species from different thermal habitats: energetics and remodelling of membrane lipids. *Journal of Experimental Biology* 210, 2999–3014. <https://doi.org/10.1242/jeb.006007>
- Pernet, F., Lagarde, F., Jeannée, N., Daigle, G., Barret, J., Le Gall, P., Quere, C., D'orbcastel, E.R., 2014. Spatial and Temporal Dynamics of Mass Mortalities in Oysters Is Influenced by Energetic Reserves and Food Quality. *PLoS ONE* 9, e88469. <https://doi.org/10.1371/journal.pone.0088469>
- Pernet, F., 2016. Lipides marins et fonctionnement des écosystèmes et des organismes . HDR.
- Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura, M., Araújo, M.B., 2011. *Ecological Niches and Geographic Distributions*. Princeton University Press.
- Peterson, A.T., Soberón, J., 2012. Species distribution modeling and ecological niche modeling: getting the concepts right. *Natureza & Conservação* 10, 102–107.
- Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190, 231–259. <https://doi.org/10.1016/j.ecolmodel.2005.03.026>

- Phillips, S.J., Dudík, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31, 161–175.
- Pineda, M.C., McQuaid, C.D., Turon, X., López-Legentil, S., Ordóñez, V., Rius, M., 2012. Tough Adults, Frail Babies: An Analysis of Stress Sensitivity across Early Life-History Stages of Widely Introduced Marine Invertebrates. *PLoS ONE* 7, e46672. <https://doi.org/10.1371/journal.pone.0046672>
- Pinsky, M.L., Eikeset, A.M., McCauley, D.J., Payne, J.L., Sunday, J.M., 2019. Greater vulnerability to warming of marine versus terrestrial ectotherms. *Nature* 569, 108–111.
- Pinsky, M.L., Selden, R.L., Kitchel, Z.J., 2020. Climate-Driven Shifts in Marine Species Ranges: Scaling from Organisms to Communities. *Annual Review of Marine Science* 12, 153–179. <https://doi.org/10.1146/annurev-marine-010419-010916>
- Plicanti, A., Domínguez, R., Dubois, S.F., Bertocci, I., 2016. Human impacts on biogenic habitats: Effects of experimental trampling on *Sabellaria alveolata* (Linnaeus, 1767) reefs. *Journal of Experimental Marine Biology and Ecology* 478, 34–44. <https://doi.org/10.1016/j.jembe.2016.02.001>
- Plicanti, A., Iacofano, D., Bertocci, I., Brutto, S.L., 2017. The amphipod assemblages of *Sabellaria alveolata* reefs from the NW coast of Portugal: An account of the present knowledge, new records, and some biogeographic considerations. *Marine Biodiversity* 47, 521–534. <https://doi.org/10.1007/s12526-016-0474-5>
- Poloczanska, E.S., Brown, C.J., Sydeman, W.J., Kiessling, W., Schoeman, D.S., Moore, P.J., Brander, K., Bruno, J.F., Buckley, L.B., Burrows, M.T., 2013. Global imprint of climate change on marine life. *Nature Climate Change* 3, 919–925.
- Porras, R., Bataller, J.V., Murgui, E., Torregrosa, M.T., 1996. Trophic Structure and Community Composition of Polychaetes Inhabiting Some *Sabellaria alveolata* (L.) Reefs Along the Valencia Gulf Coast, Western Mediterranean. *Marine Ecology* 17, 583–602. <https://doi.org/10.1111/j.1439-0485.1996.tb00419.x>

-R-

- Racault, M.-F., Le Quéré, C., Buitenhuis, E., Sathyendranath, S., Platt, T., 2012. Phytoplankton phenology in the global ocean. *Ecological Indicators* 14, 152–163. <https://doi.org/10.1016/j.ecolind.2011.07.010>
- Raffaelli, D. and Hawkins, S.J., 2012. *Intertidal ecology*. Springer Science & Business Media.
- Rahman, M.A., Henderson, S., Miller-Ezzy, P., Li, X.X., Qin, J.G., 2019. Immune response to temperature stress in three bivalve species: Pacific oyster *Crassostrea gigas*, Mediterranean mussel *Mytilus galloprovincialis* and mud cockle *Katylsia rhytiphora*. *Fish & Shellfish Immunology* 86, 868–874. <https://doi.org/10.1016/j.fsi.2018.12.017>

- Ramirez-Llodra, E., 2002. Fecundity and life-history strategies in marine invertebrates, in: *Advances in Marine Biology*. Elsevier, pp. 87–170. [https://doi.org/10.1016/S0065-2881\(02\)43004-0](https://doi.org/10.1016/S0065-2881(02)43004-0)
- Rao, C.R., 1964. The use and interpretation of principal component analysis in applied research. *Sankhyā: The Indian Journal of Statistics, Series A*, pp.329–358.
- R Core Team 2018. R: A language and environment for statistical computing (R version 3.5.1). R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- R Core Team 2019. R: A language and environment for statistical computing (R version 3.6.1). R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Reise, K., 1982. Long-term changes in the macrobenthic invertebrate fauna of the Wadden Sea: Are polychaetes about to take over? *Netherlands Journal of Sea Research* 16, 29–36. [https://doi.org/10.1016/0077-7579\(82\)90014-X](https://doi.org/10.1016/0077-7579(82)90014-X)
- Reise, K., 1991. Mosaic Cycles in the Marine Benthos, in: Remmert, H. (Ed.), *The Mosaic-Cycle Concept of Ecosystems*. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 61–82. https://doi.org/10.1007/978-3-642-75650-4_4
- Reiss, H., Cunze, S., König, K., Neumann, H., Kröncke, I., 2011. Species distribution modelling of marine benthos: a North Sea case study. *Marine Ecology Progress Series* 442, 71–86.
- Richter, R., 1927. “Sandkorallen” - Riffe in der Nordsee. *Natur und Museum* 57, 49–62.
- Ricketts, E.F., Calvin, J., Hedgpeth, J.W., Phillips, D.W., 1985. *Between pacific tides*. Stanford University Press.
- Ridley, M., 2004. *Evolution*, 3rd ed. ed. Blackwell Publishers, Malden, MA.
- Rivadeneira, M.M., Hernáez, P., Antonio Baeza, J., Boltaña, S., Cifuentes, M., Correa, C., Cuevas, A., del Valle, E., Hinojosa, I., Ulrich, N., Valdivia, N., Vásquez, N., Zander, A., Thiel, M., 2010. Testing the abundant-centre hypothesis using intertidal porcelain crabs along the Chilean coast: linking abundance and life-history variation. *Journal of Biogeography* 37, 486–498. <https://doi.org/10.1111/j.1365-2699.2009.02224.x>
- Rivest, E.B., Hofmann, G.E., 2014. Responses of the Metabolism of the Larvae of *Pocillopora damicornis* to Ocean Acidification and Warming. *PLoS ONE* 9, e96172. <https://doi.org/10.1371/journal.pone.0096172>
- Rivest, E.B., Chen, C.-S., Fan, T.-Y., Li, H.-H., Hofmann, G.E., 2017. Lipid consumption in coral larvae differs among sites: a consideration of environmental history in a global ocean change scenario. *Proceedings of the Royal Society B: Biological Sciences* 284, 20162825. <https://doi.org/10.1098/rspb.2016.2825>
- Robert, P., Escoufier, Y., 1976. A unifying tool for linear multivariate statistical methods: The RV-coefficient. *Journal of the Royal Statistical Society. Series C (Applied Statistics)*, 25(3), 257–265. <https://doi.org/10.2307/2347233>

- Robinson, L.M., Elith, J., Hobday, A.J., Pearson, R.G., Kendall, B.E., Possingham, H.P., Richardson, A.J., 2011. Pushing the limits in marine species distribution modelling: lessons from the land present challenges and opportunities: Marine species distribution models. *Global Ecology and Biogeography* 20, 789–802. <https://doi.org/10.1111/j.1466-8238.2010.00636.x>
- Robinson, L.M., Hobday, A.J., Possingham, H.P., Richardson, A.J., 2015. Trailing edges projected to move faster than leading edges for large pelagic fish habitats under climate change. *Deep Sea Research Part II: Topical Studies in Oceanography* 113, 225–234. <https://doi.org/10.1016/j.dsr2.2014.04.007>
- S-**
- Safriel, U.N., Volis, S., Kark, S., 1994. Core and peripheral populations and global climate change. *Israel Journal of Plant Sciences* 42, 331–345. <https://doi.org/10.1080/07929978.1994.10676584>
- Sagarin, R.D., Barry, J.P., Gilman, S.E., Baxter, C.H., 1999. Climate-related change in an intertidal community over short and long time scales. *Ecological Monographs* 69, 465–490. [https://doi.org/10.1890/0012-9615\(1999\)069\[0465:CRCIAI\]2.0.CO;2](https://doi.org/10.1890/0012-9615(1999)069[0465:CRCIAI]2.0.CO;2)
- Sagarin, R.D., Gaines, S.D., 2002. Geographical abundance distributions of coastal invertebrates: using one-dimensional ranges to test biogeographic hypotheses. *Journal of Biogeography* 29, 985–997. <https://doi.org/10.1046/j.1365-2699.2002.00705.x>
- Sagarin, R.D., Somero, G.N., 2006. Complex patterns of expression of heat-shock protein 70 across the southern biogeographical ranges of the intertidal mussel *Mytilus californianus* and snail *Nucella ostrina*. *Journal of Biogeography* 33, 622–630. <https://doi.org/10.1111/j.1365-2699.2005.01403.x>
- Salomon, J.-C., Breton, M., 1993. An atlas of long-term currents in the Channel. *Oceanologica Acta* 16, 439–448.
- Sanders, B.M., 1993. Stress proteins in aquatic organisms: an environmental perspective. *Critical reviews in toxicology* 23, 49–75.
- Sanderson, W.G., 1996. Rarity of marine benthic species in Great Britain: development and application of assessment criteria. *Aquatic Conservation: Marine and Freshwater Ecosystems* 6, 245–256.
- Sanfilippo, R., Rosso, A., Mastandrea, A., Viola, A., Deias, C., Guido, A., 2019. *Sabellaria alveolata* sandcastle worm from the Mediterranean Sea: new insights on tube architecture and biocement. *Journal of Morphology* 280, 1839–1849. <https://doi.org/10.1002/jmor.21069>
- Sanford, E., 2014. The biogeography of marine communities. *Marine community ecology and conservation* 131–163.

- Sarà, G., Palmeri, V., Rinaldi, A., Montalto, V., Helmuth, B., 2013. Predicting biological invasions in marine habitats through eco-physiological mechanistic models: a case study with the bivalve *Brachidontes pharaonis*. *Diversity and Distributions*. 19, 1235–1247. <https://doi.org/10.1111/ddi.12074>
- Saulquin, B., Gohin, F., Garrello, R., 2011. Regional Objective Analysis for Merging High-Resolution MERIS, MODIS/Aqua, and SeaWiFS Chlorophyll- a Data From 1998 to 2008 on the European Atlantic Shelf. *IEEE Transactions on Geoscience and Remote Sensing* 49, 143–154. <https://doi.org/10.1109/TGRS.2010.2052813>
- Savigny, J.-C., 1830. Système des Annélides, principalement de celles des côtes de l’Egypte et de la Syrie, offrant les caractères tant distinctifs que naturels des ordres, familles et genres, avec la description des espèces., in: Description de l’Egypte, recueil des observations et des recherches qui ont été faites pendant l’expédition de l’armée française. impr. de C.-L.-F. Panckoucke, Paris, pp. 325–472.
- Scheer, B.T., 1969. Carbohydrates and carbohydrate metabolism: Annelida, Sipuncula, Echiura. *Chemical zoology*, 4.
- Schimmenti, E., Musco, L., Lo Brutto S., Mikac, B., Nygren, A., Badalamenti, F., 2015 « A Mediterranean Record of *Eulalia Ornata* (Annelida: Phyllodocidae) Corroborating Its Fidelity Link with the *Sabellaria Alveolata*-Reef Habitat ». *Mediterranean Marine Science* 17(2): 359-70.
- Schlegel, R., Smit, A., 2018. heatwaveR: A central algorithm for the detection of heatwaves and cold-spells. *Journal of Open Source Software* 3(27): 821. <https://doi.org/10.21105/joss.00821>
- Schlund, E., Basuyaux, O., Lecornu, B., Pezy, J.-P., Baffreau, A., Dauvin, J.-C., 2016. Macrofauna associated with temporary *Sabellaria alveolata* reefs on the west coast of Cotentin (France). *SpringerPlus* 5, 1260.
- Schwenk, K., Padilla, D.K., Bakken, G.S., Full, R.J., 2009. Grand challenges in organismal biology. *Integrative and Comparative Biology* 49, 7–14. <https://doi.org/10.1093/icb/icp034>
- Seabra, R., Wethey, D.S., Santos, A.M., Lima, F.P., 2011. Side matters: Microhabitat influence on intertidal heat stress over a large geographical scale. *Journal of Experimental Marine Biology and Ecology* 400, 200–208. <https://doi.org/10.1016/j.jembe.2011.02.010>
- Seabra, R., Varela, R., Santos, A.M., Gómez-Gesteira, M., Meneghesso, C., Wethey, D.S., Lima, F.P., 2019. Reduced Nearshore Warming Associated With Eastern Boundary Upwelling Systems. *Frontiers in Marine Science* 6, 104. <https://doi.org/10.3389/fmars.2019.00104>
- Seers, B. 2018. fetchR: Calculate Wind Fetch. R package version 2.1-1. <https://CRAN.R-project.org/package=fetchR>

