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To cite this version:

Benjamin Benti. Behavioural responses of two cetacean species to natural and anthropogenic sounds. Acoustics [physics.class-ph]. Université de Strasbourg, 2020. English. NNT : 2020STRAJ002 . tel-03112595

HAL Id: tel-03112595
https://theses.hal.science/tel-03112595

Submitted on 17 Jan 2021

UNIVERSITÉ DE STRASBOURG

ÉCOLE DOCTORALE 414 : Sciences de la Vie et de la Santé

Équipe ECS, UMR 7247-85 CNRS, INRA, IFCE, Université de Tours

THÈSE présentée par :

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Soutenue le : **16 janvier 2020**

pour obtenir le grade de : **Docteur de l'université de Strasbourg**

Discipline/ Spécialité : écologie – éthologie

Behavioural responses of two cetacean species to natural and anthropogenic sounds

Réponses de deux espèces de cétacés aux stimuli acoustiques d'origine naturelle et anthropique

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ACKNOWLEDGEMENTS

First and foremost, I would like to thank my three Ph.D. supervisors: Charlotte Curé, Patrick Miller, and Valérie Dufour. Charlotte, merci de m'avoir proposé ce projet de recherche il y a trois ans et demi, et merci pour ton soutien et tes conseils tout au long de cette thèse. Patrick, I would like to thank you for your warm welcome in Saint Andrews. I'm glad that you encouraged me to follow up my own ideas, while providing such acute comments. Valérie, merci pour ta présence depuis notre première rencontre, lors de mon premier stage de recherche en 2013. Merci d'avoir su me recadrer à chaque fois que j'ai eu trop d'idées et pas assez de temps.

I would like to thank the research teams that hosted me during my Ph.D. Merci à l'équipe éthologie cognitive et sociale : Odile Petit, Bernard Thierry, Nancy Rebout, Thomas Huraux, et les autres. J'ai une pensée particulière pour Aïcha Mohamed Benkada, qui m'a devancé de peu sur ce long chemin qui mène au doctorat: merci pour toutes ces discussions farfelues qui nous ont remonté le moral dans les moments difficiles. Merci aux Cerema de Strasbourg et de Rouen. Merci à Cyrille Fauchard et toute son équipe pour leur accueil. I'm grateful to the Sea Mammal and Research Unit for their warm welcome and how much they taught me when I was just starting to study marine mammal biology. Thanks to Saana Isojunno and Steve Balfour, Eilidh Siegal, Gui Bortolotto, Alec Burslem, and the others.

I would like to thank all the institutions that made the research in this thesis possible. Merci à l'Ecole Normale Supérieure de Lyon et au Ministère de l'Enseignement Supérieur et de la Recherche de m'avoir donné la possibilité de me lancer dans la recherche en finançant mon contrat doctoral. I'm really grateful to the 3S consortium (Sea mammal Sonar Safety) which funded the fieldwork campaigns I took part in. Thanks to Petter Kvadsheim, Frans-Peter Lam, Lars Kleivane, Paul Wensveen, Lise Sivle, and all the others for their effort on the field and outside, and for having collected part of the data I analysed during my Ph.D. I will never forget the midnight swims in the Arctic ocean with Lucia Martin Lòpez and Rune Hansen. Nor will I forget being stuck in the Spildra harbour, with nothing to do but sip whisky in a hot tub with Takashi Iwata and wait for better weather.

I would like to thank all of my co-authors, for their useful advice and comments on the different chapters of my thesis: Martin Biuw, Heike Vester, and Florencia Noriega.

J'adresse un grand merci à toute ma famille: Maman (joyeux anniversaire !), Papa, Zack, Tom, mais aussi mes grand-parents, mes oncles et tantes, et mes cousins et cousines. Merci de m'avoir soutenu sans cesse et de m'avoir permis de m'échapper de la thèse quelques jours quand le besoin s'en est fait sentir.

Un énorme merci à Léa Lemaire, mon plus grand soutien, sans qui cette thèse n'aurait très certainement jamais vu le jour. Merci d'avoir toujours essayé de comprendre mes travaux et de les avoir parfois éclairés d'une lumière nouvelle. Merci d'avoir veillé à

mon sommeil et à mon alimentation lorsque le travail les reléguait au rang d'options. Ti amo.

Merci à tous mes amis de Lyon : Ronan Duchesne, mon ex-colocataire préféré, Baptiste Busi, Valentin Lefèvre, Robin Frot, Alexandre Torzynski, Thomas Cometx, Antonin Lentz, et tous les autres. Merci à Grégoire Beaudoire, Pierre-Louis Alzieu, et François Bojarski pour ces repas à peu près mensuels où tout était permis. Merci aux volleyeurs et volleyeuses de l'Ecole Normale Supérieure de Lyon: Chloé Serrÿn, Sébastien Maulat, Céleste Odier, Margaux Galland, ...

And thanks to all the ones I have forgotten who had a part in these three and a half years of Ph.D. Et merci à tous ceux et celles que j'oublie mais qui ont joué un rôle durant ces trois ans et demi de thèse.

EXTENDED SUMMARY (IN FRENCH)

Les stimuli environnementaux peuvent être porteurs d'information sur la localisation, la quantité, ou la qualité des ressources et des menaces existantes pour les individus. Il est crucial pour ces derniers d'identifier la signification biologique des signaux perçus afin d'adopter des réponses comportementales adaptées. Ne pas répondre à un stimulus lorsqu'il est présent peut exposer les animaux à un risque létal, si le stimulus est associé à une menace de prédation, ou à la pénurie alimentaire, si le stimulus permet de localiser un type de nourriture. Inversement, répondre à un stimulus alors qu'il n'est pas présent peut avoir un double coût pour les individus : le coût de la réponse comportementale déclenchée, et la perte des bénéfices liés à l'activité interrompue. Le risque de prédation fait partie des menaces les plus importantes qui pèsent sur les animaux. Il existe de nombreuses stratégies de réponse au risque de prédation : certaines d'entre elles visent à éviter de rencontrer le prédateur, d'autres ont pour but de survivre à une rencontre avec lui. Certaines de ces stratégies nécessitent de détecter le prédateur avant que celui-ci ne lance son attaque. Dans l'environnement, plusieurs types de signaux peuvent indiquer un risque immédiat de prédation et permettre d'exprimer de telles stratégies comportementales en amont d'une éventuelle attaque. On distingue les signaux de communication, qui sont dirigés depuis un émetteur vers un receveur et modifient le comportement de ce dernier, et les signaux interceptés, qui ne sont pas intentionnellement émis vers l'individu qui les reçoit. Les signaux de communication sont communément échangés entre individus de la même espèce, mais peuvent également être dirigés vers des individus d'autres espèces dans des contextes comme la prédation et la compétition. Parmi les signaux interceptés, on peut séparer l'interception de signaux involontairement émis et l'interception de signaux de communication échangés entre tierce parties (« eavesdropping »). Ces différents types de signaux peuvent passer par une ou plusieurs modalités sensorielles comme le toucher, la vision, l'odorat, ou l'ouïe. Chaque modalité sensorielle présente des avantages et des inconvénients liés à la nature des signaux, leurs propriétés de transmission dans le milieu environnant, et l'écologie et la biologie des espèces. Dans le milieu marin, les sons sont la principale source d'information. Dans l'océan, la lumière disparaît rapidement avec la profondeur et la turbidité de l'eau, et les signaux chimiques ne diffusent pas aussi librement que dans l'air. Les sons, quant à eux, se propagent cinq fois plus vite que dans l'air et sont peu absorbés, surtout dans les basses fréquences, par l'eau de mer. En milieu marin, les sons fournissent un support d'information rapide et longue portée comparé aux autres types de signaux sensoriels. D'ailleurs, les cétacés utilisent les sons pour de nombreuses fonctions biologiques essentielles à leur survie, comme la navigation, l'alimentation, la cohésion au sein des groupes sociaux, et la reproduction. Les cétacés se répartissent en deux sous-ordres : les mysticètes, ou baleines à fanons, et les odontocètes, ou baleines à dents. Les mysticètes sont des baleines de grande taille qui se nourrissent par filtration à travers des fanons.

La plupart des mysticètes migrent annuellement entre des aires de reproduction dans les eaux tropicales et des aires d'alimentation dans les eaux tempérées ou polaires. Les mysticètes produisent et ont une audition adaptée aux sons basse fréquences (ordre de grandeur : de 10 Hz à 10 kHz). Ils ne peuvent pas utiliser l'écholocation. Les odontocètes sont des baleines de taille variable. La plupart d'entre eux vivent en groupes sociaux tout au long de l'année. Tous les odontocètes produisent des clics d'écholocation dont ils se servent pour détecter les obstacles présents dans leur environnement et pour trouver leur nourriture. La production vocale des différentes espèces d'odontocètes est variable, mais leur répertoire vocal se décline en catégories de sons distinctes : les clics d'écholocation, les sifflements (des sons harmoniques dont la fréquence fondamentale est très modulée), et les cris pulsés (des répétitions de clics à haute fréquence qui paraissent tonales à l'oreille humaine). Les gammes de fréquence audibles par les cétacés se recoupent largement entre espèces, et les sons se propagent sur de longues distances dans l'océan ; ainsi, les cétacés sont susceptibles de détecter les sons produits par d'autres espèces de cétacés et d'en tirer des informations. Parmi ces sons, les sons d'orques présentent un intérêt particulier pour les autres espèces de cétacés. Les orques sont une espèce cosmopolite qui interagit avec la plupart des autres espèces de cétacés. Ce sont des prédateurs apicaux qui peuvent chasser la majorité des espèces de mammifères marins présentes dans leur habitat. De nombreuses espèces de cétacés adoptent des réponses anti-prédatrices en présence d'orques : certaines espèces s’enfuient quand elles rencontrent des orques, d’autres se regroupent et montrent des réponses agressives. Toutefois, toutes les interactions entre les orques et les autres espèces de cétacés n’impliquent pas des relations de prédation. De nombreuses observations font état de cétacés voyageant ou se reposant en groupes mixtes avec des orques sans montrer de réaction. Certaines espèces, comme les baleines à bosse, se nourrissent parfois dans la même zone que les orques, et occasionnellement de la même proie. Cette variabilité dans la nature des interactions entre les orques et les autres cétacés est à relier à la variabilité écologique des orques et de leurs relations trophiques avec les autres cétacés. Dans certaines populations, il existe des écotypes sympatriques qui ont des régimes alimentaires et des comportements différents. Les premiers écotypes d’orques ont été décrits dans le Pacifique nord : les orques « resident » se nourrissent majoritairement de poisson, alors que les orques « transient » chassent exclusivement des mammifères marins (surtout des pinnipèdes, mais aussi des odontocètes et des mysticètes). Ces deux écotypes ont également des comportements vocaux différents ; notamment, les orques « resident » se servent de l’écholocation pour trouver leur proie, alors que les orques « transient » chassent en silence et ne deviennent vocales que lorsqu’elles lancent une attaque. Les cris et sifflements des orques « resident » sont plus forts, plus longs, et de plus haute fréquence que les cris et sifflements des orques « transient ». Toutes les populations d’orques ne présentent pas une différentiation aussi marquée que les orques « resident » et « transient ». Néanmoins, l’existence de différences comportementales, et plus particulièrement de différences de comportement vocal, entre les orques se nourrissant à différents niveaux trophiques se retrouve dans plusieurs populations d'orques, dont celle du nord-est Atlantique. Les différents écotypes d'orques produisent donc des sons différents, et sont engagés dans des relations écologiques différentes avec les autres cétacés : il serait avantageux pour les autres espèces de cétacés de différentier les sons des écotypes d'orques et d'adapter leur réponse au type d'orque identifié.

Le premier axe de ma thèse a porté sur les réponses des cétacés aux sons hétérospécifiques, avec l'étude des réponses comportementales aux repasses de sons de différents écotypes d'orques. La capacité à discriminer entre les sons de différents écotypes d'orques a été démontrée chez une espèce de pinnipède, le phoque commun, et une espèce d'odontocètes, le globicéphale noir. Dans la première partie de ma thèse (chapitre 1), j'ai étudié les réponses comportementales d'une espèce de mysticète, la baleine à bosse, à des repasses (« playbacks ») de sons d'orques afin de déterminer si elles pouvaient différentier les sons produits par différents écotypes d'orques. J'ai utilisé les sons de deux écotypes d'orques : les orques mangeuses de mammifères marins du nord-est Pacifique (« transient »), et les orques mangeuses de hareng de Norvège. J'ai effectué les expériences de repasse de ces sons d'orques à des baleines à bosse au large de la Norvège. Les individus testés étaient familiers avec les orques mangeuses de hareng : les deux espèces se nourrissent de la même proie dans les fjords en hiver.

L'hypothèse émise est que les sons d'orques mangeuses de hareng pourraient signaler la présence d'un compétiteur (et donc éventuellement la présence de nourriture). Les baleines à bosse testées en Norvège étaient au contraire non-familières avec les sons des orques mangeuses de mammifères marins du Pacifique. L'hypothèse émise est que ce stimulus, de par sa nouveauté et ses caractéristiques communes aux sons d'orques mangeuses de mammifères marins, pourrait être perçu comme une menace intense par les baleines à bosse. J'ai suivi le comportement des baleines à bosse avant, pendant, et après la diffusion des sons d'orques en combinant des observations visuelles du comportement exprimé en surface et le déploiement de balises multi-capteur non-invasives (accrochées aux individus pour quelques heures avec des ventouses). J'ai analysé la réponse comportementale des baleines à bosse en me focalisant sur les déplacements horizontaux, en quantifiant l'approche ou l'évitement de la source sonore en réponse à la présentation du stimulus ainsi que la tortuosité de la trajectoire de baleines à bosse, et de mouvement verticaux, en mesurant la profondeur et la durée maximale de plongée des baleines à bosse avant, pendant, et après la diffusion des sons d'orques. J'ai démontré que les baleines à bosse répondent différemment aux sons de différents écotypes d'orques, et qu'elles étaient donc capables de différentier ces sons. Pendant la repasse de sons d'orques compétitrices familières, les baleines à bosse se sont approchées du haut-parleur (situé à environ 8 m de profondeur) et se sont mises à plonger plus profondément. En comparaison, les baleines à bosses ont eu tendance à éviter horizontalement la source des sons d'orques potentiellement prédatrices et non-familières. De plus, les réponses comportementales des baleines à bosse aux sons d'orques n'étaient pas les mêmes au large pendant l'été et en hiver dans les fjords : l'évitement horizontal était clair et très marqué au large pendant l'été, et plus mitigé (réponses variables et moins marquées) pendant l'hiver dans les fjords. La composante verticale de la réponse présentait également des différences entre les deux contextes écologiques. J'ai émis deux hypothèses pour expliquer cette différence de réponses entre les deux contextes. D'une part, les baleines à bosse avaient des réserves lipidiques réduites au large pendant l'été, qui correspondait au début de la saison d'alimentation : les baleines avaient passé toute la saison de reproduction dans les eaux tropicales, ainsi que les migrations dans les deux sens, en se nourrissant peu ou pas. En hiver dans les fjords, la saison d'alimentation touchait à sa fin et les baleines étaient en condition optimale, prêtes à partir vers les aires de reproduction. De ce fait, pendant l'été, les baleines à bosses étaient à la fois plus vulnérables à la prédation par les orques, et avaient également plus de besoins énergétiques que pendant l'hiver, ce qui a pu influencer leur prise de décision. D'autre part, la présence d'orques mangeuses de hareng, compétitrices des baleines à bosse, en grand nombre dans les fjords pendant l'hiver aurait pu réduire la capacité des baleines à bosse à reconnaître les sons d'orques non-familières potentiellement prédatrices.

Les activités humaines, qui ne cessent de croître dans l'environnement, représentent une autre source d'information pour les animaux. Les stimuli sensoriels produits par les activités humaines, aussi appelés stimuli anthropiques, jouent un double rôle pour les animaux : ils peuvent représenter une source de nuisance directe pour les animaux, et ils peuvent signaler certains risques associés aux activités humaines, tels que des blessures physiques et des dommages physiologiques. En milieu marin, l'utilisation des sonars militaires fait partie des sources de perturbations anthropiques (ici, des sons) les plus intenses. La corrélation spatiale et temporelle entre des exercices impliquant des sonars militaires et des échouages massifs de cétacés a soulevé des préoccupations sur les impacts des sonars militaires sur l'écosystème marin, et sur les cétacés en particulier. Les émissions sonar peuvent provoquer des dommages physiques directs chez les cétacés (pertes temporaires et permanentes d'audition), perturber leur comportement, et masquer les signaux de communication et d'écholocation qui sous-tendent de nombreuses de leurs fonctions biologiques. Au cours des deux dernières décennies, plusieurs projets de recherche se sont succédé pour caractériser les réponses comportementales des cétacés aux sonars militaires. Les réponses les plus communément observées ont été l'évitement (horizontal ou vertical) et l'interruption de certaines activités fonctionnelles importantes pour la survie des individus, comme l'alimentation et le repos. D'autres réponses comportementales observées ont montré des changements de comportements sociaux (e.g. regroupement et perte de cohésion sociale), des changements du profil de plongée, et des modifications du comportement vocal. Toutefois, les réponses comportementales des cétacés aux sonars militaires sont très variables entre les espèces et entre les individus. Certaines espèces, comme les baleines à bec, apparaissent très sensibles aux sonars militaires : lorsqu'elles sont exposées aux sonars militaires, elles cessent de se nourrir et quittent leur zone d'alimentation pendant plusieurs heures après la fin de la transmission sonar. Au contraire, certaines espèces comme le globicéphale noir semblent moins sensibles aux sonars militaires : leurs réponses comportementales sont déclenchées à des niveaux sonores plus élevés, et cessent généralement avec la fin de la transmission sonar. Mais les réponses comportementales des cétacés exposés au sonar militaire varient également au sein d'une espèce, en fonction du type de signal, de l'activité comportementale dans laquelle les individus sont engagés avant l'exposition au sonar, et de la procédure d'émission des signaux sonar. Il est donc nécessaire de mieux caractériser les réponses des cétacés aux sonars militaires. Il faut aussi parvenir à interpréter la signification biologique des comportements que les cétacés adoptent en réponse au sonar militaire. En effet, les sons anthropiques comme les sonars militaires ont fait irruption récemment dans l'environnement, à l'échelle évolutive. De fait, les coûts et bénéfices évolutifs des stratégies de réponses des cétacés au sonar n'ont certainement pas encore été intégrés au processus de sélection naturelle. Une des approches méthodologiques possibles pour comprendre la signification biologique des réponses comportementales aux sonars militaires est de les comparer aux réponses provoquées par des stimuli naturels perturbation de signification biologique connue (e.g. risque immédiat de prédation). Les réponses comportementales aux stimuli naturels sont stables évolutivement si les bénéfices qu'elles apportent à long terme sont plus importants que leurs coûts à court terme (en temps, en énergie, en opportunités perdues). Par exemple, les réponses comportementales au risque de prédation sont coûteuses (fuite, affrontement), mais le bénéfice à long-terme (la survie) est plus important que leurs coûts. Les réponses aux stimuli naturels devraient modeler les réponses aux stimuli anthropiques. Ainsi, même si les coûts et bénéfices exacts des différentes réponses ne sont pas les mêmes, comparer les réponses comportementales aux sonars militaires aux réponses anti-prédation permet d'évaluer le niveau de menace auquel sont perçus les sonars militaires par les animaux. En milieu marin, les stimuli utilisés pour simuler le risque de prédation sont les sons d'orques. Le second axe de ma thèse a porté sur l'étude des réponses comportementales des cétacés à un stimulus anthropique, le sonar militaire, et leur comparaison aux comportements anti-prédateurs exprimés en réponse à la détection de sons d'orques, afin d'interpréter leur signification biologique.

Dans la seconde partie de ma thèse (qui regroupe les chapitres 2 et 3), j'ai étudié en particulier les réponses vocales des globicéphales noirs à certains types de sonars militaires communément utilisés à l'échelle internationale, et à des repasses de sons d'orques simulant la présence de ces derniers. Une partie des réponses comportementales des globicéphales noirs aux sonars militaires est présentée dans de précédentes publications, mais leurs réponses vocales n'avaient que peu été étudiées. Les globicéphales noirs produisent des sons typiques d'odontocètes : des clics d'écholocation, des sifflements et des cris pulsés. Leurs cris pulsés sont composés de plusieurs sous-unités qui peuvent être harmoniques, pulsées, ou bruitées, voire présenter des sons intermédiaires entre ces différents types de sons. Les globicéphales ont un répertoire vocal étendu : l'inspection audio-visuelle d'enregistrement a permis de définir 125 types de cris. Cette classification manuelle s'est concentrée sur les cris stéréotypés, mais la plupart des vocalisations de globicéphale noir semblent varier graduellement le long d'un continuum, ce qui rend leur classification particulièrement difficile. Dans le chapitre 2 de cette thèse, j'ai développé un algorithme de classification autonome qui prend en compte l'aspect graduel, ou non-stéréotypé, des vocalisations animales. Cet algorithme repose sur le principe du « fuzzy clustering » et sur les coefficients cepstraux en fréquence Mel. Au lieu d'assigner à chaque vocalisation un unique type, comme le font les procédures de classification strictes, le « fuzzy clustering » définit des stéréotypes apparents dans le jeu de données : chaque cri a un score d'appartenance à chaque catégorie, qui correspond à sa similarité avec le stéréotype de la catégorie. Les stéréotypes apparents sont définis à partir de la distribution des vocalisations dans le jeu de donnée : ni le nombre de catégories, ni leurs caractéristiques ne sont renseignées par l'utilisateur. Afin de décrire les vocalisations, j'ai eu recours aux coefficients cepstraux en fréquence Mel. Cette méthode, initialement utilisée pour automatiser la segmentation et l'identification des phonèmes dans la production vocale humaine, est de plus en plus utilisée pour étudier les comportements vocaux des animaux. En effet, les coefficients cepstraux en fréquence Mel représentent une méthode efficace pour comprimer l'information sur la distribution de l'énergie le long du spectre fréquentiel en un nombre réduit de variables. Dans un but de classification, ils sont donc à la fois plus complets que les paramètres acoustiques mesurés sur les spectrogrammes, et ont un sens acoustique plus clair que d'autres méthodes de description basées sur les descripteurs d'images ou impliquant des procédures de transformation des paramètres. Les coefficients cepstraux en fréquence Mel présentent aussi l'avantage d'être définis pour tous les types de cris (harmoniques, pulsés, bruités, …), contrairement à d'autres paramètres acoustiques comme ceux liés à la fréquence fondamentale. J'ai testé cette procédure de classification sur un jeu de 279 cris de globicéphale noir. Ces cris ont été préalablement classés selon le catalogue le plus récent pour l'espèce. Ce jeu de données représente une fraction du répertoire vocal des globicéphales noirs : il contient huit types de cris (dix en incluant les sous-types) sur les 125 définis. La procédure de classification que j'ai développée n'a pas atteint la même précision que celle impliquant des opérateurs humains entraînés quatre catégories vec le « fuzzy clustering » contre huit types de cris du catalogue défini par les opérateurs. Les catégories définies par le « fuzzy clustering » étaient basées sur la présence ou absence de motifs de distribution d'énergie à l'échelle du cri complet, alors que l'identification des cris définis dans le catalogue est basée sur l'association de sous-unités séparées par des courts silences ou des changements dans les caractéristiques fréquentielles. Cette différence de résolution temporelle peut être à l'origine de la précision moindre du « fuzzy clustering ». Toutefois, la procédure du « fuzzy clustering » fournit des outils pour quantifier et visualiser la variation graduelle des vocalisations entre les stéréotypes apparents. Ces outils pourraient permettre d'analyser les aspects fonctionnels de cette variation graduelle.