- Shaw, R.G., 2019. From the past to the future: considering the value and limits of evolutionary prediction. *The American Naturalist* 193, 1–10.
- Sheehan, E.V., Bridger, D., Attrill, M.J., 2015. The ecosystem service value of living versus dead biogenic reef. *Estuarine, Coastal and Shelf Science* 154, 248–254. <https://doi.org/10.1016/j.ecss.2014.12.042>
- Siems, D.P. and Sikes, R.S., 1998. Tradeoffs between growth and reproduction in response to temporal variation in food supply. *Environmental Biology of Fishes*, 53(3), 319–329.
- Sieracki, C., Sieracki, M., Yentsch, C., 1998. An imaging-in-flow system for automated analysis of marine microplankton. *Marine Ecology Progress Series* 168, 285–296. <https://doi.org/10.3354/meps168285>
- Simkanin, C., Dower, J.F., Filip, N., Jamieson, G., Therriault, T.W., 2013. Biotic resistance to the infiltration of natural benthic habitats: Examining the role of predation in the distribution of the invasive ascidian *Botrylloides violaceus*. *Journal of Experimental Marine Biology and Ecology* 439, 76–83. <https://doi.org/10.1016/j.jembe.2012.10.004>
- Simpson, J., Edelsten, D., Edwards, A., Morris, N., Tett, P., 1979. The Islay front: physical structure and phytoplankton distribution. *Estuarine and Coastal Marine Science* 9, 713–IN1.
- Smale, D.A., Wernberg, T., Yunnice, A.L., Vance, T., 2015. The rise of *Laminaria ochroleuca* in the Western English Channel (UK) and comparisons with its competitor and assemblage dominant *Laminaria hyperborea*. *Marine ecology* 36, 1033–1044.
- Soberón, J. and Peterson, A. T. 2005. Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics* 2: 1–10.
- Sorte, C., Hofmann, G., 2004. Changes in latitudes, changes in aptitudes: *Nucella canaliculata* (Mollusca: Gastropoda) is more stressed at its range edge. *Marine Ecology Progress Series* 274, 263–268. <https://doi.org/10.3354/meps274263>
- Soudant, P., Marty, Y., Moal, J., Masski, H., Jean François Samain, 1998. Fatty acid composition of polar lipid classes during larval development of scallop *Pecten maximus* (L.). *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 121, 279–288. [https://doi.org/10.1016/S1095-6433\(98\)10130-7](https://doi.org/10.1016/S1095-6433(98)10130-7)
- Soudant, P., Van Ryckeghem, K., Marty, Y., Moal, J., Samain, J.F., Sorgeloos, P., 1999. Comparison of the lipid class and fatty acid composition between a reproductive cycle in nature and a standard hatchery conditioning of the Pacific Oyster *Crassostrea gigas*. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology* 123, 209–222. [https://doi.org/10.1016/S0305-0491\(99\)00063-2](https://doi.org/10.1016/S0305-0491(99)00063-2)
- Sourie, R., 1954. Contribution à l'étude écologique des côtes rocheuses du Sénégal, Mémoires de l'Institut français d'Afrique noire. IFAN, Dakar.

- Southward, A.J., Hawkins, S.J., Burrows, M.T., 1995. Seventy years' observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. *Journal of Thermal Biology* 20, 127–155. [https://doi.org/10.1016/0306-4565\(94\)00043-1](https://doi.org/10.1016/0306-4565(94)00043-1)
- Stanley, D.W., Howard, R.W., 1998. The biology of prostaglandins and related eicosanoids in invertebrates: cellular, organismal and ecological actions. *American zoologist* 38, 369–381.
- Stark, J., Lehman, R., Crawford, L., Enquist, B.J., Blonder, B., 2017. Does environmental heterogeneity drive functional trait variation? A test in montane and alpine meadows. *Oikos* 126, 1650–1659. <https://doi.org/10.1111/oik.04311>
- Stearns, S.C., 1992. The evolution of life histories (No. 575 S81).
- Stein, A., Gerstner, K., Kreft, H., 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters* 17, 866–880. <https://doi.org/10.1111/ele.12277>
- Stillman, J.H., Tagmount, A., 2009. Seasonal and latitudinal acclimatisation of cardiac transcriptome responses to thermal stress in porcelain crabs, *Petrolisthes cinctipes*. *Molecular ecology* 18, 4206–4226.
- Stone, R., Callaway, R., Bull, J.C., 2019. Are biodiversity offsetting targets of ecological equivalence feasible for biogenic reef habitats? *Ocean & Coastal Management* 177, 97–111. <https://doi.org/10.1016/j.ocecoaman.2019.04.003>
- Straub, S.C., Wernberg, T., Thomsen, M.S., Moore, P.J., Burrows, M.T., Harvey, B.P., Smale, D.A., 2019. Resistance, Extinction, and Everything in Between – The Diverse Responses of Seaweeds to Marine Heatwaves. *Frontiers in Marine Science* 6, 763. <https://doi.org/10.3389/fmars.2019.00763>
- Stuart-Smith, R.D., Edgar, G.J., Barrett, N.S., Kininmonth, S.J., Bates, A.E., 2015. Thermal biases and vulnerability to warming in the world's marine fauna. *Nature* 528, 88–92. <https://doi.org/10.1038/nature16144>
- Sunday, J.M., Bates, A.E., Dulvy, N.K., 2012. Thermal tolerance and the global redistribution of animals. *Nature Climate Change* 2, 686–690.
- Swetnam, T.W., Allen, C.D., Betancourt, J.L., 1999. Applied historical ecology: using the past to manage for the future. *Ecological Applications* 9, 1189–1206. [https://doi.org/10.1890/1051-0761\(1999\)009\[1189:AHEUTP\]2.0.CO;2](https://doi.org/10.1890/1051-0761(1999)009[1189:AHEUTP]2.0.CO;2)

- Talluto, M.V., Boulangeat, I., Ameztegui, A., Aubin, I., Berteaux, D., Butler, A., Doyon, F., Drever, C.R., Fortin, M.-J., Franceschini, T., Liénard, J., McKenney, D., Solarik, K.A., Strigul, N., Thuiller, W., Gravel, D., 2016. Cross-scale integration of knowledge for predicting species ranges: a metamodelling framework: Integrated models of species ranges. *Global Ecology and Biogeography* 25, 238–249. <https://doi.org/10.1111/geb.12395>
- Tessier, B., 1993. Upper intertidal rhythmites in the Mont-Saint-Michel Bay (NW France): perspectives for paleoreconstruction. *Marine Geology* 110, 355–367.
- Tewksbury, J.J., Huey, R.B., Deutsch, C.A., 2008. Ecology: Putting the Heat on Tropical Animals. *Science* 320, 1296–1297. <https://doi.org/10.1126/science.1159328>
- Tolman, H., 2009. User manual and system documentation of WAVEWATCH III-version 3.14 (Tech. rep.): NOAA / NWS / NCEP / MMAB Technical Note-276.
- Tremblay, R., Olivier, F., Bourget, E., Rittschof, D., 2007. Physiological condition of *Balanus amphitrite* cyprid larvae determines habitat selection success. *Marine Ecology Progress Series* 340, 1–8.
- Treurnicht, M., Pagel, J., Tonnabel, J., Esler, K.J., Slingsby, J.A., Schurr, F.M., 2020. Functional traits explain the Hutchinsonian niches of plant species. *Global Ecology and Biogeography* 29, 534–545. <https://doi.org/10.1111/geb.13048>
- Trnka, M., Rötter, R.P., Ruiz-Ramos, M., Kersebaum, K.C., Olesen, J.E., Žalud, Z., Semenov, M.A., 2014. Adverse weather conditions for European wheat production will become more frequent with climate change. *Nature Climate Change* 4, 637–643. <https://doi.org/10.1038/nclimate2242>
- Turner, J.A., Babcock, R.C., Kendrick, G.A., Hovey, R.K., 2019. How does spatial resolution affect model performance? A case for ensemble approaches for marine benthic mesophotic communities. *Journal of Biogeography* 46, 1249–1259. <https://doi.org/10.1111/jbi.13581>
- Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F., De Clerck, O., 2012. Bio-ORACLE: a global environmental dataset for marine species distribution modelling: Bio-ORACLE marine environmental data rasters. *Global Ecology and Biogeography* 21, 272–281. <https://doi.org/10.1111/j.1466-8238.2011.00656.x>

-U-

- University Of North Wales, Bangor., 2018. 1778-1998 Ivor Rees North Wales Marine Fauna Ad-hoc sightings shore and ship-based surveys. <https://doi.org/10.17031/35PRLF>
- Urian, A.G., Hatle, J.D., Gilg, M.R., 2011. Thermal constraints for range expansion of the invasive green mussel, *Perna viridis*, in the southeastern United States. *Journal of Experimental Zoology* 315A, 12–21. <https://doi.org/10.1002/jez.644>

-V-

- Vandermeer, J.H., 1972. Niche Theory. *Annual Review of Ecology and Systematics* 3, 107–132.
- Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional! *Oikos* 116, 882–892. <https://doi.org/10.1111/j.0030-1299.2007.15559.x>
- Violle, C., Jiang, L., 2009. Towards a trait-based quantification of species niche. *Journal of Plant Ecology* 2, 87–93. <https://doi.org/10.1093/jpe/rtp007>
- Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C., Jung, V., Messier, J., 2012. The return of the variance: intraspecific variability in community ecology. *Trends in Ecology & Evolution* 27, 244–252. <https://doi.org/10.1016/j.tree.2011.11.014>
- Violle, C., Reich, P.B., Pacala, S.W., Enquist, B.J., Kattge, J., 2014. The emergence and promise of functional biogeography. *Proceedings of the National Academy of Sciences* 111, 13690–13696.

-W-

- Waldvogel, A.-M., Feldmeyer, B., Rolshausen, G., Exposito-Alonso, M., Rellstab, C., Kofler, R., Mock, T., Schmid, K., Schmitt, I., Bataillon, T., Savolainen, O., Bergland, A., Flatt, T., Guillaume, F., Pfenninger, M., 2020. Evolutionary genomics can improve prediction of species' responses to climate change. *Evolution Letters* 4, 4–18. <https://doi.org/10.1002/evl3.154>
- Wallingford, P.D., Morelli, T.L., Allen, J.M., Beaury, E.M., Blumenthal, D.M., Bradley, B.A., Dukes, J.S., Early, R., Fusco, E.J., Goldberg, D.E., Ibáñez, I., Laginhas, B.B., Vilà, M., Sorte, C.J.B., 2020. Adjusting the lens of invasion biology to focus on the impacts of climate-driven range shifts. *Nature Climate Change* 10, 398–405 <https://doi.org/10.1038/s41558-020-0768-2>
- Waltari, E., Hickerson, M.J., 2013. Late Pleistocene species distribution modelling of North Atlantic intertidal invertebrates. *Journal of Biogeography* 40, 249–260. <https://doi.org/10.1111/j.1365-2699.2012.02782.x>
- Wang, W., Wang, J., Choi, F.M., Ding, P., Li, X., Han, G., Ding, M., Guo, M., Huang, X., Duan, W., 2020. Global warming and artificial shorelines reshape seashore biogeography. *Global Ecology and Biogeography* 29, 220–231.
- Wenger, S.J., Olden, J.D., 2012. Assessing transferability of ecological models: an underappreciated aspect of statistical validation. *Methods in Ecology and Evolution* 3, 260–267.
- Wernberg, T., Smale, D.A., Tuya, F., Thomsen, M.S., Langlois, T.J., de Bettignies, T., Bennett, S., Rousseaux, C.S., 2013. An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nature Climate Change* 3, 78–82. <https://doi.org/10.1038/nclimate1627>

- Wessel, P., Smith, W.H.F., 1996. A global, self-consistent, hierarchical, high-resolution shoreline database. *Journal of Geophysical Research: Solid Earth*. 101, 8741–8743. <https://doi.org/10.1029/96JB00104>
- Wethey, D.S., 1983. Geographic Limits and Local Zonation: the Barnacles *Semibalanus* (Balanus) and *Chthamalus* in New England. *The Biological Bulletin* 165, 330–341. <https://doi.org/10.2307/1541373>
- Wethey, D.S., 1984. Sun and Shade Mediate Competition in the Barnacles *Chthamalus* and *Semibalanus*: A Field Experiment. *The Biological Bulletin* 167, 176–185. <https://doi.org/10.2307/1541346>
- Wethey, D.S., 2002. Biogeography, Competition, and Microclimate: The Barnacle *Chthamalus fragilis* in New England. *Integrative and Comparative Biology* 42, 872–880. <https://doi.org/10.1093/icb/42.4.872>
- Wethey, D.S., Woodin, S.A., 2008. Ecological hindcasting of biogeographic responses to climate change in the European intertidal zone. *Hydrobiologia* 606, 139–151. <https://doi.org/10.1007/s10750-008-9338-8>
- Wethey, D.S., Woodin, S.A., Hilbish, T.J., Jones, S.J., Lima, F.P., Brannock, P.M., 2011. Response of intertidal populations to climate: Effects of extreme events versus long term change. *Journal of Experimental Marine Biology and Ecology* 400, 132–144. <https://doi.org/10.1016/j.jembe.2011.02.008>
- Whittaker, R. H., 1975. *Communities and ecosystems*. 2nd edition. New York: Macmillan.
- Wiens, J.A., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H.V., Damschen, E.I., Jonathan Davies, T., Grytnes, J., Harrison, S.P., 2010. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology letters* 13, 1310–1324.
- Wiens, J.A., Stralberg, D., Jongsomjit, D., Howell, C.A., Snyder, M.A., 2009. Niches, models, and climate change: Assessing the assumptions and uncertainties. *Proceedings of the National Academy of Sciences* 106, 19729–19736. <https://doi.org/10.1073/pnas.0901639106>
- Wilson, D.P., 1929. The larvae of the British sabellarians. *Journal of the Marine Biological Association of the United Kingdom* 16, 221–268.
- Wilson, D. 1968. The settlement behaviour of the larvae of *Sabellaria alveolata* (L.). *Journal of the Marine Biological Association of the United Kingdom*, 50, 1-45.
- Wilson, D.P., 1971. *Sabellaria* Colonies At Duckpool, North Cornwall, 1961–1970. *Journal of the Marine Biological Association of the United Kingdom* 51, 509. <https://doi.org/10.1017/S002531540001496X>
- Winder, M., Carstensen, J., Galloway, A.W.E., Jakobsen, H.H., Cloern, J.E., 2017. The land-sea interface: A source of high-quality phytoplankton to support secondary production: Nutritious phytoplankton support coastal systems. *Limnology and Oceanography* 62, S258–S271. <https://doi.org/10.1002/lno.10650>

Woodin, S.A., Hilbish, T.J., Helmuth, B., Jones, S.J., Wethey, D.S., 2013. Climate change, species distribution models, and physiological performance metrics: predicting when biogeographic models are likely to fail. *Ecology and Evolution* 3(10), 3334-3346. <https://doi.org/10.1002/ece3.680>

-Y-

Yesson, C., Bush, L.E., Davies, A.J., Maggs, C.A., Brodie, J., 2015. Large brown seaweeds of the British Isles: evidence of changes in abundance over four decades. *Estuarine, coastal and shelf science* 155, 167–175.