Dans le chapitre 3 de cette thèse, j'ai utilisé l'outil de classification développé dans le chapitre 2 pour analyser les réponses vocales des globicéphales noirs à différents types de sonar militaires ainsi qu'à la repasse de sons d'orques potentiellement prédatrices. J'ai enregistré le comportement vocal de globicéphales noirs à l'aide de balises accrochées temporairement sur le dos des individus par des ventouses. En plus des enregistrements effectués par la balise, des paramètres sur la taille du groupe et sa cohésion étaient notées lors d'observations visuelles réalisées depuis la surface. J'ai utilisé trois types de sonar militaire : des signaux en augmentation hyperbolique de 1 à 2 kHz, en augmentation hyperbolique de 6 à 7 kHz, et en diminution hyperbolique de 2 à 1 kHz. Les trois sonars étaient pulsés et suivaient le même schéma de transmission : des signaux de 1 s séparés par des silences de 19 s. Comme dans les conditions d'exercices militaires, les sonars militaires étaient transmis depuis une source sonore remorquée par un navire (le navire source). Le navire source approchait un globicéphale noir focal pendant les transmissions. Pour tester l'effet de l'approche du navire tractant la source sonar seule (sans transmission sonar), j'ai également effectué des expériences lors desquelles le navire remorquant la source sonar approchait l'individu focal, mais sans émettre de signal. Pour interpréter les réponses vocales des globicéphales noirs aux sonars militaires, j'ai aussi effectué des repasses de sons d'orques mangeuses de mammifères marins. J'ai utilisé deux types de signaux contrôles pour les expériences de repasse : des enregistrements de bruits ambiant sans vocalisations d'orques (contrôle négatif) et des signaux artificiels de 1 s dont la fréquence augmentait de façon hyperbolique de 1 à 2 kHz (contrôle positif). Je me suis intéressé à trois paramètres du comportement vocal des globicéphales noirs : le niveau global d'activité vocale, le type de cris produits, et la typicalité (c'est-à-dire le caractère stéréotypé ou graduel) des cris produits. J'ai mesuré l'activité vocale des globicéphales noirs en utilisant les enregistrements acoustiques de la balise. Toutes les vocalisations de globicéphales noirs ont été annotées dans les enregistrements : des opérateurs entraînés ont noté leur temps de commencement et de fin, et les ont classés en signaux d'écholocation ou en signaux sociaux. J'ai compté le nombre de cris annotés et leur durée cumulée avant, pendant, et après l'exposition des globicéphales noirs aux différents stimuli acoustiques. Je n'ai pris en compte que les cris dont le rapport signal sur bruit dépassait 3 dB (mesuré en comparant la moyenne quadratique du niveau sonore entre le cri de globicéphale noir et une fenêtre de bruit ambient de 0.2 s juste avant le cri). Toutes les phases expérimentales (avant, pendant, et après l'exposition) n'ayant pas la même durée, j'ai divisé le nombre et la durée cumulée des cris par la durée de chaque phase expérimentale. De plus, les balises n'enregistrent pas uniquement les vocalisations de l'individu balisé, mais aussi celles produites par ses congénères situés à proximité. Le nombre et la durée cumulée des cris sont donc des mesures de l'activité vocale au niveau du groupe social de l'individu balisé. J'ai divisé ces paramètres vocaux par la taille moyenne du groupe de l'individu balisé (estimée lors des observations visuelles à la surface) pendant chaque phase expérimentale pour obtenir une mesure de l'activité individuelle des membres du groupe de l'individu balisé. Pour déterminer le type et la typicalité des cris, j'ai classé les vocalisations enregistrées par la balise en utilisant la procédure définie au chapitre 2. J'ai pris en compte les cris dont le rapport signal sur bruit dépassait 6 dB et qui n'étaient pas recoupés par d'autres cris, par des signaux d'écholocation, et pas des bruits ambiants. J'ai mesuré le changement des scores d'appartenance moyens des cris (une mesure du changement d'utilisation des différents types de cris) et le changement de la typicalité moyenne des cris (une mesure du caractère stéréotypé ou graduel des cris) entre les phases expérimentales. J'ai observé une augmentation de l'activité vocale en réponse au sonar de 1 à 2 kHz et à la repasse de signaux artificiels. Les changements d'activité vocale en réponse aux autres type de sonar (de 6 à 7 kHz et de 2 à 1 kHz), aux repasse de sons d'orques, et aux différentes expériences contrôles étaient variables. J'ai observé des changements dans les types de cris utilisé en réponse à toutes les expériences. Toutefois, aucun type de cris n'était constamment produit en réponse aux stimuli acoustiques diffusés. Les réponses aux sonars militaires étaient globalement plus importantes que les réponses aux repasses de sons d'orques. Le sonar de 1 à 2 kHz semblait être perçu différemment des autres signaux sonars. La ressemblance des réponses à la repasse de sons d'orques et de signaux artificiels ayant la même structure que le sonar de 1 à 2 kHz (même type de cri utilisé pendant la présentation des deux stimuli) m'a mené à l'hypothèse que la combinaison de la bande de fréquence et du motif de modulation fréquentielle du sonar de 1 à 2 kHz pourraient s'approcher de a structure acoustique des sons d'orques par rapport à d'autres signaux sonar, et engendreraient des réponses plus proches des réponses anti-prédation. Les différences dans les conditions d'exposition des cétacés aux sonars militaires (grand navire remorquant la source sonore, transmission initialement longue distance puis approche de l'individu balisé, niveaux sonores intenses jusqu'à 214 dB re 1 μPa) et aux sons d'orques (sons diffusés depuis un plus petit navire, moteur à l'arrêt pendant la diffusion, à une distance moyenne de l'individu balisé, et à plus bas niveaux sonores) peuvent expliquer une partie des différences entre les réponses comportementales aux sons d'orques et aux sonars militaires. Au cours de cette thèse, j'ai démontré qu'une espèce de mysticète, la baleine à bosse, répondait différemment aux sons d'écotypes d'orques indiquant des situations écologiques différentes (risque de prédation et présence d'un compétiteur alimentaire), et qu'elles étaient donc capables de différencier ces stimuli. Cette capacité à différencier les sons de différents écotypes d'orques et à adopter une réponse comportementale adaptée à la relation écologique avec le type d'orque détecté a également été démontrée chez une espèce de pinnipède, le phoque commun, et une espèce d'odontocète, le globicéphale noir. Il semblerait donc que cette capacité soit répandue chez les mammifères marins. Les cétacés manifestent des réponses comportementales diverses lorsqu'ils sont exposés au sonar militaire. Certaines similitudes entre les réponses comportementales des cétacés au sonar militaire et au risque de prédation (simulé par la diffusion de sons d'orques prédatrices) semblent indiquer que les sonars militaires sont perçus comme une menace par les cétacés, mais pas aussi pressante que le risque de prédation. Toutefois, les réponses au sonar militaire et au risque de prédation présentent également des spécificités. Les conditions d'exposition contrastées entre les expositions contrôlées au sonar militaires et les repasses de sons d'orques (caractéristiques du signal, taille et déplacements de la source sonore, niveaux sonores) doivent être prises en compte pour interpréter la signification biologique et le niveau de sévérité des réponses comportementales observées. Des travaux supplémentaires sont nécessaires pour comprendre dans leur ensemble les interactions acoustiques entre les espèces de cétacés et le degré de perturbation des sources sonores anthropiques sur leur mode de vie.

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1: GENERAL INTRODUCTION

1.1: External stimuli carry vital information about the environment

Adopting appropriate responses to environmental stimuli has a crucial influence on animal fitness. Diverse stimuli that animals receive from various external sources may carry information about the location, quantity, and quality of both resources and threats in the surrounding area.

For instance, the risk of predation is one of the main threats faced by animals, and effective responses to predation risk indicators will increase the fitness of individuals. There are numerous strategies to respond to perceived predation risk: animals may fight against predators, form groups or schools to reduce the individual risk of predation, seek refuge, or try and avoid detection. These responses may be broadly categorised as fight, flight, or stealth strategies (Ford and Reeves, 2008). They can be expressed at the individual (individual escape manoeuvres: Ford et al., 2005; Whitford et al., 2017) or the collective scale, in same-species groups (group silencing in beaked whales: Soto et al., 2018) or mixed-species assemblages (Hurd, 1996; Dutour et al., 2017). According to their timing within a predator attack, we distinguish primary and secondary responses: 'primary responses' occur before predators are able to detect their prey and aim to avoid physical encounter with predators, and 'secondary responses' happen once predators have launched their attack and focus on surviving the encounter (Ford and Reeves, 2008).

In some contexts, it may be adaptive to be aware of factors that influence predation risk ahead of time or from a distance. There are multiple sources of information and several kinds of signals in the environment which may carry such valuable information for animals. Vigilance to cues and signals that precede or indicate potential increases in risk would allow the triggering of primary anti-predator responses. Such primary responses could be used to avoid fights against predators and subsequent injuries and would be a mean to decrease the costs of predation.

1.1.1: Communication signals

Communication refers to the directed transmission of a signal from a signaller to a receiver, which influences the behaviour of the receiver (Bradbury and Vehrencamp, 2011). Communication typically takes place within a species: con-specifics may exchange signals to maintain social cohesion (individual vocal signatures in bottlenose dolphins: King et al., 2018; group-specific calls of killer whales: Miller and Bain, 2000; collective movements in primates: Schlenker et al., 2016), to signal the boundaries of their territories to neighbours (vocal displays: Schmidt et al., 2007; olfactory marking: Zub et al., 2003), or to signal the presence of an external threat to group members (Collier et al., 2017).

However, communication is not limited by species boundaries: some signals are directed towards members of other species. For instance, alarm and mobbing calls may be directed towards hetero-specific animals to recruit them to a mobbing event (Suzuki, 2016; Dawson Pell et al., 2018), or towards predators to make detection known to them and thereby deter their attack (Curio et al., 1978) or to confuse them (Corcoran and Conner, 2017). Individuals may direct their signals toward prey species to manipulate their behaviour (Ford et al., 2005; Simon, 2005) or towards competitors to reduce their efficiency (Wollerman, 1999).

1.1.2: Intercepted signals

Animals may also intercept signals, i.e. detect signals that were not intended for them and infer information from such cues. We can distinguish two kinds of signals that can be intercepted.

First, individuals may perceive involuntary cues. These cues are not intentionally broadcasted signals, but they can still be informative for eavesdroppers. For instance, chemical and visual cues play a central role in the context of predation: predators make use of involuntary prey cues to detect them (Koivula and Viitala, 1999; Bouchard et al., 2019), whereas prey are likely to make appropriate defensive responses, such as fleeing, upon detection of predator cues (Schoeppner and Relyea, 2009; Amo et al., 2008; Billings et al., 2015).

The second kind of signal that animals can intercept is communication signals directed to a third-party. We refer to such interception of communication signals as eavesdropping (McGregor, 1993). Individuals can intercept communication signals exchanged between con-specifics (satellite males in crickets: Cade and Cade, 1992; food signalling in songbirds: Hillemann et al., 2019). Eavesdropping on hetero-specific communication signals can be informative as well. Communication signals intercepted from prey from prey may be used to increase foraging efficiency (Barrett-Lennard et al., 1996; Corcoran and Conner, 2017), and signals intercepted from predators to avoid predation (Billings et al., 2015). Signals from species sharing common predators could signal predator presence (Mahr and Hoi, 2018; Dawson Pell et al., 2018) or absence (Lilly et al., 2019). Vigilance to competitor signals may help locate resources (Jourdain and Vongraven, 2017; Pollock et al., 2017) or avoid areas of high-intensity competition (Evans et al., 2009). Cases of hetero-specific eavesdropping occur both within taxa (Dawson Pell et al., 2018) and across taxa (Fuong et al., 2014; Lilly et al., 2019).

1.1.3: Anthropogenic sources

Human activities present a number of risks for animal populations. These risks include physical and physiological damage: collisions with vehicles are responsible for an average of 4 % of annual roe deer deaths in Europe (Bruinderink and Hazebroek, 1996); pile-driving sounds can trigger hearing loss in harbour seals (Finneran, 2015; Kastelein et al., 2018); urban environments result in elevated stress levels in birds (Slabbekoorn and Ripmeester, 2008). Apart from damage risks, human activities can also alter the behaviour of animals. Human-related light sources influences the migratory route of birds (McLaren et al., 2018). Vessel traffic noise can mask biological sounds (Jensen et al., 2009a) or displace populations from biologically important areas (Glockner-Ferrari and Ferrari, 1990). Urban noise can alter inter-specific interactions: for instance, prey may have reduced abilities to detect predators in noisy habitats (Francis et al., 2009).

Sounds associated with human activities, referred to as anthropogenic sounds, can play a double role in this context. On the one hand, they can represent direct perturbation sources themselves (masking of biological sounds, ear damage for intense sounds); on the other hand, they could serve as hints indicating the presence of human activities and their potential threats to the animals.

1.1.4: The costs of misinterpreting environmental stimuli

Environmental stimuli, including signals produced by hetero-specific animals and anthropogenic sources, may carry valuable information about the environment. It is essential to accurately recognise the ecological significance of such stimuli, or at least to consistently associate them with appropriate behavioural responses to gain the fitness-enhancing benefits of the response. False negatives, i.e. the failure to display an appropriate response in the presence of a stimulus, incur a shortfall of resource acquisition (if the stimulus is associated to the presence or location of a resource) or a risk to be killer or injured (if the stimulus is related to the presence of a threat). False positives, i.e. triggering a behavioural response to a stimulus in its absence, can also reduce fitness. Uncalled for changes in behaviour imply excess energy expenditures and the loss of the benefits related to the functional behavioural state that was disturbed (Isojunno et al., 2016).

The importance of environmental stimuli for the gathering of information is heightened in unpredictable environments such as the marine environment. The marine environment is also a type of environment with limited access to information.

1.2: The marine environment is a prime setting for the study of eavesdropping

1.2.1: Sounds are a primary support of information in the marine environment

Environmental stimuli can be perceived through one or several sensory modalities such as: touch (Thomas and Gruffydd, 1971), olfaction (Zub et al., 2003; Mahr and Hoi, 2018), vision (Rauber and Manser, 2018), and audition (Billings et al., 2015). Each of these modalities presents limitations, due to the nature of the signals, the transmission properties of the environment, and the species ecology. For instance, tactile stimuli only exist at very short-range. Visual information requires a minimum amount of light to be detected, and they cannot be transmitted through opaque obstacles. Chemicals signals remain for a long-term in the environment, but do not diffuse over large range: they are not very suitable for highly mobile species.

In the marine environment, light is absorbed strongly by the seawater, so ambient light quickly fades with depth and visual detection distances are limited. Moreover, the turbidity of seawater further reduced the propagation of light. Visual signals are typically most usable at close ranges when animals are close enough to the sea surface for ambient light to be present. Most marine species, in particular marine mammals, have large habitat ranges and could not rely on chemical signals for communication, even though they may be used during foraging (Bouchard et al., 2019). By comparison, the acoustic channel provides an efficient means for unimodal, adjustable, fast, long-range information transfer in the marine environment. Indeed, sounds travel five times faster underwater than in the air, and acoustic signals suffer little absorption in sea water. Acoustic energy absorption levels are frequency-dependent and particularly low for low frequency sounds (e.g. Munk et al., 1994). The content of acoustic signals can vary in the frequency, the time, and the amplitude domains, providing wide degrees of freedom to encode information in sounds.

1.2.2: Cetaceans

Most species of marine mammals and cetaceans in particular are highly mobile, which may magnify the prominent benefit of using sounds to detect features in the marine environment. Indeed, cetaceans rely on acoustic signals for multiple biological functions: navigation and foraging (Miller et al., 2004), maintenance of social cohesion (Nousek et al., 2006; King et al., 2018), and reproduction (Herman, 2017) for instance.

There are two sub-orders of cetaceans: the mysticetes, or baleen whales, and the odontocetes, or toothed whales (Würsig et al.,2018). Mysticetes are larger whales which share adaptations for filter feeding (large heads and mouths, laryngeal grooves for expansion, and baleens for filtering: Cade et al., 2016). Most species migrate annually between high-latitude, cold water feeding grounds and tropical, warmer waters breeding grounds (e.g. humpback whales: Clapham and Mead, 1999; gray whales: Cummings and Thompson, 1971). Mysticetes are adapted for the production and reception of low-frequency sounds, but do not produce echolocation signals (Au et al., 2006; Berchok et al., 2006; Parks et al., 2019).

Odontocetes vary in size: from small dolphin species, 1.5 m (e.g. Commerson dolphins: Yoshida et al., 2014) to sperm whales, 15 m (Würsig et al., 2018). Though some, as adult sperm whales, are thought to be solitary, many odontocetes live in social groups all year long (e.g. Ottensmeyer and Whitehead, 2003; Fearnbach et al., 2014). All odontocetes share the morphological adaptations for the use of echolocation (Racicot et al., 2019).

Toothed whales produce a variety of sounds: whistles, echolocation clicks, and pulsed calls. Whistles are tonal, frequency modulated signals. They seem to be used for short-range communication (Thomsen et al., 2001). Clicks are broadband pulses mostly used in trains for echolocation (Miller et al., 2004). The length of the interval between successive clicks is correlated with the range to the echolocation target. At close range, individual clicks cannot be distinguished anymore: such rapid click trains with increasing click rate are referred to as buzzes. Buzzes seem to be associated with prey capture attempts. Not all click-based signals are used for echolocation: sperm whales use group-specific click trains, called codas, during social interactions (Gero et al., 2016). Buzz-like signals, referred to as bursts or rasps, show varying click rate evolution patterns and are not associated with foraging (Yoshida et al., 2014; Sørensen et al., 2018). Pulsed calls are fast pulse train which appear tonal to the human ear and form horizontal bands on spectrograms. The apparent tonal frequency corresponds to the pulse repetition rate (Watkins, 1966). Pulsed calls can make up a substantial proportion of some species' communication signals (Miller and Bain, 2000). The frequency ranges used by toothed whales vary greatly from one species to another: species are sorted into three groups according to the hearing and frequency ranges. High-frequency cetaceans include sperm whales, beaked whales and large delphinid species such as killer whales and pilot whales (Southall et al., 2019). Porpoises and some species of dolphins form the group of very high-frequency cetaceans (Southall et al., 2019).

The hearing ranges of the different groups of cetaceans overlap to a large extent (Southall et al., 2019). Given the fast and long-range propagation of sounds underwater, cetaceans should be able to detect acoustic signals from a multitude of sources, including other species of cetaceans and anthropogenic sources. They provide an ideal setting to investigate how animals might be able to detect and use the signals present in their environment.

1.2.3: Methodological limitations in the marine environment

Studying the behaviour of cetaceans is challenging. Mysticetes species are too large to be held in captivity. Smaller species may develop abnormal behaviour in captivity. In addition, not all aspects of behaviour can be observed from captive animals. Monitoring the behaviour of free-ranging cetaceans is also difficult. Cetaceans spend most of their time underwater and thus visual observations at the surface only provide a partial record of their behaviour. The recent development of animal-borne sensors made possible to study the underwater behaviour of wild cetaceans in detail. These tags can be attached to the animal temporarily (with suction cups for instance: Johnson and Tyack, 2003) or for extended periods of time (with barbs: Alves et al., 2010) and record diverse aspects of cetaceans' behaviour: their position at the surface, their depth, their orientation and movement patterns, or their acoustic scene. In addition, the natural range of some species is limited to remote areas (e.g. narwhals in arctic waters: Laidre et al., 2006), which increases the material and logistical costs of field studies (boat, crew, tracking material, tags).

1.3: Case study of hetero-specific signal eavesdropping: killer whale sounds

1.3.1: Ecological relationships between killer whales and other cetacean species

Killer whales are a cosmopolitan species, particularly common in high-latitude coastal areas (Jefferson et al., 1991). They are apex predators known to prey on a large variety of species including members of all marine mammal families they encounter in their natural range. Most cases of killer whale predation on marine mammals involve pinnipeds, but killer whales were also reported to hunt other toothed whales and baleen whales (Jefferson et al., 1991). Killer whale attacks on pinnipeds and small whales generally involve groups of six to ten individuals, which use collective herding strategies to corral their prey. When attacking large whales, killer whales usually form larger groups, in which small sub-groups (one to five individuals) harass a single prey at a time (Whitehead and Glass, 1985; Jefferson et al., 1991; Jourdain et al., 2017). The predation pressure that killer whales exert on other marine mammal species is difficult to estimate precisely (Trites et al., 2007), but is thought to be responsible for the lowest incidence of whistling dolphins in temperate waters (Rankin et al., 2013) and the evolution of migration in large whales (Steiger et al., 2008).

Marine mammals exhibit a diversity of responses toward killer whale attacks, which encompasses fight, flight and stealth behavioural strategies (Ford and Reeves, 2008). Sperm whales, with their large body size, and mysticetes with robust body shapes (such as humpback whales, bowhead whales, or grey whales) can use fight strategies against killer whales: they thrash their flukes and flippers towards their assailants. In some species, groups form marguerites or spokes: individuals form a circle with their heads towards the circle and flip their tails towards predators (Whitehead and Glass, 1985; Jefferson et al., 1991; Ford and Reeves, 2008). Pilot whales, despite their smaller body size, form larger, tighter groups in the presence of killer whales and were observed to chase them away (Jefferson et al., 1991; De Stephanis et al., 2015). Baleen whales with hydrodynamic body shapes (such as blue whales and fin whales) rely on flight strategies: when attacked by killer whales, they engage high speed directional escapes. However, if the killer whales catch up to them, they exhibit little or no defence: they may roll belly up so as to get their appendages out of the attackers' reach (Jefferson et al., 1991; Ford et al., 2005; Ford and Reeves, 2008). Many species incorporate stealth in their responses to killer whale attacks: silencing (Jefferson et al., 1991; Laidre et al., 2006; Soto et al., 2018) or hiding in the shallows or in kelp beds, and behind ice clocks and boats (Jefferson et al., 1991).

However, not all interactions between killer whales and other marine mammal species are of a predatory nature. Some cases of killer whale attacks do not result in death, but rather resemble harassment (Whitehead and Glass, 1985; Jefferson et al., 1991). Killer whales are frequently observed in close proximity with other marine mammal species: some dolphin species travel and rest with killer whales, porpoises sometimes ply around killer whales (Jefferson et al., 1991). Killer whales can be observed feeding in the same place as other species (Jefferson et al., 1991), sometimes on the same prey (e.g. herring: Jourdain and Vongraven, 2017). There are also cases of marine mammals avoiding killer whales in the absence of apparent attack intent (Jefferson et al., 1991), and reports of marine mammals chasing killer whales away or harassing them (De Stephanis et al., 2015; Pitman et al., 2017).

The variability in the nature of the interactions between killer whales and other marine mammal species can be linked to the ecological variability of killer whales. Indeed, there are several distinct populations of killer whales around the globe, and some of them present evidence of the existence of sympatric ecotypes: that is, ensembles of individuals or groups sharing ecological adaptations (morphology, behaviour) irrespective of their genealogy (de Bruyn et al., 2013).

1.3.2: Killer whale ecotypes

The first killer whale ecotypes were described in the northeast Pacific. Researchers identified two sympatric populations, referred to as resident killer whales and transient killer whales, which do not mix socially (Morton, 1990; Baird et al., 1992) and show clear dietary specialisations. Resident killer whales feed on fish (mostly salmon) and transient killer whales hunt marine mammals (mainly pinnipeds and porpoises, but occasionally larger cetaceans) (Morton, 1990).

Killer whale ecotypes are engaged in different trophic relationships with other cetacean species. Some ecotypes prey on marine mammals, some compete with other cetacean species for a common resource such as prey or habitat, and some display apparently neutral relationships with other cetacean species. It would be adaptive for cetacean species to discriminate between killer whale ecotypes in order to respond appropriately to the type of killer whale they encounter. The dietary specialisation of resident and transient killer whales is associated with differences in behaviour between these ecotypes, including differences in social organisation and in vocal behaviour. Marine mammals may eavesdrop on killer whale ecotype-specific vocal characteristics to adapt their behaviour to the type of killer whale detected, as has been shown for harbour seals (Deecke et al., 2002).

All killer whale ecotypes produce typical odontocete sounds: pulsed calls, clicks, and whistles, with pulsed calls representing the majority of killer whale communication signals (Miller and Bain, 2000). Overall, transient killer whales produce fewer clicks and pulsed calls than resident killer whales (Ford, 1984; Barrett-Lennard et al., 1996). Resident killer whales produce clicks and calls in almost all behavioural contexts (Morton, 1990), while transient killer whales are only vocal during attacks, after a kill, and when socialising at the surface (Deecke et al., 2005; Ford et al., 2005; Riesch and Deecke, 2011). In particular, resident killer whales rely on echolocation clicks to find their prey (Simon et al., 2007), while transient killer whale remain silent until the attack when hunting (Barrett-Lennard et al., 1996; Deecke et al., 2005). Transient killer whales show little, if any, differential usage of call types between contexts (Deecke et al., 2005), whereas the usage of certain call types vary according to contexts in resident killer whales (whistles preferentially used during rest and socialising, bi-phonated calls used more during foraging and travel in spread out groups: Miller, 2006; Riesch and Deecke, 2011). Each pod of resident killer whales has a repertoire of 7 to 17 stereotyped pulsed call types (Ford, 1991). Pod-specific call types, different usage rates of shared call types, and variation in the structure of individual call types carry pod, matriline, and individual markers (Miller and Bain, 2000; Nousek et al., 2006). Transient killer whales present a smaller repertoire which is distinct from the vocal repertoire of resident killer whales. Moreover, most call types are apparently shared by all members of the population (Deecke et al., 2002; Riesch and Deecke, 2011). Lastly, the calls of resident killer whales are usually louder, longer, and of higher frequency and wider bandwidth than calls of transient killer whales (Deecke et al., 2005; Foote and Nystuen, 2008; Riesch and Deecke, 2011; Filatova et al., 2015a).