-Z-

Zacharias, M.A., Roff, J.C., 2001. Explanations of patterns of intertidal diversity at regional scales: Patterns of intertidal diversity at regional scales. *Journal of Biogeography* 28, 471–483. <https://doi.org/10.1046/j.1365-2699.2001.00559.x>

APPENDICES

APPENDIX 1 CHAPTER I SUPPLEMENTARY MATERIAL	205
APPENDIX 2 CHAPTER II SUPPLEMENTARY MATERIAL	206
APPENDIX 3 GBIF AND PRESENT STUDY OCCURRENCE RECORDS	212
APPENDIX 4 SUMMARY OF THE OBSERVATION RECORDS USED FOR THIS STUDY.	214
APPENDIX 5 PREDICTOR VARIABLES	222
APPENDIX 6 IPCC MODELS RCP SCENARIOS	225
APPENDIX 7 MODELLING METHODS USED.....	226
APPENDIX 8 BINARY MAPS OF PRESENT-DAY PRESENCE/ABSENCE	227
APPENDIX 9 MODEL EVALUATION THROUGH INDEPENDENT TRUE ABSENCE RECORDS. ...	228

APPENDIX 1 CHAPTER I SUPPLEMENTARY MATERIAL

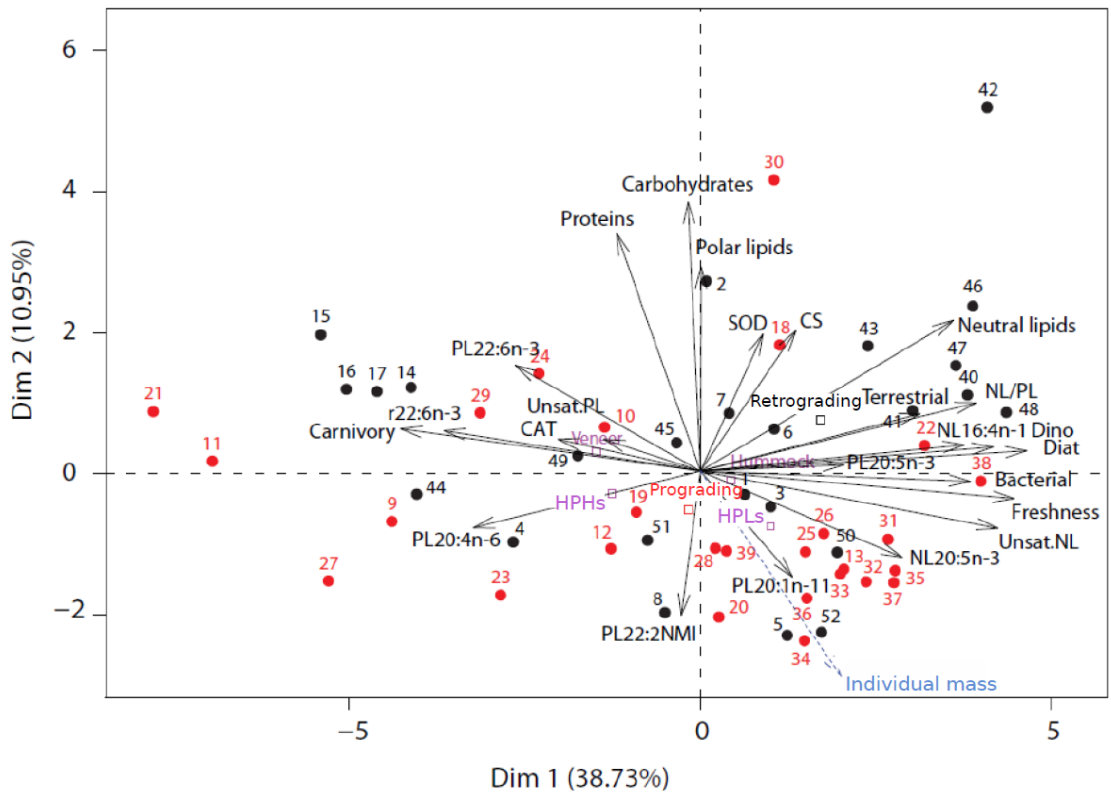


Figure 37 Principal Component Analysis (PCA) biplot of 52 female *Sabellaria alveolata* individuals and 26 biochemical variables. Individual mass is considered as an illustrative quantitative variable, and reef type and phase are considered as illustrative qualitative variables. The first two dimensions of the PCA express 49.68% of the total dataset inertia. Individuals are coloured after their category for the variable “Reef Phase”: progradation phase individuals are in red, retrogradation phase individuals are in black. PCA calculated using the PCA function of the “FactoMineR” package (Lê et al., 2008).

APPENDIX 2 CHAPTER II SUPPLEMENTARY MATERIAL

Table 13. Field locations and sampling dates. Numbers in italic represent the number of viable individuals retained after FlowCAM quality controls.

Site name	Site abbreviations	GPS coordinates (decimal degrees)	Summer 2017 Sampling dates & No. of viable individuals	Winter 2018 Sampling dates & No. of viable individuals
Maryport	MAR	54.718869 -3.507036	21/08/2017 24	17/03/2018 6
Llanddulas	LLA	53.294723 -3.634655	21/08/2017 13	17/03/2018 5
Criccieth	CRI	52.916712 -4.230685	21/08/2017 28	17/03/2018 9
Dunraven	DUN	51.444295 -3.608907	11/06/2017 -	17/03/2018 5
Champeaux	CHA	48.732365 -1.552953	25/07/2017 28	01/03/2018 31
Douarnenez- plage du Ris	RIS	48.098813 -4.294829	24/07/2017 24	04/03/2018 31
La Fontaine aux Bretons	LFB	47.09958 -2.072538	22/07/2017 34	03/03/2018 29
Oléron	OLE	45.970809 -1.393057	21/07/2017 28	02/03/2018 28
Moledo do Minho	MOL	41.8417722 -8.9	25/07/2017 24	29/03/2018 16
Buarcos	BUA	40.1787 -8.9068	23/07/2017 2	30/03/2018 6

Table 14. Meteorological variable sources, units and horizontal resolution. All data were calculated over the thirty day period prior to the sampling dates.

Variable	Abbreviated variable name	Unit	Source	Horizontal resolution
Air temperature	air	Degrees Kelvin	ARPEGE*	~10km
Cold spells – air	arp_cs_n_event	No. of events over the 30-day period	HeatwaveR	~10km
Heatwaves – air	arp_hw_n_event	No. of events over the 30-day period	HeatwaveR	~10km
Seawater temperature	swtemp	Degrees Celsius	CMEMS†	~3km
Cold spells – water	cop_cs_n_event	No. of events over the 30-day period	HeatwaveR	~3km
Heat waves – water	cop_hw_n_event	No. of events over the 30-day period	HeatwaveR	~3km
Seawater Salinity	salinity	psu	CMEMS	~3km
Current Velocity	current_velocity	m.s ⁻¹	CMEMS	~3km
Tidal amplitude	tide_amp	Meters	OTIS-OSU‡	~9km (1/12°)
Suspended Particulate Inorganic Matter	spim	mg.m ⁻³	OC5	~1km
Chlorophyll <i>a</i>	chl _a	µg.m ⁻³	OC5	~1km
Wave exposure index	wave_exposure	(m.s ⁻¹) ²	Adapted from Burrows et al. 2008	~10km

* = Météo-France European Centre for medium-range Weather Forecasts (ECMWF) atmospheric model (Déqué et al., 1994) † = EU Copernicus Marine Environment Monitoring Service (CMEMS) operational IBI (Iberian Biscay Irish) Ocean Physics Analysis and Forecast Product (IBI_ANALYSIS_FORECAST_PHYS_005_001) ‡= Oregon State University Tidal Inversion Software - Regional Tidal Solution (Egbert & Erofeeva, 2010)

Figure 38 Correlations between the *in-situ* temperature loggers and the meteorological models over the 30-day period prior to sampling, for all REEHAB project sampling dates (2016-2018 summer and winter, winter 2019). Please note that Maryport and Llanddulas loggers were not retrieved in summer 2017, and Maryport, Llanddulas and Douarnenez loggers were not retrieved in winter 2018. The red points and line, labelled "Emersion", represent the correlation between the ARPEGE model air temperature variable daily average and the logger readings at low-tide. The blue points and line, labelled "Immersion", represent the correlation between the CMEMS model seawater surface temperature daily average and the logger readings at high-tide. All correlations were significant at the $p < 0.001$ level.