The differentiation between these north Pacific killer whale ecotypes is clear and well-defined. It has served as a template to study other killer whale populations around the world. In some cases, similar differentiations were discovered (for instance, in the Russian Far East: Filatova et al., 2015b). However, this model of sympatric differentiation of ecotypes does not hold in every area (reviewed in de Bruyn et al., 2013). For instance, in the north Atlantic, several morphotypes of killer whales have been described, but their ecology appears more complex than in the north Pacific and their ecotypic and dietary status remains unclear. There are three killer whale populations in the north Atlantic, associated with the herring, mackerel, and bluefin tuna stock (Foote et al., 2011, 2012). Two ecotypes have been proposed in the north Atlantic: type 1, a generalist feeding mostly on fish; and type 2, a specialist hunting baleen whales (de Bruyn et al., 2013). In the northeast Atlantic, killer whales appear to belong to the type 1 ecotype but their diet remains unclear. Seal-hunting killer whales near the Shetland Islands are socially related to herring-feeding killer whales in Iceland (Beck et al., 2012). Killer whales identified as herring-feeding in Norway were observed taking harbour seals, harbour porpoises, and minke whales (Vester and Hammerschmidt, 2013). It remains unknown whether seal-eating killer whales in Norway are full-time marine mammal hunters, show seasonal dietary specialisation, or switch opportunistically between prey types (Jourdain et al., 2017). Isotopic analyses revealed that at least some individuals may switch between fish and marine mammal prey, and that the proportions of each type of prey in their diet vary over their lifetime (Foote et al., 2012; Samarra et al., 2017).

Despite unclear ecological differentiation, consistent differences in behaviour, including in vocal behaviour, still exist between killer whales feeding on different prey (Simon et al., 2007; Samarra, 2015). Herring-feeding killer whales in Norway produce many echolocation clicks, bi-phonated calls, and use tail slaps (which produce multi-pulsed broadband sounds) to herd fish into tight balls near the surface (Simon, 2005; Shapiro, 2008). When hunting seals, north Atlantic killer whales move in small groups and reduce their vocal output (Jourdain et al., 2017; Riesch et al., 2012). Marine mammal-eating killer whales worldwide seem to adopt this silent hunting strategy (in the Pacific: Deecke et al., 2005; in the Crozet archipelago: Guinet et al., 2000; in the north Atlantic: Deecke et al., 2011). In addition, the calls of north Atlantic killer whales are higher in frequency than the calls of transient killer whales (Foote and Nystuen, 2008; Filatova et al., 2015a).

1.3.5: Study species: the humpback whale (Megaptera novaeangliae)

Humpback whales inhabit most of the world seas: there is a large population in the southern hemisphere, and two populations in the north Atlantic and Pacific. They favour coastal and shelf waters, but occasionally cross deep waters (Clapham and Mead, 1999; MacKay et al., 2016). Mature individuals measure an average of 13 meters for males and 14 meters for females. Their large flippers amount to one third of the animal length make them particularly manoeuvrable and can be used as a weapon to defend against assailants (Clapham and Mead, 1999; Ford and Reeves, 2008). In the northern hemisphere, humpback whales migrate annually between summer and fall feeding grounds in high-latitude waters and winter breeding grounds in subtropical areas (Payne and McVay, 1971; Clapham and Mead, 1999). They show high fidelity towards feeding grounds, and whales from several feeding grounds converge to large breeding areas (Clapham and Mead, 1999; Stevick et al., 2006). On breeding grounds, humpback whales adopt a polygamous mating system in which associations between individuals are transient (Baker and Herman, 1984; Andriolo et al., 2014). On feeding grounds, they either form large, temporary aggregations spread over several square kilometres when feeding on plankton, or small groups that are stable over the years when feeding on schooling fish (Baker and Herman, 1984). In the northeast Atlantic, humpback whales feed on plankton and capelin (*Mallotus villosus*) off Iceland, Bear Island, and Jan Mayen (Nøttestad et al., 2014). During winter, part of the population stops in the Norwegian waters to feed upon wintering herring (*Clupea harengus*) before their southward migration (Jourdain and Vongraven, 2017). Humpback whales are the most vocal mysticetes (Payne and McVay, 1971). They produce two kinds of sounds: the song, a structured vocal display produced exclusively by males and mostly on the breeding grounds (Payne and McVay, 1971; Herman, 2017), but occasionally during migration and on the feeding grounds (Magnúsdóttir et al., 2014; Herman, 2017; Ryan et al., 2019; pers. obs.); and social sounds which include vocalisation and surface impacts with flippers and body, produced by all individuals, including females and calves, all year round (Thompson et al., 1986; Dunlop et al., 2007; Stimpert et al., 2011; Rekdahl et al., 2013; Kavanagh et al., 2017). The frequency range of songs and social sounds ranges from 30 Hz to over 20 kHz (Thompson et al., 1986; Au et al., 2006; Dunlop et al., 2013). Little is known about humpback whales' hearing abilities. Humpback whales should be able to detect killer whale sounds, as the frequency ranges of both species overlap (under the assumption that an animal could hear the frequencies it produces). An audiogram for humpback whales was modelled from anatomical observations on stranded individuals and known frequency-position functions from cats and humans (Houser et al., 2001). It concluded that humpback whales had a typical mammalian U-shaped audiogram spanning from 30 Hz to 18,000 Hz, with best hearing between 700 and 10,000 Hz and maximum sensitivity between 2 and 8 kHz. Sound exposure experiments confirmed that humpback whales could detect sounds in the 5-2,000 Hz range (Dunlop et al., 2015; Sivle et al., 2015).

Humpback whales interact with killer whales all along their migratory cycle. These interactions are frequent and variable in nature. Along their migratory cycle, humpback whales are led to interact with various populations and ecotypes of killer whales. Killer whale sounds may assume a wide range of ecological significances for humpback whales.

Interactions between humpback whales and killer whales are often predatory. Reports of killer whale attacks on humpback whales describe mostly non-lethal attacks (Whitehead and Glass, 1985; Jefferson et al., 1991; Saulitis et al., 2015) and some lethal attacks (Florez-Gonzalez et al., 1994; Naessig and Lanyon, 2004; Pitman et al., 2015). Attacks target calves preferentially, and they are concentrated on the breeding grounds and on the annual migration toward the feeding grounds (McCordic et al., 2014). Attacks are rarely directly observed: lethal attacks do not usually leave traces (except when carcasses are found: Saulitis et al., 2015), but non-lethal attacks do. The prevalence of killer whale scarring is high in humpback whales (15-40 %: Whitehead and Glass, 1985; Naessig and Lanyon, 2004; Steiger et al., 2008; McCordic et al., 2014), and indicates that attacks by killer whales may be more frequent than previously thought. The low number of recent scars on adult humpback whales confirms that most attacks target calves (Naessig and Lanyon, 2004). Humpback whales are more scarred on breeding grounds than on feeding grounds (14 vs 6%: Steiger et al., 2008), which is consistent with the annual repartition of attacks inferred from direct observations. Anatomical observations seem to indicate that humpback whales are fight strategists (Ford and Reeves, 2008). Their large flippers incrusted with barnacles could be used to strike attackers. Humpback whales form tight groups in response to killer whale attacks. They protect the calves, appendages, and soft ventral sides from attackers. They often thrash fluke, flippers, or head towards killer whales (Whitehead and Glass, 1985; Jefferson et al., 1991; Florez-Gonzalez et al., 1994; Pitman et al., 2015). However, humpback whales have also been observed to go silent and to avoid killer whales (flight strategies: Jefferson et al., 1991; Ford and Reeves, 2008; Curé et al., 2015).

As is the case for marine mammals in general, not all interactions between humpback whales and killer whales involve predation: there are also cases of competition and interference for instance. There are documented cases of humpback whales avoiding killer whales which showed no apparent attack intent and observations of both species in close proximity with no response from either one (Jefferson et al., 1991). Humpback whales sometimes travel with identified fish-eating killer whales (Pitman et al., 2017). Humpback whales feed on schooling fish in some areas (Clapham and Mead, 1999). As a result, they may compete with killer whale for the exploitation of this common resource. Concurrent feeding of both species is common (Jefferson et al., 1991), as in Norway during winter where they both feed upon herring in mixed-species aggregations (Jourdain and Vongraven, 2017). These aggregations are initiated most often by killer whales, and humpback whales join once the herring has been herded near the surface (Jourdain and Vongraven, 2017). Humpback whales were also observed interfering with killer whale attacks on other marine mammals: they were reported to join other humpback whales under attack by killer whales, or even other marine mammals (reviewed in Pitman et al., 2017). Humpback whales harassed more than half of the attacking killer whales regardless of the species of the prey although the interference was less intense when preys were not humpback whales (Pitman et al., 2017). Some humpback whales travelled several kilometres to reach the site of a killer whale attack, which seems to indicate that killer whale or prey sounds were the cues attracting humpback whales (Pitman et al., 2017). However, playback of marine mammal-eating killer whale sounds to humpback whales off Norway revealed strong avoidance responses (Curé et al., 2015). Interestingly, no observation of humpback whale interference with killer whale attack was made in the northeast Atlantic (Pitman et al., 2017).

By conducting playback experiments, we tested whether humpback whales could discriminate between the sounds of killer whale ecotypes, which should be associated with distinct ecological meanings.

1.4: Case study of behavioural responses to anthropogenic signals: sonar signals

1.4.1: Naval sonar, a particular source of concern

The marine environment is a place of particular concern about the impacts of human activities on the ecosystem (reviewed in Williams et al., 2015). Increasing human activities (vessel traffic, fishery, pile driving, seismic prospection, naval sonar) have especially large areas of influence because of the fast and long-range propagation of anthropogenic sounds (e.g. Fristrup et al., 2003). Moreover, cetacean species exhibit a double vulnerability to human-related disturbances, because of the importance of sounds in their ecology and because of the low population size of some species resulting from industrial whaling (Rocha et al., 2015).

Sonar sources produce high intensity signals to probe into underwater environments. Space and time correlations between naval sonar transmissions and mass stranding events (Parsons, 2017) placed sonar under the scrutiny of research. Several international research groups, such as the 3S consortium (sea mammal sonar safety) in which my Ph.D. was conducted, coordinated their effort to study the negative impacts of naval sonar on marine ecosystems. Studies have identified a variety of impacts of sonar on marine mammals. First, researchers focused on physical injury and observed temporary and permanent hearing loss in animals exposed to sonar transmission (Southall et al., 2007). Tissue damages from gas bubble formation in stranded individuals hinted at unusual dive cycles upon reception of sonar signals (Cox et al., 2006). The focus of researchers shifted towards the identification of behavioural responses to sonar (Southall et al., 2016). These responses are less obvious than physical damage, but they can potentially translate to severe detrimental effects at the population scale. The most common behavioural response to naval sonar is avoidance (Miller et al., 2012; Goldbogen et al., 2013; Sivle et al., 2015), sometimes for prolonged periods (Miller et al., 2015), and interruption of foraging which can also last longer than the exposure to sonar (Miller et al., 2012; Sivle et al., 2015; Isojunno et al., 2016). A particularly severe observed response was the separation of a mother-calf pair (Miller et al., 2012). Other responses include cessation of resting (Curé et al., 2016), alteration of diving behaviour (Frankel and Clark, 2000; Visser et al., 2016), and modifications of the vocal behaviour. Delphinids in particular have been reported to mimic sonar signals by producing vocalisations with similar frequency modulation patterns as sonar pings (DeRuiter et al., 2013; Alves et al., 2014). In addition, sonar signals can potentially mask natural communication signals. Cetaceans can display compensatory mechanisms for masking: they produce more, louder, and longer calls in areas of higher background noise; they shift the frequency of their vocalisations to avoid masked frequency bands (Rendell et al., 1999; Parks et al., 2007, 2011); and they may switched to less masked means of communication such as clicks and surface impacts (Kavanagh et al., 2017; Marrero Pérez et al., 2017).

Behavioural responses to sonar show high inter-individual variability according to species, sonar signal characteristics, or the behavioural state of individuals (Goldbogen et al., 2013; Harris et al., 2015). There exists a need to better characterise the behavioural responses of cetaceans to sonar.