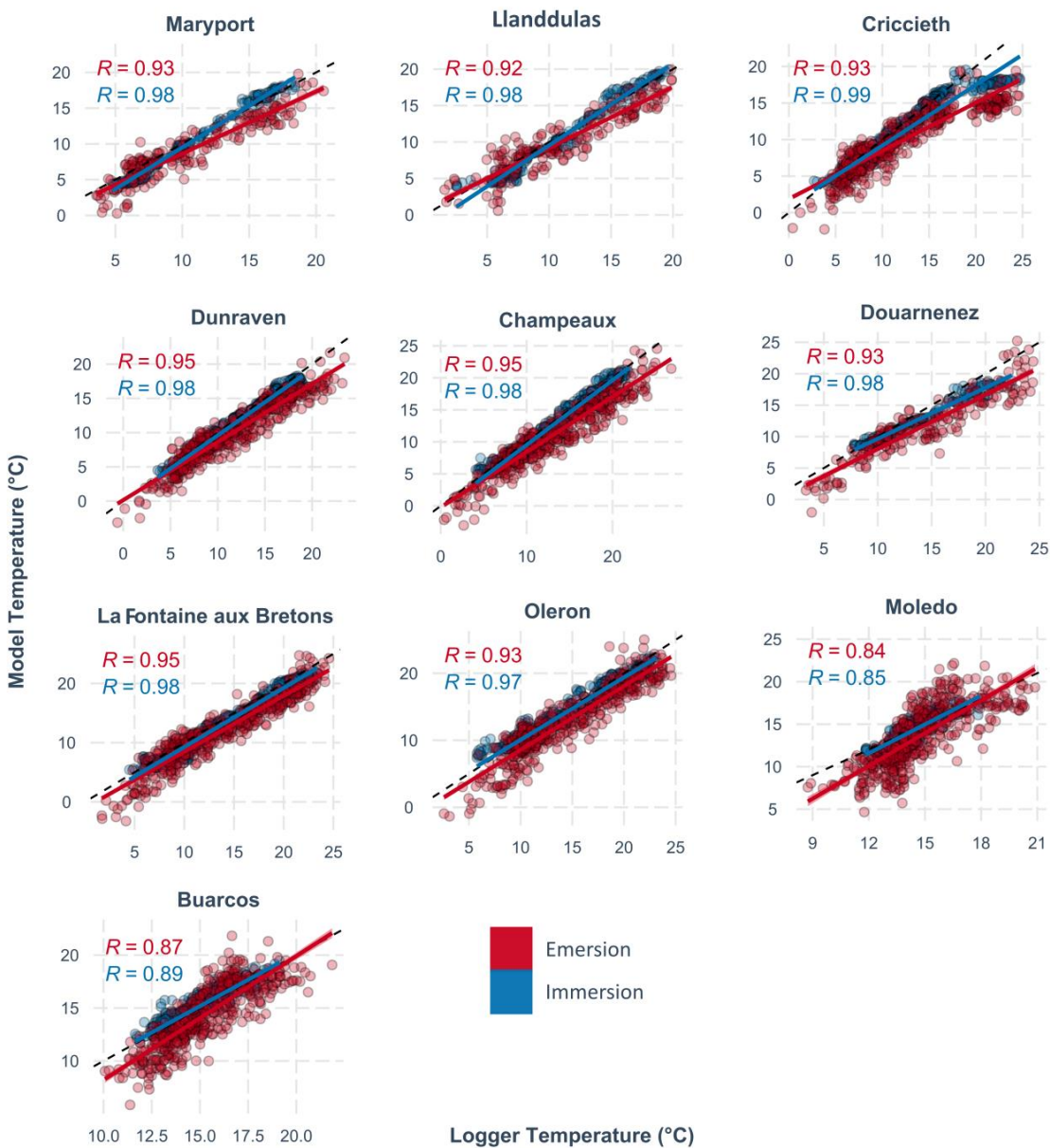
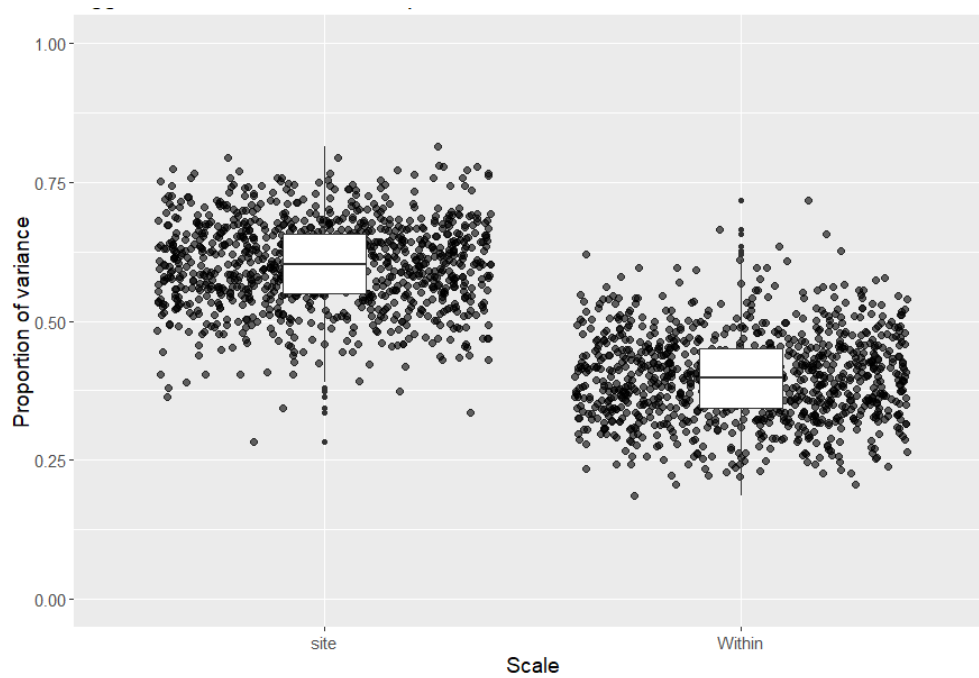
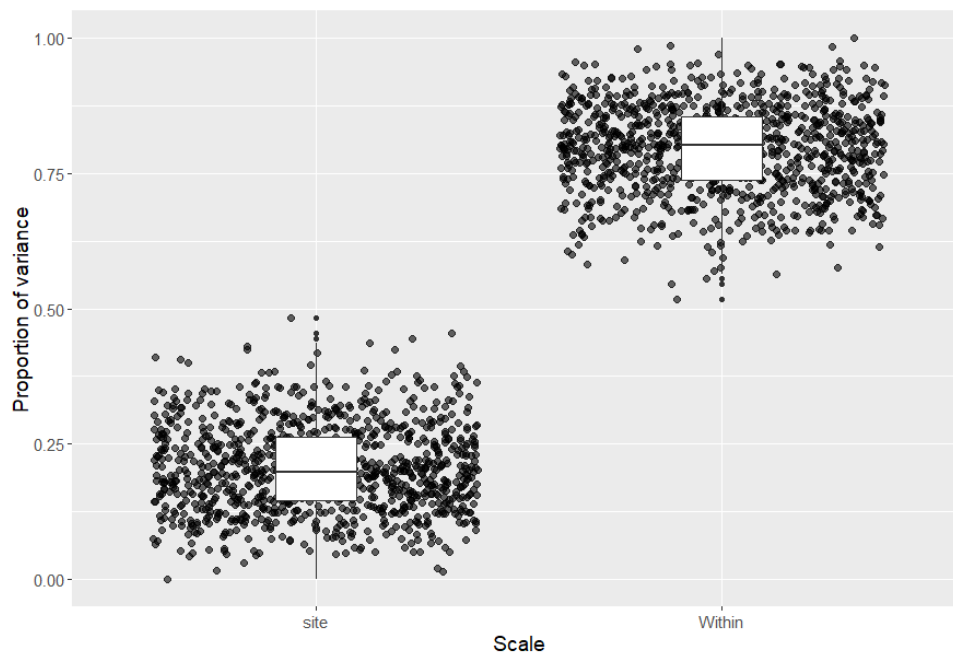


Figure 39 Boxplots of variance component analyses across two nested scales, using a decomposition (varcomp function) of variance on the restricted maximum likelihood (REML) method (lme function), on 1000 resampling of 5 individuals per site for a) summer total egg diameter b) winter total egg diameter c) summer relative fecundity and d) winter relative fecundity. See Messier et al. (2010) for more information.

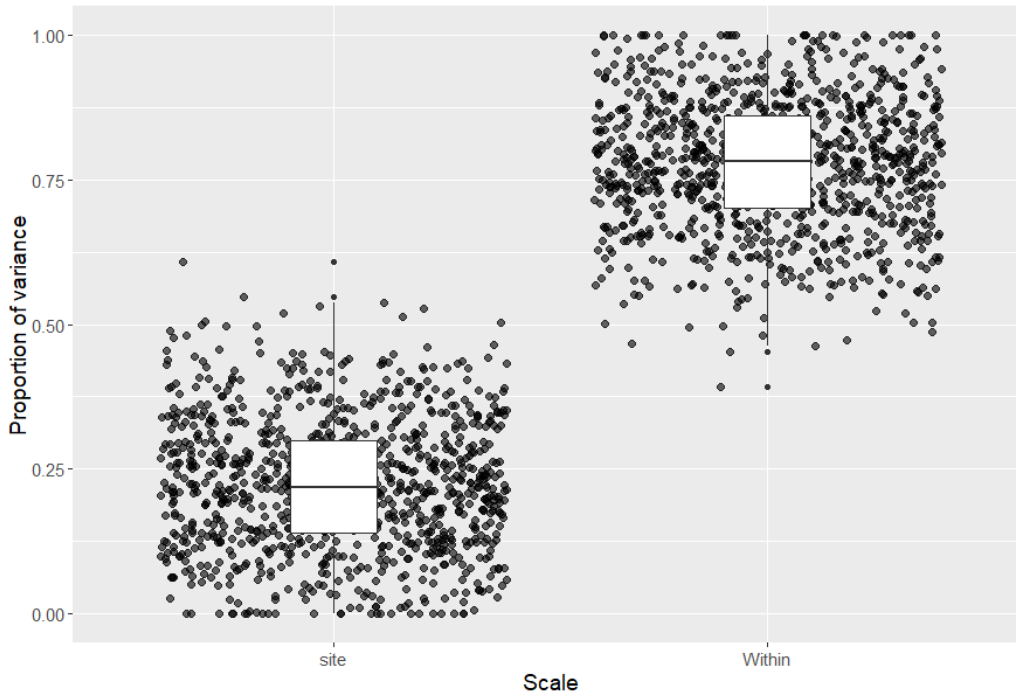
a) Summer total egg diameter, 1000 resampling, 60% site, 40% intra-site



b) Winter total egg diameter, 1000 resampling, 21% site, 79% intra-site



c) Summer relative fecundity, 1000 resampling, 22% site, 77% intra-site



d) Winter relative fecundity, 1000 resampling, 41% site, 59% intra-site

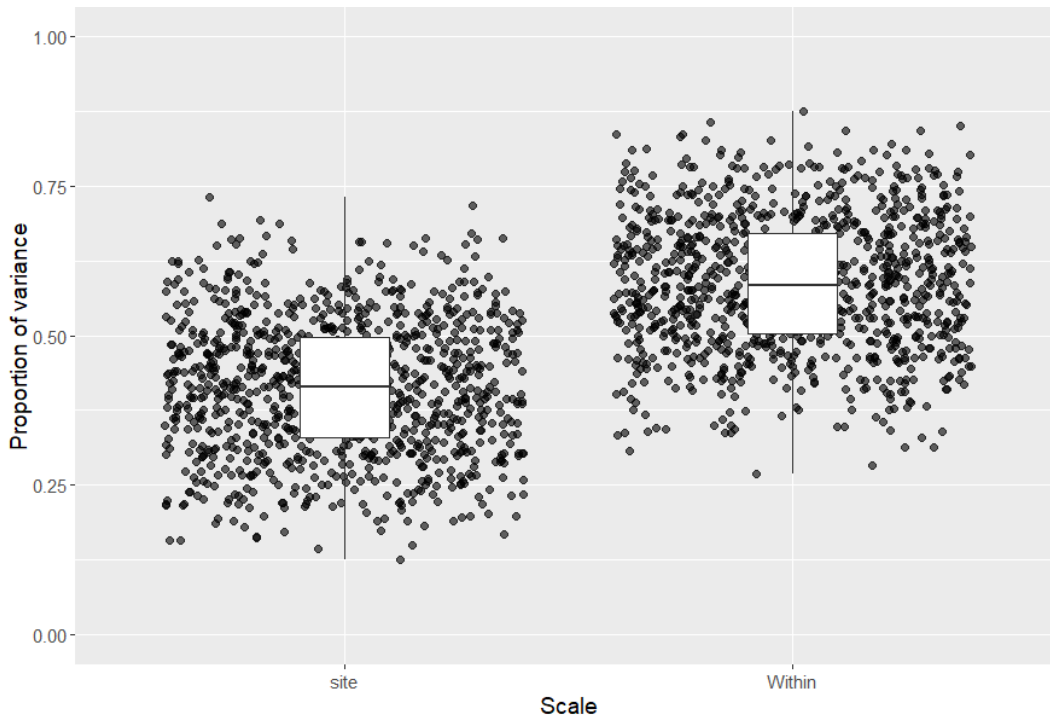
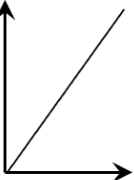
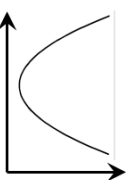
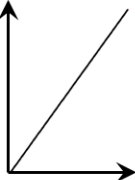
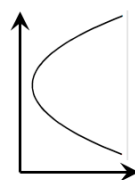
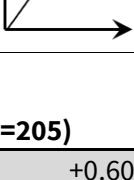
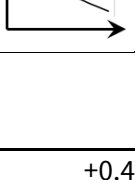
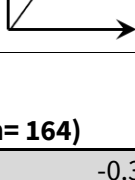
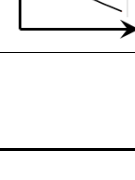


Table 15 Key reproductive, meteorological and biochemical variables and their relationship with linear and quadratic latitude. Values are Pearson’s correlation r .

*** = $p \leq 0.001$, ** = $p \leq 0.01$, * $p \leq 0.05$. NS = non-significant. When both patterns were significant, residuals were checked for normality

	Summer 2017		Winter 2018	
	Linear	Quadratic	Linear	Quadratic
58° N				
40° N				
Response variables	(n=205)		(n= 164)	
Total egg diameter	+0.60***	+0.44***	-0.34***	NS
Relative fecundity	NS	NS	NS	-0.43***
Circle Fit	+0.20**	-0.31***	-0.26***	NS
Symmetry	+0.27***	-0.41***	-0.24**	-0.28***
Meteo. variables	(n=9)		(n=10)	
Air	-0.75 *	NS	-0.72*	NS
Air SD	NS	-0.79 *	NS	NS
Seawater	NS	-0.67 *	-0.97 ***	NS
Seawater SD	NS	NS	NS	NS
Chl.a	+0.79*	NS	NS	NS
Chl.a SD	NS	NS	NS	NS
Salinity	NS	NS	NS	NS
SPIM	NS	NS	NS	NS
Wave exposure	NS	NS	NS	NS
Biochemical variables (n=60)				
CS			+0.25*	+0.54***
SOD			+0.45***	NS
PL AA			+0.34**	NS
PL EPA			NS	NS
PL DHA			NS	+0.73***

APPENDIX 3 GBIF AND PRESENT STUDY OCCURRENCE RECORDS

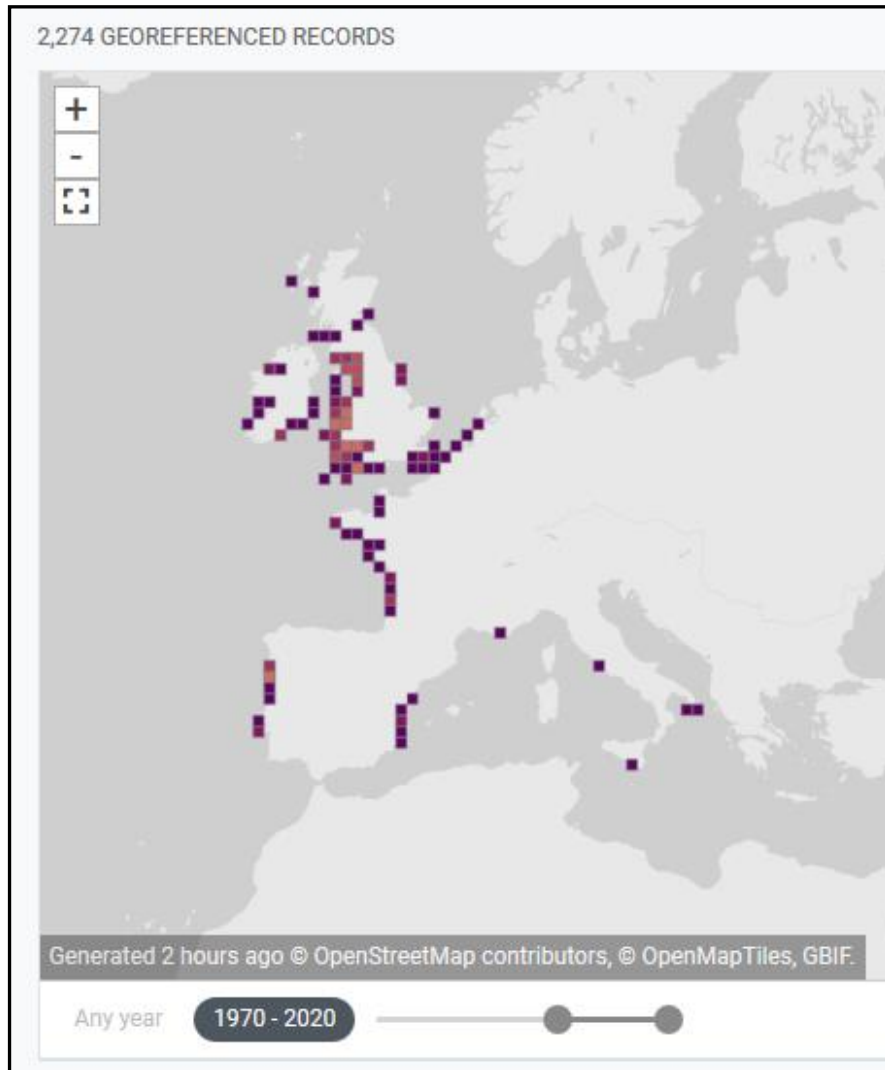


Figure 40. Screenshot of the 2274 georeferenced records for ‘*Sabellaria alveolata*’ held in the Global Biodiversity Information Facility (GBIF - accessed 12-03-2020). The records situated in the eastern English Channel and around the North Sea are all issued from citizen science programs (i.e. the Shore Thing and BioBlitz in the United Kingdom, Observation.org from the Netherlands).

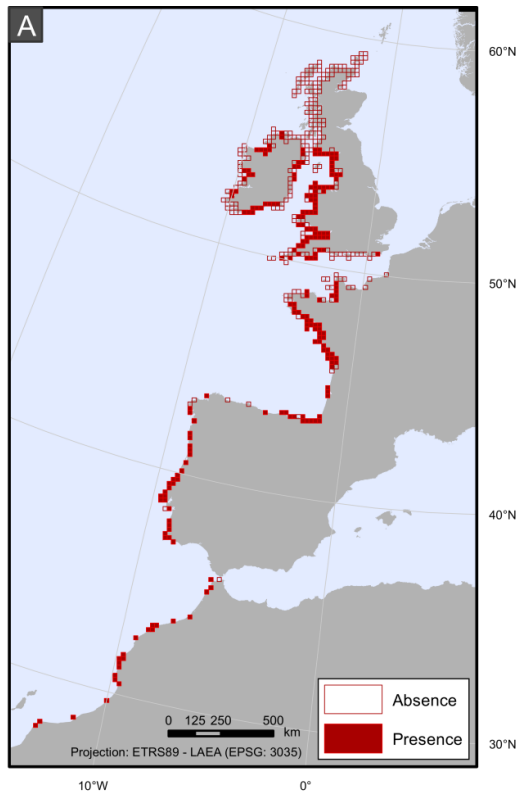
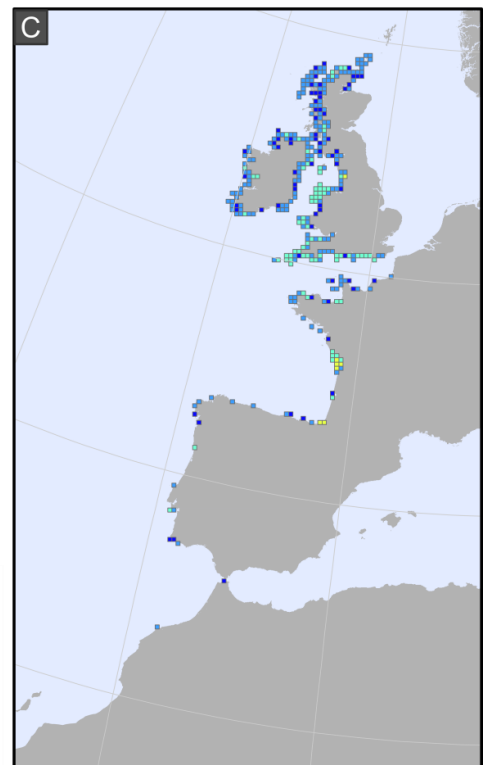
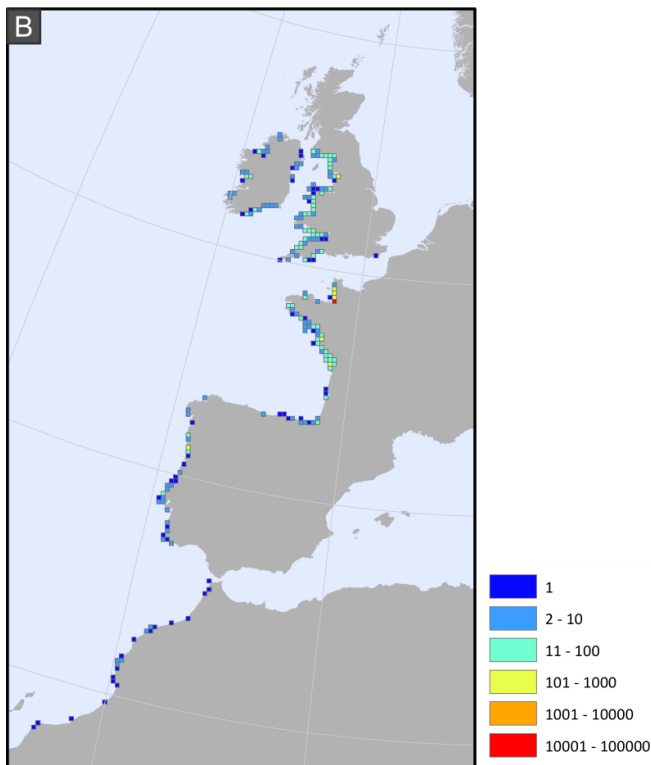


Figure 41 Maps illustrating the distribution and density of the 19354 collated *Sabellaria alveolata* records along the North-east Atlantic coast, where A) shows presence and absence records project onto a 20km grid – grid cells with a majority of presence are filled, those with a majority of absences are outlined; B) the density of the 14960 presence records (2000-2019) per 20km grid cell according to a log base 10 scale; C) the density of the 4394 absence records (1970-2019) per 20km grid cell according to a log base 10 scale.



APPENDIX 4 SUMMARY OF THE OBSERVATION RECORDS COLLATED AND USED FOR THIS STUDY.

Table 16 Databases *via* which 22 of the 109 sources were accessed. See colour-coding scheme in Table 17 below

Database name and URL	Pres.	Abs.
	2000-2019	1970-2019
BDESTAMP - OFB - https://estamp.afbiodiversite.fr/	22	0
French Biodiversity Agency, CARTOMER - http://cartographie.afbiodiversite.fr/	355	1454
Global Biodiversity Information Facility (GBIF) - GBIF.org	21	6
Ifremer, SEXTANT - https://sextant.ifremer.fr/	1667	56
NBN Atlas - https://nbnatlas.org	495	1864

Table 17 List of all the sources of *Sabellaria alveolata* records collated across the Northeast Atlantic. When records were retrieved from an online database, they were colour-coded as per Table 16.

Sources	Pres.	Abs.
	2000-2019	1970-2019
Agence des aires marines protégées, Parc naturel marin d'Iroise, 2016. Récifs d'hermelles (habitat 1170-4) de la Baie de Douarnenez - Parc naturel marin d'Iroise (état 2008-2016).	30	0
Agence Française pour la biodiversité, 2019. BDESTAMP: Suivi des habitats benthiques et des usages de la zone intertidale au sein des Aires Marines Protégées. https://estamp.afbiodiversite.fr .	22	0
Allen, J.H., Billings, I., Cutts, N., Elliott, M., 2002. Mapping, Condition & Conservation Assessment of Honeycomb Worm <i>Sabellaria alveolata</i> Reefs on the Eastern Irish Sea Coast (No. Z122- F-2002). Institute of Estuarine & Coastal Studies / University of Hull.	61	20
Allen, J.R., Wilkinson, S.B., Hawkins, S.J., Hartnoll, R.G., Russel, G., 1991. Baseline survey of the Cumbrian shores from St Bees Head to Maryport (Unpublished report to Acer Environmental for North West Water Ltd.). Liverpool University Port Erin Marine Laboratory, Port Erin.	0	1
Aquafact International Services Ltd, The Foods Standard Agency in Northern Ireland, 2012. Sanitary Survey Report and Sampling Plan for Killough Harbour.	1	0
Basuyaux, O., Lecornu, B., 2019. Cartographie des hermelles <i>Sabellaria</i>	1587	0

<i>alveolata</i> sur la façade ouest du département de la Manche 2009-2019, SMEL. www.smel.fr .		
Becker, P.T., Lambert, A., Lejeune, A., Lanterbecq, D., Flammang, P., 2012. Identification, Characterization, and Expression Levels of Putative Adhesive Proteins From the Tube-Dwelling Polychaete <i>Sabellaria alveolata</i> . <i>The Biological Bulletin</i> 223, 217–225. https://doi.org/10.1086/BBLv223n2p217	1	0
Bell, J.J., 2005. Influence of occupant microhabitat on the composition of encrusting communities on gastropod shells. <i>Marine Biology</i> 147, 653–661. doi:10.1007/s00227-005-1587-8	6	0
Bertocci, I., Araújo, R., Incera, M., Arenas, F., Pereira, R., Abreu, H., Larsen, K., Sousa-Pinto, I., 2012. Benthic assemblages of rock pools in northern Portugal: seasonal and between-pool variability. <i>Scientia Marina</i> 76. https://doi.org/10.3989/scimar.03669.21A	1	0
Bonifazi, A., 2018. <i>Sabellaria</i> from larvae to reef: growth, ecological role and habitat mapping (Ph.D. Thesis). Università' degli studi di Roma.	1	0
Bonnot-Courtois, C., Guilpain, P., Legendre, V., Le Vot, M., Massé, M., Moré, F., Panizza, A., Prevost, C., Schoorens, J., Toupoint, N., 2007. Cartographie morpho-sédimentaire intertidale de la baie du Mont Saint-Michel. État 2002. CNRS, UMR 8586 PRODIG, Laboratoire de Géomorphologie et Environnement littoral. EPHE.	1503	46
Bouleau, A.-M., 2012. Fécondation chez les Hermelles - <i>Sabellaria alveolata</i> [WWW Document]. Académie de Nantes. Espace pédagogique. URL https://www.pedagogie.ac-nantes.fr/sciences-de-la-vie-et-de-la-terre/enseignement/ressources-pedagogiques/fecondation-chez-les-hermelles-sabellaria-alveolata-100483.kjsp?RH=PEDA	22	0
Bredèche, M., Le Borgne, M., 2019. Suivi des récifs d'hermelles sur les sites Natura 2000 "Côte de Granit rose - Sept-Iles" et "Rivière du Léguer". Lannion-Trégor Communauté.	35	0
Bretagne Vivante, 2017. Observations de <i>Sabellaria alveolata</i> venant des bénévoles sur la période 2010-2015. Association Bretagne Vivante, Brest.	15	0
Brinkmann, N., Wanninger, A., 2008. Larval neurogenesis in <i>Sabellaria alveolata</i> reveals plasticity in polychaete neural patterning. <i>Evolution & Development</i> 10, 606–618. https://doi.org/10.1111/j.1525-142X.2008.00275.x	1	0
Bush, L., 2016. Stability and variability of the ecosystem engineer <i>Sabellaria alveolata</i> on differing temporal and spatial scales (PhD Thesis). Bangor University.	215	123
Bustamante, M., Tajadura-Martín, F.J., Saiz-Salinas, J.I., 2010. Temporal and spatial variability on rocky intertidal macrofaunal assemblages affected by an oil spill (Basque coast, northern Spain). <i>Journal of the Marine Biological Association of the United Kingdom</i> , 90, 1305–1317. https://doi.org/10.1017/S0025315410000056	10	2
Cajeri, P., Curti, C., Lafon, V., Launay, R., Sauriau, P.-G., 2012. Cartographie des habitats intertidaux des sites Natura 2000 des Pertuis charentais: complémentarité des approches inventaire terrain, télédétection et SIG, in: Actes Des XIIèmes Journées Nationales Génie Côtier – Génie Civil. Paralia, Cherbourg, pp. 855–864. https://doi.org/10.5150/jngcgc.2012.093-C	116	0