1.4.2: Interpretation of behavioural responses to sonar

Anthropogenic sounds emerged recently in the environment (on the evolutionary time scale) and do not correspond to natural situations. It is thus challenging to determine the biological significance and relevance of the behavioural responses they elicit in animals.

One approach is to extrapolate the effects of the individual behavioural responses to the population scale, based on the species biology. Prolonged avoidance and cessation of foraging may result in a decline in body condition and reproductive success in populations routinely exposed to sonar. Avoidance responses may also displace populations from biologically crucial area, such as feeding hotspots or breeding grounds. Prolonged masking from sonar signals may reduce the efficiency of information transfer and provoke a reduction in social cohesion or an increase of the energy and time budget for communication.

Another approach is to compare the behavioural responses to anthropogenic sounds with behavioural responses to natural disturbing stimuli of known ecological meaning. The risk of predation is a particularly strong ecological signal (Lima and Dill, 1990); therefore, cues indicating a heightened risk of predation are generally used for comparison. They usually trigger clear and strong biologically costly responses from prey. The risk disturbance hypothesis predicts that the costs of responses to anthropogenic sounds perceived as a threat should be shaped by the costs of responses to natural threats (Frid and Dill, 2002). For cetacean species, killer whale sounds are an appropriate template to interpret the biological significance of responses of other cetacean species to sonar (see Curé et al., 2016 for an example). Killer whales prey on most marine mammal species, and should therefore be perceived as a threat. Even in species that are not under strong predation pressure from killer whales, such as pilot whales, we observe strong reactions to the presence of killer whales: pilot whales chasing killer whales (De Stephanis et al., 2015). Killer whales appear to be perceived as a threat or competitor by other marine mammals.

However, not all populations of killer whales are threatening for marine mammals. The sounds of different populations of killer whales may be perceived differently by marine mammals. That's why we tested the sounds of different killer whale populations to define an optimal template for the interpretation of the responses of marine mammals to sonar.

1.4.2: Study species: the long-finned pilot whales (Globicephala melas)

Long-finned pilot whales are the second largest species of delphinids after killer whales: mature males measure 6.5 metres and mature females 5.5 metres (Augusto et al., 2013). They occur in shelf-edge and deep waters in the southern hemisphere and in the north Atlantic (Isojunno et al., 2017). Long-finned pilot whales are deep-diving whales that rely on echolocation to feed upon deep sea cephalopods, and occasionally on mesopelagic fish (Gygax, 2002). They migrate between inshore and offshore water to follow the distribution of their prey (Vester, 2017). They spend most of their time neat the surface, with occasional series of foraging deep dives to 300-1000 meters (Sivle et al., 2012; Isojunno et al., 2017).

Long-finned pilot whales live in cohesive social groups all year long (Visser et al., 2014). Both male and female offspring remain with their mother (Amos et al., 1993) and form matrilines: groups of 11-14 individuals from several generations (Ottensmeyer and Whitehead, 2003). Matrilines associate in a mix of long-term (months, years) and short-term (hours, days) relationships: such groups are called pods (Ottensmeyer and Whitehead, 2003). Matrilines form tight subgroups within pods (Visser et al., 2014). Individuals within a pod synchronise their behaviour to a large extent (Senigaglia and Whitehead, 2012; Visser et al., 2014). Synchronisation is thought to improve foraging efficiency, to have hydrodynamic advantages, to play a role in social bonding, and to reduce predation risks (Senigaglia and Whitehead, 2012; Senigaglia et al., 2012). Long-finned pilot whales synchronise their foraging bouts to a large extent; however, when foraging, groups break into smaller sets of individuals which do not perform foraging dives in synchrony. This could be a strategy to reduce foraging interference at depth (Senigaglia and Whitehead, 2012; Visser et al., 2014). On the contrary, synchronisation becomes more precise in large groups, in the presence of calves, or when multiple boats are present in the area: it may be a general response to stressful situations (Senigaglia et al., 2012).

The responses of long-finned pilot whales to sonar experiments have been identified through sound exposure experiments, such as the ones performed by the 3S consortium (Sea mammal Sonar Safety). Even if long-finned pilot whale stranding events have been associated with sonar activity (Parsons, 2017), they do not appear to be particularly sensitive to sonar transmission compared to other species, such as killer whales or beaked whales: they respond at higher received sound levels, and their responses are usually shorter in duration, rarely extending after the sonar transmission (Miller et al., 2012; Antunes et al., 2014). The observed behavioural responses of long-finned pilot whales to sonar include short-duration avoidance, modifications of the dive cycle such as the interruption of deep diving (thus a probable cessation of feeding) and surfacing in synchrony with sonar pings, and increases in social group size and cohesion (Miller et al., 2012; Sivle et al., 2015; Visser et al., 2016; Isojunno et al., 2017). As in other species, long-finned pilot whales exhibit large inter-individual differences according to sonar type (more responses to 1-2 kHz signals than to 6-7 kHz ones: Miller et al., 2012) and behavioural state (response patterns differed between foraging and non-foraging individuals: Harris et al., 2015). Changes in vocal activity in response to sonar exposure were also reported; however, they report global vocal activity levels (e.g. call rate: Rendell and Gordon, 1999; Visser et al., 2016), or focus on specific vocal patterns (mimicry of sonar signals: Alves et al., 2014).

The vocal responses of long-finned pilot whales to naval sonar have not been reported in detail because of the challenges of describing this species' vocal behaviour. Long-finned pilot whales display high-levels of vocal activity in all behavioural contexts (Popov et al., 2017). Bouts of vocalisations are usually separated by short pauses, but longer periods of silence are possible when pilot whales are resting in such close proximity that vocal signals are not needed for communication (Visser et al., 2014, 2017). Long-finned pilot whales produce typical odontocete sounds: echolocation clicks, whistles, and pulsed calls (Vester et al., 2016). Echolocation clicks are mainly used for echolocation and foraging (they are ideal signals for range estimation: Jiang et al., 2019), but they may have an additional role in communication in conditions adverse to call production (e.g. at depth: Jensen et al., 2011). Long-finned pilot whales produce rasps, rapid series of clicks which, unlike buzzes, are not related to prey capture attempts (Vester, 2017). In the closely related congener short-finned pilot whale species, individuals may somewhat shift their communication towards click-based signals at depth, even if they keep producing tonal calls up to 800 m (Jensen et al., 2011; Marrero Pérez et al., 2017). Whistles and pulsed calls are mainly used for communication (these signals are optimal for speed estimation and information transfer robust to the differential speed of producer and receiver: Jiang et al., 2019). The frequency range of long-finned pilot whale whistles cover the human audible range and extend to the ultrasonic range, with most whistles between 20 and 40 kHz (Vester et al., 2017). Long-finned pilot whales produce a variety of pulsed calls. However, they do not fall into discrete categories but rather form a continuum of graded calls with intermediate forms between pulsed and tonal signals (Visser et al., 2014; Vester et al., 2017), as has been observed in other delphinid species (short-finned pilot whales: Sayigh et al., 2013; beluga whales: Garland et al., 2015; false killer whales: Murray et al., 1998).

This level of variation causes the categorisation of long-finned pilot whales vocalisations to be fundamentally challenging. Initial attempts at classification relied on the definition of broad classes based on entire call frequency modulation patterns (Taruski, 1979). The latest descriptions of the vocal repertoire of long-finned pilot whales described calls as sequences of subunits with consistent frequency contours separated by silent gaps (segments) of shifts in frequency (elements). They identified 129 call types and 25 subtypes (Vester et al., 2017). In addition, long-finned pilot whale calls can also be bi-phonated, with two independently modulated frequency component (the low frequency component or LFC and high frequency component or HFC: Vester et al., 2017). Most calls have relative simple structure (around 10% of calls had several segments: Vester et al., 2017) and contained a single frequency component – the LFC by convention (75%: Nemiroff and Whitehead, 2009; Vester et al., 2017). The maximal number of elements was eight for LFC calls and seven for bi-phonated calls (Vester et al., 2017). Each pod of long-finned pilot whales produce between seven and 54 call types, some of which are shared with other groups (15-81% of shared call types: Vester et al., 2016). Pods of pilot whales which share a portion of their repertoire form a vocal clan (De Stephanis et al., 2008). Long-finned pilot whales may use individual-specific whistles or calls in multi-pod associations to maintain contact with matriline members (Weilgart and Whitehead, 1990). In short-finned pilot whales, individuals have a predominant, specific bi-phonated call type which could be used to signal individual identity or group membership (Quick et al., 2018).

Long-finned pilot whales display specific pattern of vocal behaviour. For instance, calls with little frequency modulation are produced in all contexts, whereas highly modulated ones tend to be more frequent around the start and the end of deep foraging dives (Visser et al., 2017). Repeated call sequences, the repetition of similar calls with regular spacing for up to several minutes, were among the first observation of the vocal behaviour of long-finned pilot whales (Zwamborn and Whitehead, 2017a). They make up a significant portion of the species' vocal behaviour. As a result, some call types, referred to as principal call types, represent most of pilot whale recordings (Nemiroff and Whitehead, 2009; Sayigh et al., 2013; Vester et al., 2017). Within repeated call sequences, repetition is not accurate: half of the transitions involve slight modifications, either embellishments – discrete changes to part of the calls – or morphings – non-discrete changes across the calls (Zwamborn and Whitehead, 2017b). It is unclear whether repeated call sequences are produced by one or several individuals (Sayigh et al., 2013). The possible functions of repeated call sequences are not known. The type of calls repeated and the rate of repetition may convey information, as well as the modifications of calls within the sequences (Zwamborn and Whitehead, 2017b, 2017a). Repeated call sequences may also be a by-product of the fluid nature of long-finned pilot whales' vocal repertoire (Zwamborn and Whitehead, 2017b). Another pattern worthy of attention is the overlapping of calls, frequent in this species (Alves et al., 2014). Overlapping is usually an agonistic signal which reduces communication efficiency for both overlapper and overlapped, but it may also be used to address specific individuals, or a result of excitement (Todt and Naguib, 2000). Delphinids, among which long-finned pilot whales, have a tendency to match signals produced by conspecifics and are known to mimic anthropogenic sounds (DeRuiter et al., 2013; Alves et al., 2014). Call-matching may be used to attract a caller's attention and to retain it in noisy environments (Todt and Naguib, 2000; Sewall, 2012). It is also a means to display group membership and group size (Sewall, 2012).

I decided to focus on the vocal behaviour of long-finned pilot whales in response to sonar exposure. A more in-depth analysis of pilot whale vocal behaviour is necessary to explore the functional aspects of sound use in this species. I used an analysis of vocal responses of long-finned pilot whales to playback of killer whale sounds as a tool to interpret the biological significance of their responses to sonar. Other aspects of the behavioural responses of long-finned pilot whales to these stimuli have already been analysed by the 3S consortium (Miller et al., 2012; Curé et al., 2013; Sivle et al., 2015; Visser et al., 2016; Isojunno et al., 2017; Curé et al., 2019), and provide strong supporting information to augment a study of their vocal behaviour.

1.5: Research questions and thesis outline

My PhD is centred on two research questions:

How do cetaceans detect and process hetero-specific in relation with the ecological relationships between the involved species?

How do cetaceans respond to anthropogenic sounds? How do these responses compare to responses to biologically significant, natural signals?

The specific studies in my PhD are organised in three chapters.

1.5.1: Chapter 1 – Behavioural responses to heterospecific sounds are influenced by trophic relationships and ecological contexts

I performed playbacks of killer whale sounds to humpback whales in northern Norway. We used the sounds of unfamiliar, predatory killer whales (transient whales from Alaska) and the sounds of familiar, competitor species (herring-feeding killer whales from Norway). In addition, we performed playback experiments in the Norwegian fjords during winter (both stimuli) and offshore during summer (unfamiliar, predatory killer whales only). We combined visual observations and the deployment of multi-sensor tags to monitor the behaviour of humpback whales before, during, and after the playback.

I hypothesised that humpback whales would be able to discriminate between the different killer whale stimuli and would respond differently to each. I expected fish-eating killer whale sounds to have to signal the presence of food patches to humpback whales, and thus trigger approach and exploration responses. I expected the sounds of predatory killer whales to be perceived as a threat, and to trigger flight responses. The different contexts of presentation represent two different positions along the starvation-risk of predation trade-off, and also vary in bathymetry.