Centre for Environmental Data and Recording, 2019. Ulster Museum Marine Surveys.	1	4
Chouikh, N., Gillet, P., Langston, W.J., Cheggour, M., Maarouf, A., Mouabad, A., 2019. First investigation of the composition and spatial distribution of polychaete feeding guilds from Essaouira protected costal area (Atlantic coast of Morocco). <i>Applied Ecology and Environmental Research</i> 17, 3231–3249. https://doi.org/10.15666/aeer/1702_32313249	12	0
Cofnod – North Wales Environmental Information Service, 2019. NRW Regional Data: North Wales. https://doi.org/10.15468/KRLJPU	3	0
Cole, V., Chapman, M., 2007. Patterns of distribution of annelids: taxonomic and spatial inconsistencies between two biogeographic provinces and across multiple spatial scales. <i>Marine Ecology Progress Series</i> 346, 235–241. https://doi.org/10.3354/meps07061	7	0
Communauté de Communes de l’Ile de Noirmoutier, 2013. Réalisation d’aménagements de stabilisation du trait de côte. Etude réglementaire. (Etude d’impact No. ARCADIS/ 12-002928).	15	0
Cooney, B., 2016. Intertidal Indicators of Climate Change (BSc. thesis). University College Cork.	1	4
Cordier, Jean-Yves, n.d. Le moteur de la Tante Yvonne, plage de Postolonnec à Crozon. [WWW Document]. Le blog de jean-yves cordier. URL http://www.lavieb-aile.com/article-le-moteur-de-la-tante-yvonne-plage-de-postollonec-a-crozon-112582549.html (accessed 8.17.17).	1	0
CREOCEAN, IMA, Centre de la Mer de Biarritz, 2012. NATURA 2000 en mer - Lot 4 Aquitaine - Côte Basque: Cartographie et évaluations des habitats marins. CARTHAM - AAMP.	80	422
CREOCEAN, LIENSs, EPOC, RE NATURE ENVIRONNEMENT, IODDE, 2012. Inventaire et Cartographie des habitats marins du périmètre d’étude du projet de Parc naturel marin de l’Estuaire de la Gironde et des Pertuis Charentais. CARTHAM - AAMP.	245	1032
Crisp, D.J., Southward, A.J., n.d. Field notebooks.	0	5
Cruz da Costa, A.C., 2012. Caracterização e cartografia da fauna intertidal das praias rochosas de Matosinhos. Universidade do Porto.	109	73
Culloty, S.C., Favier, E., Ní Riada, M., Ramsay, N.F., O’Riordan, R.M., 2010. Reproduction of the biogenic reef-forming honeycomb worm <i>Sabellaria alveolata</i> in Ireland. <i>Journal of the Marine Biological Association of the United Kingdom</i> , 90, 503. https://doi.org/10.1017/S0025315409990932	3	0
Cunningham, P.N., Hawkins, S.J., Jones, H.D., Burrows, M.T., 1984. The biogeography and ecology of <i>Sabellaria alveolata</i> in England, Wales and Scotland, with investigations into the community structure of and the effects of trampling on <i>Sabellaria alveolata</i> colonies (Report to the Nature Conservancy Council No. HF3/11/22). Department of Zoology, University of Manchester, Manchester.	0	146
Davenport, J., Moloney, T.V., Kelly, J., 2011. Common sea anemones <i>Actinia equina</i> are predominantly sessile intertidal scavengers. <i>Marine Ecology Progress Series</i> 430, 147–156. https://doi.org/doi:10.3354/meps08861	1	0

De Montaudouin, X., Lamarque, B., Lavesque, N., Gouillieux, B., Costes, L., 2016. Rechargement et restauration des plages du Pyla sur Mer: impact sur les peuplements benthiques (année 13). Université de Bordeaux.	13	15
Domínguez, R., Domínguez Godino, J., Freitas, C., Machado, I., Bertocci, I., 2015. Habitat traits and patterns of abundance of the purple sea urchin, <i>Paracentrotus lividus</i> (Lamarck, 1816), at multiple scales along the north Portuguese coast. Estuarine, Coastal and Shelf Science 155, 47–55. https://doi.org/10.1016/j.ecss.2014.12.048	9	0
DORIS, n.d. <i>Sabellaria alveolata</i> [WWW Document]. DORIS. URL http://doris.ffessm.fr/Especies/Sabellaria-alveolata-Hermelle-1373/%28rOffset%29/0 (accessed 10.6.17).	2	0
Dubois, S., Barillé, L., Barillé, A.-L., Gruet, Y., 2004. Conditions de préservation des formations récifales à <i>Sabellaria alveolata</i> (L.) en baie de Bourgneuf (Rapport d'étude dans le cadre de la mise en place du réseau Européen Natura 2000). Université de Nantes.	303	0
Dubois, S., Commito, J.A., Olivier, F., Retière, C., 2006. Effects of epibionts on <i>Sabellaria alveolata</i> (L.) biogenic reefs and their associated fauna in the Bay of Mont Saint-Michel. Estuarine, Coastal and Shelf Science 68, 635–646.	1	0
Edwards, H., 2017. The Honeycomb worm <i>Sabellaria alveolata</i> in the North of Ireland 1985 to 2016. Department of Agriculture and Rural Affairs (DAERA).	6	1
Egerton, S., 2014. Distribution mapping and health assessment of honeycomb worm, <i>Sabellaria alveolata</i> , reefs on Heysham Flat, Lancashire (Report to the North Western Inshore Fisheries and Conservation Authority). North Western IFCA, The Wildlife Trusts.	215	200
Favier, E., 2001. An investigation into the aspects of the ecology and reproductive biology of the honeycomb worm, <i>Sabellaria alveolata</i> (B.Sc thesis). University College Cork.	7	10
Fingal County Council, 2005. Ecological Study of the Coastal Habitats in County Fingal Phase IV: Intertidal Habitats.	0	6
Firth, L.B., Harris, D., Blaze, J.A., Marzloff, M.P., Boyé, A., Miller, P.I., Curd, A., Nunn, J.D., O'Connor, N.E., Power, A.M., Mieszkowska, N., O'Riordan, R.M., Burrows, M.T., McGrath, D., Bordeyne, F., Bush, L.E., David, C., Davies, A.J., Dubois, S., Edwards, H., Foggo, A., Gribben, P., Knights, A.M., Lima, F.P., Noël, L.M.L.I., Nunes, F.L.D., Patterson, A., Seabra, R., Simkanin, C., Vasquez, M., Hawkins, S.J., 2020. Climate and meso-scale processes influence the distribution, abundance and biogeography of an ecosystem engineer at its leading range edge in Ireland over the last 180 years. Unpublished manuscript.	114	136
Fournier, J., CNRS, 2017. pers. comm.	7566	0
Frost, M.T., Leaper, N., Mieszkowska, N., Moschella, P., Murua, J., Smyth, C., Hawkins, S.J., 2004. Recovery of a Biodiversity Action Plan Species in Northwest England: possible role of climate change, artificial habitat and water quality amelioration (Report to English Nature). Marine Biological Association of the United Kingdom.	16	12
Garcia-Regeira, X., Tato, R., Moreira, J., Urgorri, V., 2010. Temporal evolution of polychaete assemblages on intertidal hard substrata at two localities of the galician coast after the “PRESTIGE” oil spill.	2	0

Thalassas 26, 33–45.		
Green, D., Crowe, T., 2013. Physical and biological effects of introduced oysters on biodiversity in an intertidal boulder field. <i>Marine Ecology Progress Series</i> 482, 119–132. https://doi.org/10.3354/meps10241	1	0
Gruet, Y., 1972. Faune associée des “récifs” d’Hermelles Polychète Sabellariidé: <i>Sabellaria alveolata</i> (Linné): cas de récifs morts à Crève-Coeur (La Bernerie, Loire Atlantique). <i>Bulletin de la Société Scientifique de Bretagne</i> 47, 69–80.	0	1
Gruet, Y., n.d. Unpublished raw data.	0	14
Hammond, N., 2000. <i>S. alveolata</i> report: Solway Firth (Draft report to the Solway Firth Partnership).	49	1
Hawkins, S.J., n.d. Field notebooks.	11	8
IFREMER, 2020. Submit Honeycomb Worm Reef Sightings [WWW Document]. <i>Sabellaria alveolata</i> biogenic reefs. URL http://www.honeycombworms.org/Submit-Honeycomb-Worm-Reef-Sightings (accessed 2.18.20).	107	4
iNaturalist, n.d. Honeycomb Worm (<i>Sabellaria alveolata</i>) [WWW Document]. iNaturalist. URL https://www.inaturalist.org/taxa/338082-Sabellaria-alveolata (accessed 04.10.19).	27	0
Joint Nature Conservation Committee, 2019. Marine Recorder Public UK snapshot - v20190730.	0	1
Kochmann, J., O’Beirn, F., Yearsley, J., Crowe, T.P., 2013. Environmental factors associated with invasion: modelling occurrence data from a coordinated sampling programme for Pacific oysters. <i>Biological Invasions</i> 15, 2265–2279. https://doi.org/10.1007/s10530-013-0452-9	1	0
La Vigie, 2011. Observation sur le projet de port à Brétignolles-sur-Mer dans le cadre de l’enquête publique sur l’impact environnemental du projet.	3	0
Last, K.S., Hendrick, V.J., Beveridge, C.M., Roberts, D.A., Wilding, T.A., 2016. Lethal and sub-lethal responses of the biogenic reef forming polychaete <i>Sabellaria alveolata</i> to aqueous chlorine and temperature. <i>Marine Environmental Research</i> 117, 44–53. doi:10.1016/j.marenvres.2016.04.001	1	0
Le Cam, J.-B., Fournier, J., Etienne, S., Couden, J., 2011. The strength of biogenic sand reefs: Visco-elastic behaviour of cement secreted by the tube building polychaete <i>Sabellaria alveolata</i> , Linnaeus, 1767. <i>Estuarine, Coastal and Shelf Science</i> 91, 333–339. https://doi.org/10.1016/j.ecss.2010.10.036	2	0
Le Rhun, J., 1982. Étude physique de la baie du Mont-Saint-Michel (Thèse de doctorat de 3ème cycle). Université Paris 1.	0	11
Lefebvre, S., Marín Leal, J.C., Dubois, S., Orvain, F., Blin, J.-L., Bataillé, M.-P., Ourry, A., Galois, R., 2009. Seasonal dynamics of trophic relationships among co-occurring suspension-feeders in two shellfish culture dominated ecosystems. <i>Estuarine, Coastal and Shelf Science</i> 82, 415–425. https://doi.org/10.1016/j.ecss.2009.02.002	1	0
Ligue pour la Protection des Oiseaux, 2018. Observations de <i>Sabellaria alveolata</i> venant de la réserve naturelle de Moëze-Oléron.	45	0
Lima, F.P., n.d. Unpublished data.	55	39

Linhares, E., 2006. Avaliação do potencial impacto do quebra-mar destacado na diversidade faunística associada aos recifes de <i>Sabellaria alveolata</i> (L.) da praia da guda (Dissertações de Mestrado). Instituto de Ciências Biomédicas de Abel Salazar, Universidade do Porto.	1	0
Lourenço, C.R., n.d. Field notebooks.	3	3
Lourenço, C.R., Zardi, G.I., McQuaid, C.D., Serrão, E.A., Pearson, G.A., Jacinto, R., Nicastro, K.R., 2016. Upwelling areas as climate change refugia for the distribution and genetic diversity of a marine macroalga. <i>Journal of Biogeography</i> 43, 1595–1607. https://doi.org/10.1111/jbi.12744	13	0
MarClim Project, 2019. https://www.mba.ac.uk/projects/marine-biodiversity-and-climate-change-marclim .	205	1854
Marine Biological Association, 2017. 2005 - Ongoing United Kingdom MarLIN Shore Thing timed search results. https://doi.org/10.15468/IKWLZR	33	22
Marine Biological Association, 2017. DASSH Data Archive Centre volunteer sightings records. https://doi.org/10.15468/XWIW3H	8	0
Marine Biological Association, 2017. DASSH Data Archive Centre volunteer survey data. https://doi.org/10.15468/PJOWTH	1	0
Maringue, M., 2016. pers. comm.	5	0
Merseyside BioBank, 2017. Merseyside BioBank (verified). https://doi.org/10.15468/AR0P6S	24	0
Nash, R., 2013. Site report Tralee Bay and Maharee Peninsula SAC (Site code 00). BEC consultants.	1	0
National Biodiversity Data Centre, 2016. General Biodiversity Records from Ireland. https://doi.org/10.15468/w8q1jm	1	0
National Parks and Wildlife Service, 2010. Site investigations for <i>Sabellaria alveolata</i> (Honey-comb worm) biogenic reefs in Ireland. NPWS.	5	0
National Parks and Wildlife Service, 2011. River Barrow and River Nore SAC (site code: 2162). Conservation objectives supporting document - marine habitats. NPWS.	1	0
Natural Resources Wales, 2017. Marine data from Natural Resources Wales (NRW) Technical Support (Research & Monitoring) Contracts, Wales. https://doi.org/10.15468/AZ7NW3	50	0
Natural Resources Wales, 2017. Marine Intertidal Phase 1 Species Dataset from the Countryside Council for Wales 1996-2005. https://doi.org/10.15468/KFLO7M	104	2
Networked Organisms, 2013. Project Noah - Organisms [WWW Document]. Project Noah. URL http://www.projectnoah.org/organisms?search=Honeycomb+worm (accessed 10.6.17).	2	0
Ni Riada, M., 2000. An investigation into the aspects of the ecology and reproductive biology of the honeycomb worm, <i>Sabellaria alveolata</i> (BSc. thesis). University College Cork.	3	0
Noernberg, M.A., Fournier, J., Dubois, S., Populus, J., 2010. Using airborne laser altimetry to estimate <i>Sabellaria alveolata</i> (Polychaeta: Sabellariidae) reefs volume in tidal flat environments. <i>Estuarine, Coastal and Shelf Science</i> 90, 93–102. doi:10.1016/j.ecss.2010.07.014	1488	0
Nunn, J., n.d. Field notebooks.	11	127