As expected, humpback whales approached the source of competitor killer whale sounds, and dove deeper around it for the duration of the playback; whereas overall they avoided the source of killer whale sounds. The avoidance responses to predatory killer whale were stronger offshore than in the fjords. This could result from the lower vulnerability of humpback whales to killer whale attacks in winter, or from a reduced ability to recognise killer whale sounds as a threat because of the high number of fish-eating killer whales in the fjords.

1.5.2: Chapter 2 – Unsupervised classification to study gradation in animal vocalisations based on fuzzy clustering and Mel frequency cepstral coefficients

To address the challenge of how to classify the diverse repertoire of sounds produced by long-finned pilot whales, I developed a procedure based on Mel frequency cepstral coefficients (MFCC) and fuzzy clustering. The objectives were to take into account the graded nature of pilot whales’ vocal repertoire and to provide objective classification criterion, in order to propose an alternative to the time-consuming, human observer-based classification schemes. I used long-finned pilot whales calls recorded in Norway with hydrophone-equipped animal-borne tags. These calls had been classified using the latest vocal repertoire as a template to evaluate the performance of the new method (dataset courtesy of Heike Vester).

The developed method achieved a lower level of precision than the catalogue-based classification: four categories were defined, versus eight (and three additional subtypes within one of the call types) according to the catalogue. The fuzzy cluster-based categories revealed consistent overlap patterns between the catalogue call types. In addition, the new method provides tools for the quantification and the visualisation of the gradation between call types.

1.5.3: Chapter 3 – Vocal responses of long-finned pilot whales to naval sonar exposures and playbacks of killer whale sounds

I analysed the vocal behaviour of long-finned pilot whales before, during, and after exposure to naval sonar or killer whale sounds. The behaviour of long-finned pilot whales was monitored with visual observations at the surface and animal-borne, sound recording tags. Movement patterns, activity budgets, and social aspects of the responses have already been analysed elsewhere, and were used as supporting information to study vocal responses. I used the method developed in chapter 2 to describe the vocal behaviour of long-finned pilot whales.

I expected the overall number of calls to change in response to disturbance (either to decrease to allow a better perception of the acoustic scene, or to increase because of the higher information transfer required for coordinated responses). I looked for call types only produced in response to disturbances (general alarm calls), or produced specifically in response to a given stimuli. I also expected the typicality of the calls, i.e. their position along the continuum from stereotyped calls to the absence of categories, to vary: either to increase as a means to compress information and increase the efficiency of communication or to decrease from the heightened information transfer required for coordinated responses. I was also interested in the distribution and characteristics of repeated call sequences and overlapping along the courses of the experiments.

I detected changes in call type usage in response to sonar exposures and playback of killer whale sounds. I could not identify general alarm of recruitment call types, or stimulus-specific call types across experiment replicates. There was no directional change in the typicality of calls in response to naval sonar or killer whale sounds.

2: GENERAL METHODS

2.1: Study species and locations

2.1.1: Humpback whales (Megaptera novaeangliae)

We conducted playback experiment of killer whale sounds to humpback whales during summer off Spitzbergen (between 73 and 79°N) and during winter in the fjords surrounding Vengsøya (69°N). In the northeast Atlantic, humpback whales feed on plankton and forage fish off Iceland, Bear Island, and Jan Mayen during summer and autumn (Clapham and Mead, 1999; Nøttestad et al., 2014; Moore et al., 2019). During winter, part of the humpback whale population stops in the Norwegian fjords to feed upon wintering herring (*Clupea harengus*) before their southward migration (Jourdain and Vongraven, 2017). Humpback whales were solitary or formed small groups (less than five individuals) in the study areas, as observed in other foraging grounds (Baker and Herman, 1984). Humpback whale songs are rarely heard on feeding grounds, but may occur before the start of the migration (Magnúsdóttir et al., 2014; Ryan et al., 2019; pers. obs.). Social sounds are routinely recorded from feeding grounds, including sound types seemingly related to coordinated foraging (Thompson et al., 1986; Parks et al., 2015).

2.1.2: Long-finned pilot whales (Globicephala melas)

We performed playback experiments of killer whale sounds and naval sonar controlled exposure experiments to long-finned pilot whales off the coast of northern Norway (between 66 and 70°N). Long-finned pilot whales exhibit fission-fusion dynamics (Ottensmeyer and Whitehead, 2003), and group size varied within and between experiments.

2.2: Experimental protocol

2.2.1: General procedure

The experiments presented in this manuscript have been executed as part of fieldwork campaigns of the 3S (Sea mammal Sonar Safety) consortium from 2008 to 2018. I took part in three campaigns: in January 2017, in June-July 2017, and in January 2018. The 3S team organises two kinds of research expeditions: the main sonar trials, which aim at exposing marine mammals to naval sonar transmissions; and the baseline trials, which aim at testing the tags and collecting baseline data. Playback experiments were conducted during baseline trials and were a secondary objective of main trials. During baseline trials, the research team was usually based on land and went at sea every day. During sonar trials, the research team spent several weeks at sea on a large research vessel (HU Sverdrup II). The research team relied on a second vessel for observations during the experiments for both kinds of trial.

Many interdisciplinary skills are needed on such fieldwork campaigns. My roles on the field were tag technician (in charge of the preparation of the tags before the deployments, the offloading and preliminary verifications of the collected data, and the investigation of any technical issue related to the tags), marine mammal observer (involving visual observation of marine mammals, identification of the tagged animal by radio-telemetry, and collection of fluke and flipper photographs for identification), and playback operator (testing the playback chain, installing the playback material on the boat, and executing playbacks).

The sequence of a sound exposure experiment was the following (Figure 1A). First, we searched for whales with visual or acoustic observations. Once a group of whales had been detected, we began tracking them and sent a second boat (a dedicated boat during baseline trials, and a small boat deployed from the research vessel during sonar trials) to equip one or two whales with tags attached with suction cups. One tagged whale became a focal whale which was followed until the tag detached to consistently track its location. Then, after a post-tagging observation phase (to ensure that the tagged whale's behaviour had returned to normal after the tag deployment) and a baseline data collection period, we exposed the focal whale (previously equipped with a tag) to a sound stimulus. We broadcasted playback stimuli from a small boat (a dedicated one during baseline trials, a small one deployed from the research vessel during sonar trials). A sonar source towed by the research vessel Sverdrup II transmitted sonar signals. We exposed focal whales to a maximum of six successive sound exposure experiments (Table 1). In all cases, a second boat continued the visual tracking of the focal whale throughout the experiments until tag detachment.

We compared the behaviour of humpback whales and long-finned pilot whales during a pre-exposure period, right before exposure to the sound stimuli, the broadcast period, and a post-exposure period immediately following the exposure. Comparison between the pre-exposure and exposure period allow the identification of behavioural responses to the stimulus. Comparison between the pre-exposure and the post-exposure periods determined whether behavioural responses extended after the exposure period or not.

2.2.2: Data collection

We combined the multi-sensor animal-borne tags attached to the whales, and visual observations at the surface from the deck of the observation vessel to record the behaviour of humpback whales and long-finned pilot whales before, during, and after the experiments. During each experiment, we equipped one or two whales with a tag, and chose one tagged whale as a focal individual, based upon the tag position on the body, and strength of the VHF radio signal received from the tag. The observation vessel was confirmed that a whale at the surface was the focal tagged whale by visually seeing the tag attached to the body, and/or by simultaneously hearing the VHF signal (which is only received when the tag is out of the water). We tagged whales opportunistically: we tried to tag an individual in the first whale group encountered in most cases, but switched to another group if we could not approach close enough for successful tagging.

2.2.2.1: Multi-sensor tags

We deployed either standard dtags (Johnson and Tyack, 2003) or custom-made mixed-tags on humpback whales and long-finned pilot whales. Dtags contain two hydrophones (sampling frequency: 96 kHz for humpback whales, 96 or 192 kHz for long-finned pilot whales), a 3-axis accelerometer (sampling frequency: 50 Hz), a 3-axis magnetometer (sampling frequency: 50 Hz), a pressure sensor (sampling frequency: 50 Hz), and a temperature sensor. Mixed-tags are custom-assembled tags which contain the sensor suite of dtags and a GPS logger (FastLoc3®, SirTrack) within 3D-printed polymer housings. Both dtags and mixed-tags were attached temporarily to the animals with suction cups. We deployed the tags with either a long hand-held pole (Figure 2A) or a pneumatic launching system (ARTS®, LKARTS: Figure 2B). All tags contained a VHF beacon and a programmable release device which allowed us to recover them quickly after the experiments. As detailed above, the VHF beacon was also used by the tracking team to identify the focal whale at the surface.

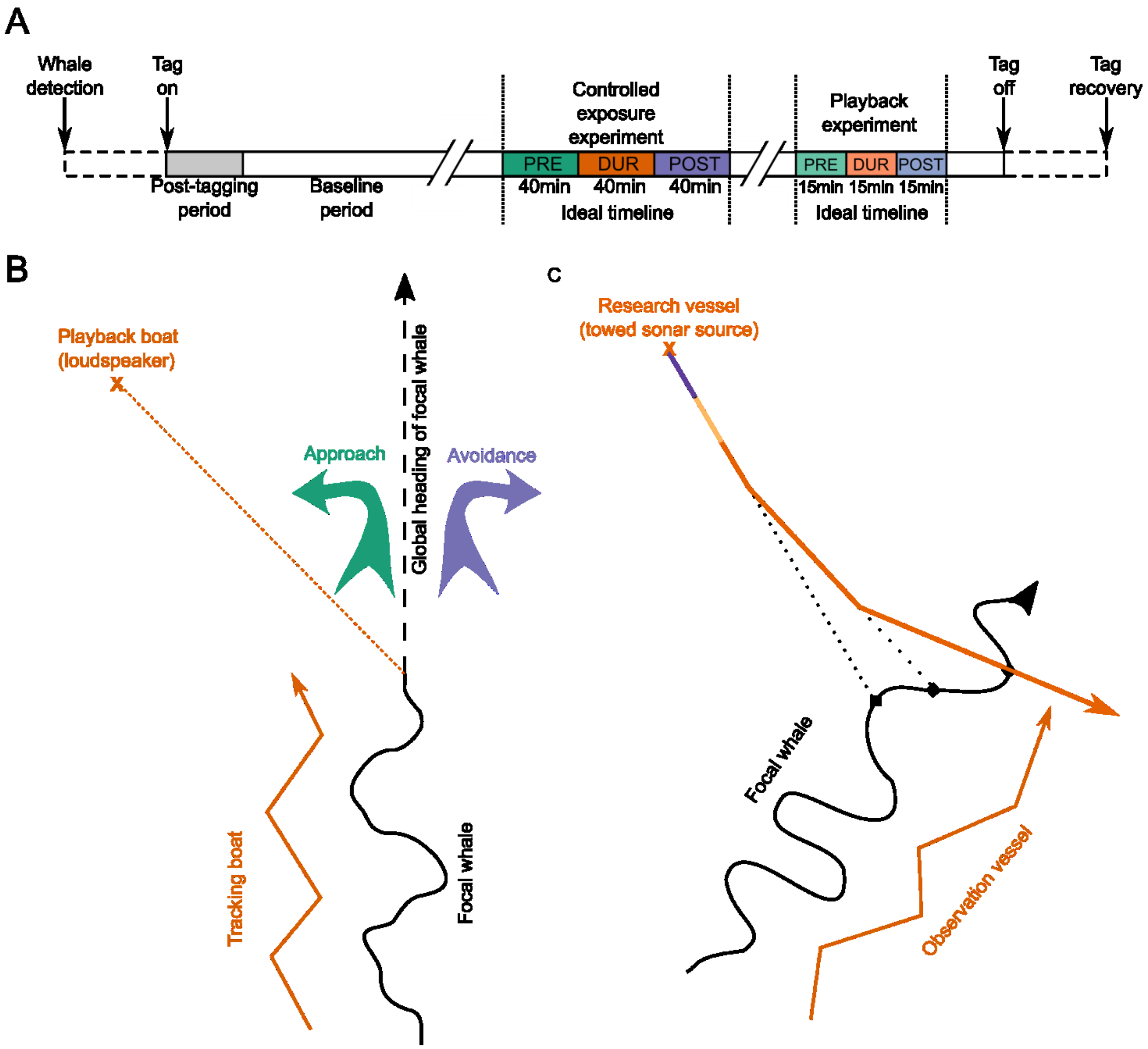

Figure 1: General protocol **A)** Experiment timeline. Once a whale was detected, we started visual observation immediately, while a vessel approached it to deploy a tag on a whale ("Tag on"). After a post-tagging period and a period of baseline behaviour collection of the tagged whale, we performed sound exposure experiments. All experiments consisted of three phases: the pre-exposure observation period ("PRE"), the exposure period ("DUR"), and the post-exposure observation period ("POST"). In the typical timeline, each period would last 40 minutes for sonar controlled exposure experiments and 15 minutes for playback experiments.