Patterson, F., 2015. There is no difference in the presence or abundance of the Honeycomb worm <i>Sabellaria alveolata</i> on intertidal rocky shores in south west Ireland (BSc thesis). University College Cork.	10	2
Plicanti, A., Iacofano, D., Bertocci, I., Brutto, S.L., 2017. The amphipod assemblages of <i>Sabellaria alveolata</i> reefs from the NW coast of Portugal: An account of the present knowledge, new records, and some biogeographic considerations. <i>Marine Biodiversity</i> 47, 521–534. doi:10.1007/s12526-016-0474-5	2	0
Preston, J., Portig, A., 2001. An assessment of the honeycom worm <i>Sabellaria alveolata</i> at several locations in county down. Aquatic and Terrestrial Environmental Consultants.	3	3
REEHAB Project, 2020. https://www.honeycombworms.org	64	2
Saldanha, L., 1974. Estudo do povoamento dos horizontes superiores da rocha litoral da costa da arrabida (Portugal). <i>Arquivos do Museu Bocage</i> 5, 1–382.	0	26
Sauriau, P.-G., Aubert, F., Breret, M., 2010. Surveillance 2009 flore masses d'eau côtière DCE FRFC01 Nord-Est Oléron: macroalgues FRFC02 Pertuis Charentais: herbier de <i>Zostera noltii</i> , Partie 1: macroalgues intertidales. CNRS.	1	0
Sauriau, P.-G., Pigeot, J., 2010. Contribution à l'inventaire de la macrofaune marine en baie de Marennes-Oléron. <i>Annales de la Société des sciences naturelles de la Charente-Maritime</i> 10.	1	0
Schlund, E., Basuyaux, O., Lecornu, B., Pezy, J.-P., Baffreau, A., Dauvin, J.-C., 2016. Macrofauna associated with temporary <i>Sabellaria alveolata</i> reefs on the west coast of Cotentin (France). <i>SpringerPlus</i> 5. https://doi.org/10.1186/s40064-016-2885-y	9	0
Scottish Natural Heritage, 2017. Species data for Scottish waters held and managed by Scottish Natural Heritage, derived from benthic surveys 1993 to 2014. https://doi.org/10.15468/FAXVGD	23	3
Seasearch, 2019. Seasearch Marine Surveys in England. https://doi.org/10.15468/KYWX6M	1	0
Seasearch, 2019. Seasearch Marine Surveys in Ireland. https://doi.org/10.15468/PYUGGE	1	0
Seasearch, 2019. Seasearch Marine Surveys in Wales. https://doi.org/10.15468/4US2HK	3	0
Serrano, A., Preciado, I., 2007. Environmental factors structuring polychaete communities in shallow rocky habitats: role of physical stress versus habitat complexity. <i>Helgoland Marine Research</i> 61, 17–29. https://doi.org/10.1007/s10152-006-0050-7	1	0
Severijns, N., 2004. Verslag van de meerdaagse excursie naar St. Germain-sur-Ay (Normandië) van 29 maart tot 3 april 2002. <i>De Strandvlo</i> 24, 57–73.	3	0
Sif, J., Rouhi, A., Gillet, P., Moncef, M., 2012. Diversité et écologie des Annélides Polychètes du littoral atlantique de la région d'El Jadida (Maroc). <i>Bulletin de l'Institut Scientifique, section Sciences de la Vie</i> 34, 95–106.	6	4
Smith, S., 2003. Porcupine field excursion to Dunbar 16 March 2002. <i>Porcupine Marine Natural History Society Newsletter</i> 12, 18–20.	1	0
Smyth, D., Roberts, D., 2010. The European oyster (<i>Ostrea edulis</i>) and its epibiotic succession. <i>Hydrobiologia</i> 655, 25–36. https://doi.org/10.1007/s10750-010-0401-x	0	1

Sousa Pinto, I., Vieira, R., 2012. Monitoring of the intertidal biodiversity of rocky beaches with schools in Portugal 2005-2010. CIIMAR - Interdisciplinary Centre for Marine and Environmental Research, Porto. https://doi.org/10.14284/38	58	0
South East Wales Biodiversity Records Centre, 2018. SEWBReC Worms (South East Wales). https://doi.org/10.15468/5VH0W8	43	0
Tato, R., Garcia-Regueira, X., Moreira, J., Urgorri, V., 2009. Inventario faunístico del intermareal rocoso de dos localidades de la costa occidental gallega (NO Península Ibérica) tras el vertido del Prestige. Nova Acta Científica Compostelana (Biología) 18, 75–94.	2	0
TBM, 2008. Site Natura 2000 - Estuaire de la Vilaine - Rapport Cartographie des habitats marin d'intérêt communautaire européen.	46	0
TBM, 2017. Cartographie des Habitats marins. Site Natura 2000 FR 5300048 "Marais de Moustierlin."	2	0
Tily, A., 2011. Marais Breton, baie de Bourgneuf, île de Noirmoutier et forêt de Monts - Site Natura 2000 FR5200653 - Cartographie des habitats naturels et des espèces d'intérêt communautaire de Marais Breton - Tome I, Notice descriptive des habitats et des espèces.	1	0
Tuthill, R.E., 2015. Are we finally seeing the effects of global climate change on intertidal biota (MSc thesis). University College Cork.	8	7
Vivarmor Nature, 2020. Observations de <i>Sabellaria alveolata</i> venant de l'inventaire "Estran22" de la zone de balancement des marées en Côte d'Armor sur la période 2010-2020. Retrieved from https://nature22.com/estran22/vers/annelides/annelides_sedentaires.html#sabellaria .	25	0
Wikipédia, 2017. <i>Sabellaria alveolata</i> [WWW Document]. Wikipédia, l'encyclopédie libre. URL https://fr.wikipedia.org/wiki/Sabellaria_alveolata (accessed 10.6.17).	1	0
Wilson, D.P., 1971. Sabellaria Colonies At Duckpool, North Cornwall, 1961–1970. Journal of the Marine Biological Association of the United Kingdom, 51, 509–580. https://doi.org/10.1017/S002531540001496X	0	1
Wüest, J., Sinniger, F., 2004. Stage de biologie marine. 25 août au 5 septembre 2004. Luc-sur-Mer, Normandie. Résultats et commentaires.	1	0
Yahoo, n.d. Flickr - Photos [WWW Document]. Flickr. URL https://www.flickr.com/search/?text=honeycomb%20worm (accessed 10.6.17).	23	0
19354 records collated from 109 sources	14960	4394

APPENDIX 5 PREDICTOR VARIABLES

Table 18 Environmental predictors used for modelling the distribution of *Sabellaria alveolata*, including whether variables were used for present-day (**P**) or future scenarios (**F**), data sources, manipulation (spatial resolution, time period and grain), types of data (RS: remote sensing; DO: direct observation; OM: ocean model; AM: atmospheric model) and units.

Environmental predictor	Source	Manipulation	Type	Units
P Sea surface temperature (SST)	<i>CMEMS</i> ^a	~3km 2016-2018 OM daily outputs		°C
SST min, P10, mean, P90, max				
P Surface current velocity	<i>CMEMS</i> ^a	~3km 2016-2018 OM daily outputs		m.s ⁻¹
Current velocity mean				
P Sea surface salinity	<i>CMEMS</i> ^a	~3km 2016-2018 OM daily outputs		PSS
Sea surface salinity mean				
P Air temperature	<i>ARPEGE</i> ^c	~10km 2012-2018 AM hourly outputs		°K
Air temperature min, P10, mean, P90, max				
P Wind speed	<i>ARPEGE</i> ^c	~10km 2012-2018 AM hourly outputs		m.s ⁻¹
Wind speed P90				
P Wave fetch	<i>Burrows et al. 2012</i> ^f	~100m		
Summed wave fetch			OM	km
P/F Significant wave height (Hs)	<i>NOC wave model</i> ^g	~12km 1975-2005 2040-2050 2090-2100 DO, AOM monthly outputs		m
Hs P90				

P/F Tidal amplitude *OTIS-Regional Tidal Solution*^h ~**9km**
 1994-2011 OM m
 Tidal amplitude (i.e. half the range) mean monthly outputs

P/F Sea surface temperature (SST) *Bio-ORACLE*^{d,e} ~**10km**
 2000-2014
 Long-term SST min, mean, max 2040-2050
 2090-2100 AOM °C
 monthly outputs

P/F Sea surface salinity *Bio-ORACLE*^{d,e}
 ~**10km**
 Salinity min, P10, mean, P90, max 2000-2014
 2040-2050
 2090-2100 AOM PSS
 monthly outputs

P/F Air temperature *WorldClim v1.4*ⁱ
 Annual mean temperature (BIO1) ~**10km**
 Max Temperature of Warmest Month (BIO 5) 1960-1990
 Min Temperature of Coldest Month (BIO 6) 2041-2060 (CCSM4)
 2061-2080 AM °C
 monthly outputs

^a EU Copernicus Marine Environment Monitoring Service (CMEMS) operational IBI (Iberian Biscay Irish) Ocean Physics Analysis and Forecast Product (IBI_ANALYSIS_FORECAST_PHYS_005_001)

^b EMODnet Bathymetry Consortium, 2018. EMODnet Digital Bathymetry (DTM 2018). EMODnet Bathymetry Consortium. <https://doi.org/10.12770/18ff0d48-b203-4a65-94a9-5fd8b0ec35f6>

^c Déqué, M., Drevet, C., Braun, A., Cariolle, D., 1994. The ARPEGE/IFS atmosphere model: a contribution to the French community climate modelling. *Climate Dynamics* 10, 249–266. <https://doi.org/10.1007/BF00208992>

^d Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F., De Clerck, O., 2012. Bio-ORACLE: a global environmental dataset for marine species distribution modelling: Bio-ORACLE marine environmental data rasters. *Global Ecology and Biogeography* 21, 272–281. <https://doi.org/10.1111/j.1466-8238.2011.00656.x>

^e Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E.A., De Clerck, O., 2018. Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modelling. *Global Ecology and Biogeography* 27, 277–284. <https://doi.org/10.1111/geb.12693>

- ^f Burrows, M., 2012. Influences of wave fetch, tidal flow and ocean colour on subtidal rocky communities. *Marine Ecology Progress Series* 445, 193–207. <https://doi.org/10.3354/meps09422>
- ^g Briceno, L.M., Wolf, J., 2018. Future Wave Conditions of Europe, in Response to High-End Climate Change Scenarios. *Journal of Geophysical Research: Oceans* 123, 8762–8791. <https://doi.org/10.1029/2018JC013866>
- ^h Egbert, G.D., Erofeeva, S.Y., Ray, R.D., 2010. Assimilation of altimetry data for nonlinear shallow-water tides: Quarter-diurnal tides of the Northwest European Shelf. *Continental Shelf Research* 30, 668–679. <https://doi.org/10.1016/j.csr.2009.10.011>
- ⁱ Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25, 1965–1978. <https://doi.org/10.1002/joc.1276>

APPENDIX 6 IPCC MODELS RCP SCENARIOS

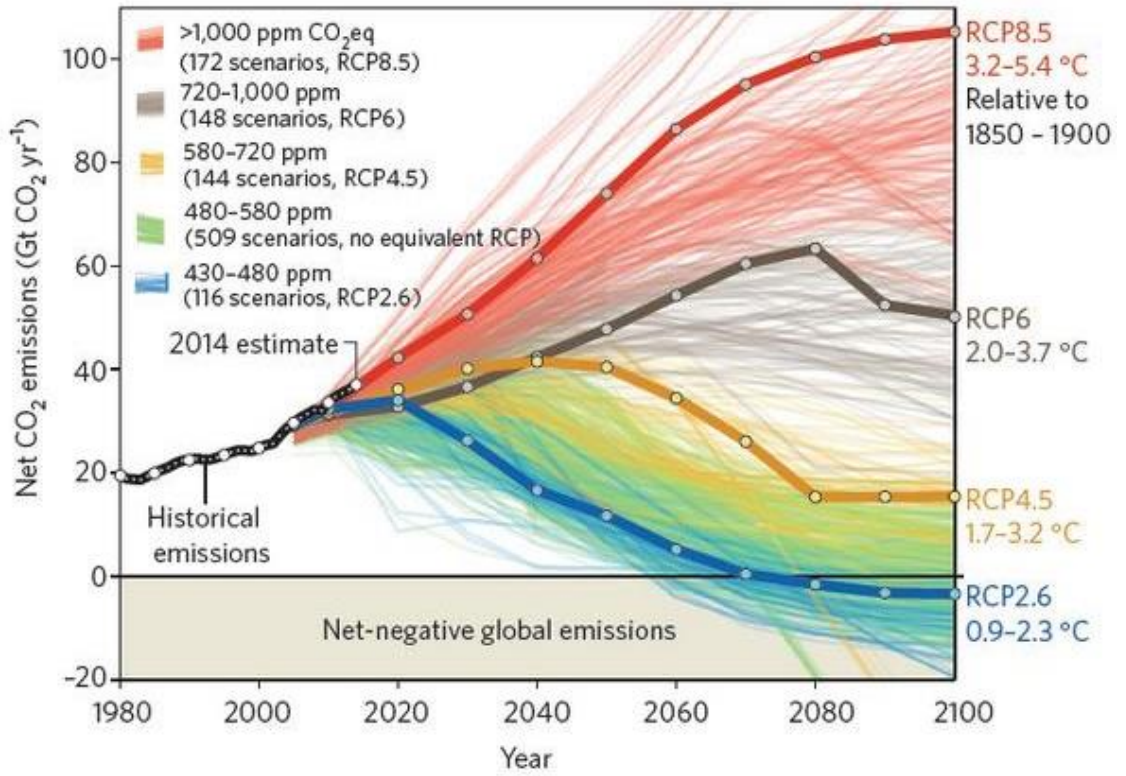


Figure 42. International Panel on Climate Change (IPCC) Representative Concentration Pathways (RCP). Image credit: Neil Craik, University of Waterloo

APPENDIX 7 MODELLING METHODS USED

Table 19. Description of modelling methods used in the study.

Modelling Technique	Description	Reference
gam: Generalized Additive Models	Regression based. Use algorithms called “smoothers” that automatically fit response curves to the data. Useful where the relationship between the variables is expected to be more complex than a linear or quadratic response.	Hastie (2017)
rf: Random Forest	Classification and regression machine-learning method. Averages the results of many classification trees constructed using a random subset of predictors.	Breiman (2001)
ens: ‘sdm’ Ensemble	Models with a TSS > 0.61 were used to build ensembles. Models were weighted based upon TSS value to produce final results.	Naimi & Araújo (2016)

APPENDIX 8 BINARY MAPS OF PRESENT-DAY PRESENCE/ABSENCE

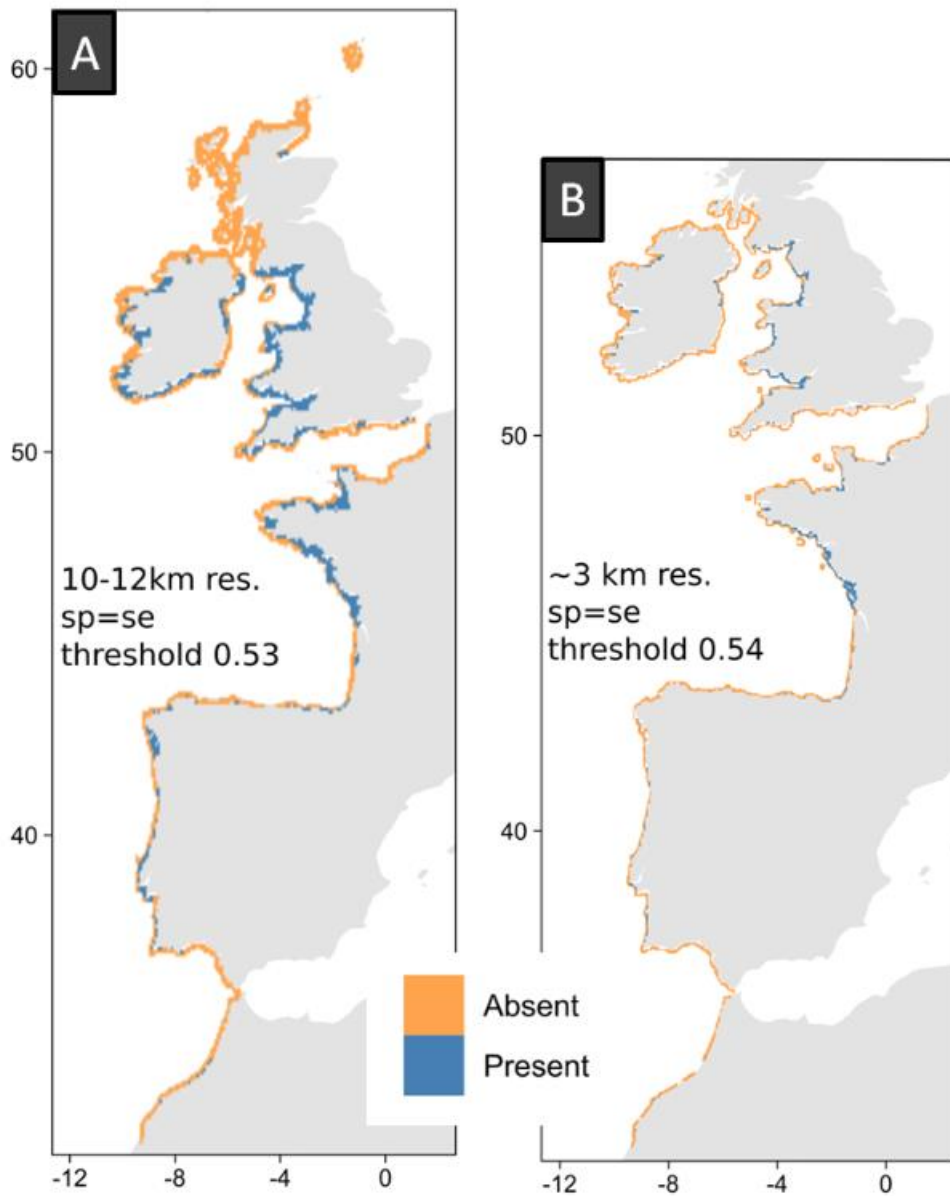


Figure 43. Binary maps of present-day presence absence for both model scales. A) 10-12km environmental predictor spatial resolution and bounding box, and B) ~3km environmental predictor spatial resolution and bounding box. The selected presence/absence threshold is the habitat suitability index score with an equal number of true positives and negatives (i.e. sensitivity equals specificity).

APPENDIX 9 MODEL EVALUATION THROUGH INDEPENDENT TRUE ABSENCE RECORDS OBTAINED FROM THE REEHAB DATASET ([HTTPS://DOI.ORG/10.17882/72164](https://doi.org/10.17882/72164)) FOR THE 1970-2019 TIME PERIOD.

Table 20 Correspondence between true absences and probability of presence for the validation dataset for the ~3km spatial resolution model. 498 true absence points, 63.5% of observations below sp=se threshold of 0.54

Probability threshold	Number of observations	% true negatives
0.0 to 0.2	114	22.9
0.2 to 0.4	128	25.7
0.4 to 0.6	113	22.7
0.6 to 0.8	94	18.9
0.8 to 1	49	9.8

Table 21 Correspondence between true absences and probability of presence for the validation dataset for the 10-12km spatial resolution model. 465 true absence points, 71.2% of observations below sp=se threshold of 0.53

Probability threshold	Number of observations	% true negatives
0.0 to 0.2	186	40.0
0.2 to 0.4	98	21.1
0.4 to 0.6	65	14.0
0.6 to 0.8	78	16.8
0.8 to 1	38	8.2

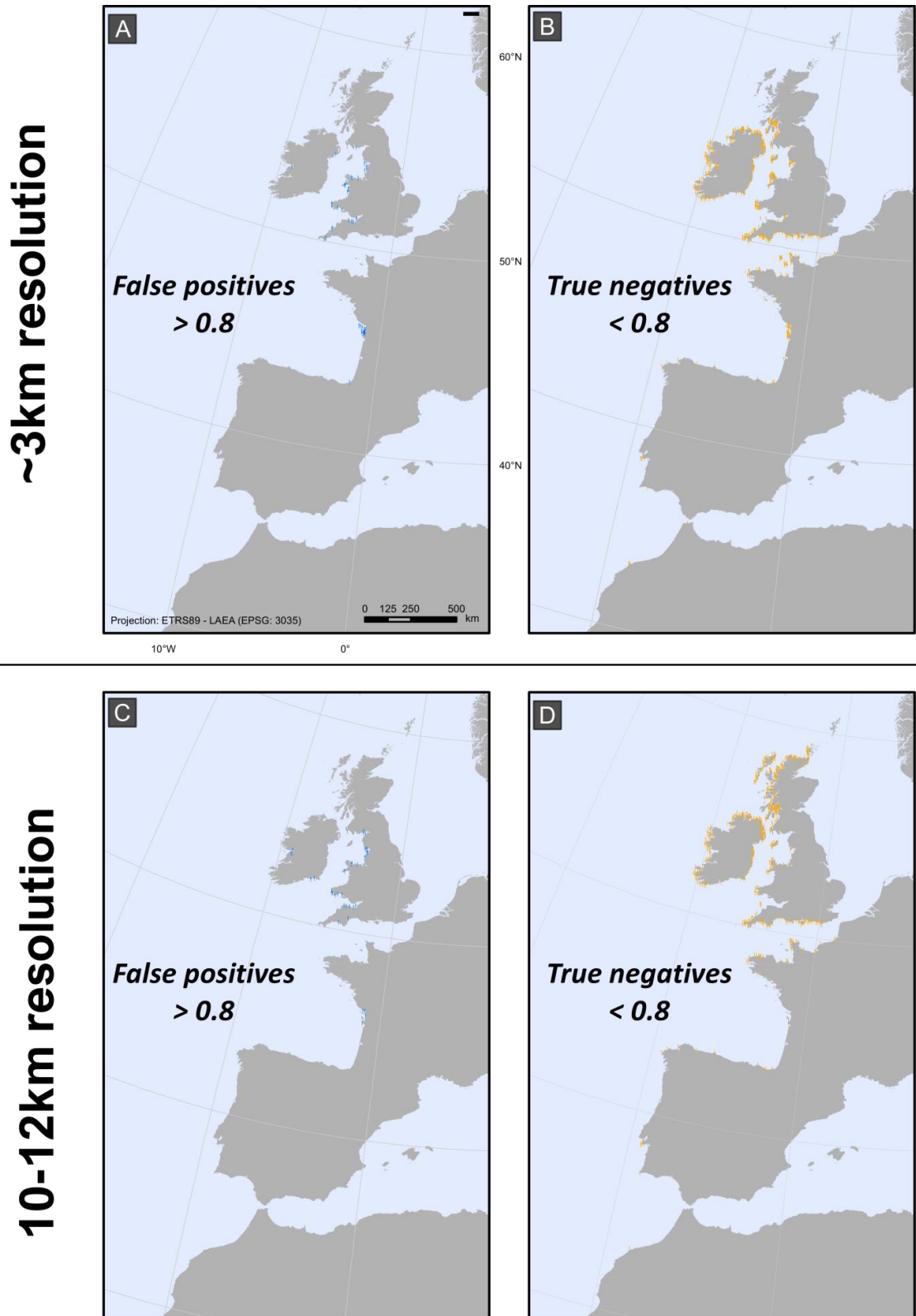


Figure 44. Maps illustrating the location of absence records, colour-coded according to the habitat suitability index threshold of 0.8. False-positive records are in blue, true negative records are in orange. The high threshold of 0.8 was selected to highlight areas with the greatest disparity between modelled habitat suitability and true absence records.

Titre : Macroécologie et distribution globale de l'espèce ingénieur *Sabellaria alveolata*

Mots clés : Biogéographie fonctionnelle ; Changement environnemental ; Habitat récifal ; Intertidal ; Macrophysiologie ; Traits biologiques

Résumé : La zone intertidale est particulièrement touchée par les changements environnementaux et les événements extrêmes des milieux terrestres et marins. A travers l'Europe, un habitat biogénique abritant une biodiversité unique atténue les écarts de température et d'énergie hydrodynamique caractéristiques de l'estran : les récifs de l'hermelle *Sabellaria alveolata*. Les critères de sélection de cet habitat d'intérêt communautaire sont en cours de définition. Pour tendre vers une définition du statut écologique, ce travail a contribué à mieux appréhender la niche écologique de *S. alveolata* à travers une approche multi-échelle et intégrée. La niche de l'espèce est explorée grâce à l'utilisation d'indicateurs biochimiques de la condition physiologique de l'organisme, reliés à l'apparence physique des bioconstructions.

La variation des traits biochimiques et reproductifs d'individus échantillonnés le long d'un gradient latitudinal européen de 15° permet de tester des théories divergentes sur la position optimale pour la reproduction de l'espèce dans son aire de distribution. Enfin, à travers la construction d'une base de données d'occurrences et un modèle statistique d'ensemble d'habitat, des cartes de prédictions présentes et futures d'habitats favorables ont pu être générées pour toute l'étendue de l'aire de répartition de l'espèce, le long de la côte Atlantique nord-est. En couplant des approches écophysiologiques et biogéographiques, ce travail apporte de nouvelles connaissances mécanistes sur une espèce ingénierant un habitat protégé, et jette les bases pour l'intégration des processus écologiques à large échelle, à travers le développement d'une approche biogéographique fonctionnelle.

Title: On the Macroecology and Global Distribution of the Ecosystem Engineer; *Sabellaria alveolata* in a Changing World

Keywords : Biological traits; Environmental Change; Functional Biogeography; Intertidal; Macrophysiology; Reef habitat

Abstract: The intertidal zone is affected by environmental change in both the marine and the terrestrial realms. All along Europe's coast, a unique biogenic habitat buffers the shores' environmental extremes for the high-diversity fauna it hosts: the reefs of the honeycomb worm *Sabellaria alveolata*. Despite being listed as a priority European Union habitat, the criteria for assessing candidate reefs have yet to be defined. As a prerequisite to defining the habitat's ecological status, the aim of this thesis was to further our knowledge of *S. alveolata*'s ecological niche through an integrated, multi-scale approach. Its niche was explored through the identification and analysis of physiological condition biochemical indicators, which were linked to the outward physical appearance of the bioconstructions in which the individuals resided.

Spatial and intraspecific variation in reproductive and biochemical traits were analysed in individuals sampled in ten sites between North Wales and central Portugal. This made it possible to test two divergent theories on the optimal position and environmental conditions for reproduction within a species range. Finally, by constructing a broad-scale occurrence records database which served as the response variable in a species global distribution model, predictive 'range-long' maps of present and future suitable habitats were generated for the whole north-east Atlantic coastline. By integrating ecophysiological and biogeographical approaches, this thesis has brought mechanistic insight to the broad-scale processes shaping the distribution of this key habitat-forming species.