Focal whales were exposed to two to six sound exposure experiments. Tracking continued throughout the experiments until tag detachment ("Tag off") and tag recovery **B)** Playback disposition. An operator on the tracking boat specified the position where the playback boat transmitted sounds during playback experiments. We aimed to place the playback boat ahead of the focal whale, at an angle of 45°: this geometry eased the detection of both approach and avoidance responses **C)** Sonar controlled exposure experiment setup. The research vessel towing the source started transmitting sonar pings 7-8 km away from the tagged whale, and then continued transmission with one sonar ping every 20s while approaching the tagged whale at 7-8 knots. The source level of sonar signals increased during the first 10 minutes of the experiment, and was then held at maximal power. The research vessel adjusted its approach course towards the surfacing points of the focal whale (communicated by the observation vessel). The course of the focal vessel was fixed once it reached 1000 m from the focal whale. It continued transmitting sonar for five minutes after crossing the focal whale's path.

We constructed the dive profile of the tagged whale from the recording of the output of the pressure sensor in the tag. We reconstructed the 3D orientation of the whale underwater with the accelerometer and magnetometer data from the tag (Wensveen et al., 2015). We used the dive profile, the orientation of the whale, and the flow noise recorded by the hydrophones to interpolate the position of the whale between surfacing events (recorded either with the GPS loggers or from visual observations). We confirmed the reception of the sound stimuli on the tags recordings (we also set a recording system to monitor the broadcasts near the source). Human observers checked the tag recordings and noted the start and end times of vocalisations. For long-finned pilot whales, they classified the signals as social sounds (pulsed calls and whistles) or click signals (click sequences and buzzes) based on the presence or absence of horizontal bands in the spectrograms.

2.2.2.2: Visual tracking

Immediately after tagging, an observation vessel started to track the focal whale visually, using visual sighting of the tag or the radio signal from the VHF beacon to identify it. For both species of whales, we recorded the position (based upon range and bearing from the observation vessel) and heading of the focal whale when it surfaced, as well as the size of the group it was in and the spacing between group members (if any).

We used a more detailed visual protocol for long-finned pilot whale groups, because group size was larger and group composition was fluid (see Visser et al., 2014 for details). We defined the focal area as a 200 m radius around the focal animal. The focal group comprised all individuals interacting or showing a certain degree of synchrony within 15 body length (around 100 m) from the focal individual. We took note of the size of the focal group; the number of individuals in the focal area; the number of groups in the focal area; the distance between the focal group and the nearest other group; the spacing between individuals within the focal group; the level of synchrony and milling within the focal group. The behavioural state of the focal group was estimated as travelling (directed swimming), resting (logging, milling), socialising (increased contacts and surface events), or foraging (long tail-out dives, presence of seabirds). We aimed at making one observation every two or three minutes. We made all visual tracking records in Logger 2010 (courtesy of the International Fund for Animal Welfare).

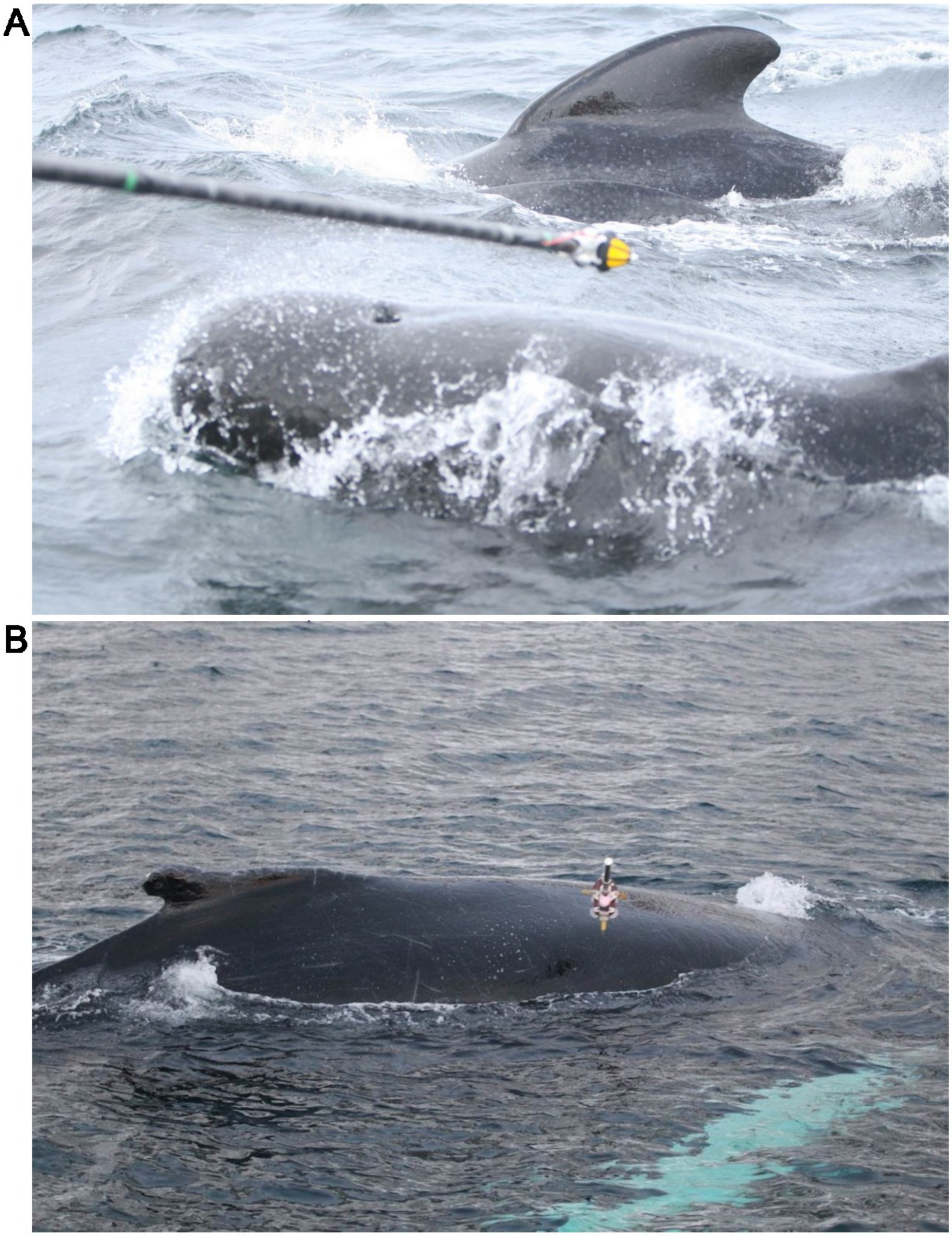

Figure 2: Tag deployment **A)** Deployment of a dtag on a long-finned pilot whale using a hand-held pole **B)** Deployment of a mixed-tag on a humpback whale using the ARTS pneumatic launching system. Picture credits: 3S project

2.2.3: Playback experiments

2.2.3.1: Stimuli used

We used the feeding sounds recorded from two killer whale populations for playback experiments: transient killer whales from southeast Alaska, and herring-feeding killer whales from Norway. We hypothesised that these stimuli would have different ecological consequences for humpback whales and long-finned pilot whales. Transient killer whales are specialised marine mammal eaters. The Norwegian study populations of humpback whales and long-finned pilot whales are most likely unfamiliar with the sounds produced by this Pacific population of killer whales. We assumed that their sounds would be highly threatening, because marine mammal-eating killer whales worldwide seem to adopt similar vocal behaviours, or because the novelty of the killer whale sounds may be threatening by itself (other marine mammals habituate selectively to local, non-predatory, killer whale populations: Deecke et al., 2002). In contrast, the sounds produced by Norwegian herring-feeding killer whales should be familiar to sympatric humpback whales and long-finned pilot whales. These killer whales exploit the same food resource as humpback whales in Norway, sometimes in mixed-species groups (Jourdain and Vongraven, 2017). We expected their sounds to signal the presence of competitors or of a food patch to humpback whales. Long-finned pilot whales and herring-feeding killer whales feed mainly on different prey, but occupy the same foraging areas. Herring-feeding killer whale sounds may signal the presence of another species in the area to long-finned pilot whales, or may indirectly signal the presence of a food patch to pilot whales, as they sometimes feed on cod which itself feeds on herring (Nøttestad et al., 2015).

All stimuli were recorded in natural behavioural contexts with dtags attached to whales in the group. All recorded killer whale groups contained around five individuals. Transient killer whales were recorded harassing and feeding on marine mammal prey and herring-feeding killer whales were recorded during active foraging. We removed sections of the recording containing sounds not produced by killer whales (for instance, sections with high flow noise or sounds from the tag breaking the water surface) and looped the resulting files so that all stimuli would last 15 minutes. We amplified the stimuli to reach 140-155 dB re 1 μPa @ 1 m for the loudest calls (within the range of natural source levels for killer whales sounds: Miller, 2006). The main difference between the two kinds of sound stimuli is the presence of many clicks, buzzes, and tail slaps in addition to calls in the herring-feeding killer whale stimuli, whereas the marine mammal-eating killer whale stimuli contained almost exclusively calls.

We also used negative and positive controls during the playback experiments. We selected sequences of recordings without killer whale sounds to use as negative controls. These sequences were cleaned and looped in the same way as killer whale stimuli. We amplified them to the same root-mean-square sound level as killer whale stimuli. We used artificial signals as positive controls, to check if humpback whales and long-finned pilot whales responded to any frequency-modulated signals. The positive control sounds were 1 s, 1 to 2 kHz hyperbolic upsweeps repeated every 20 s. We broadcasted them at the same root-mean-square sound pressure level as killer whale stimuli. We constructed several versions of each stimulus, except the artificial positive control, to reduce pseudoreplication.

2.2.3.2: Procedure

Each playback experiment was designed to last 45 minutes: 15 minutes of pre-exposure observation, 15 minutes of broadcast, and 15 minutes of post-exposure observation (Figure 1A). We performed generally two, up to four playback experiment per focal whale (Table 1). This experiment timeline ensure that at least 30 minutes separated successive exposures. We tried and observed an additional pause of 30 minutes so that there would be one hour between successive broadcasts. In practice, this procedure was not always respected and the time between successive broadcasts was sometimes reduced by constraints such as bad weather (mostly in early experiments, between 2008 and 2010).

The tracking boat team determined the position where the playback boat should get in position based on the distance and the direction between the surfacing positions of the focal whale. We aimed to place the sound source roughly 800m ahead of the focal whale but not directly in its path (Figure 1B). This geometry eases the detection of horizontal approach and avoidance responses, and does not force reactions from the focal whale. Once in position, the playback boat turned its engine off and lowered the loudspeaker 8m underwater (Figure 2). At the end of the playback experiment, the visual tracking team determined the position of the playback boat for the next playback experiment.

The playback chain consisted of a player (M-Audio Micro Track II recorder or DR40-Tascam recorder), a resistor, an amplifier (Cadence Z8000 or Sony XM-N502), and a loudspeaker (Lubell LL9642T or LL9162T, frequency range 0.2-20 kHz). We monitored the broadcasts with a calibrated hydrophone (Bruel and Kjaer 8105) placed one meter above the loudspeaker, connected to an amplifier (Bruel and Kjaer 2635) and a recorder (M-Audio Micro track II recorder or DR40-Tascam recorder).

2.2.4: Controlled exposure experiments

2.2.4.1: Procedure

We performed controlled exposure experiments of active sonar to long-finned pilot whales in the northeast Atlantic. We used a towable sonar source (Socrates, TNO, the Netherlands: Figure 3) which produced 1 s pings every 20 s (5% duty cycle). We used three different ping characteristics: 1 to 2 kHz hyperbolic up sweeps (LFAS: low frequency active sonar), 2 to 1 kHz hyperbolic down sweeps (LFASDS: LFAS down sweeps), and 6 to 7 kHz hyperbolic upsweeps (MFAS: medium frequency active sonar).

Figure 3: The Socrates towed sonar source used during sonar exposure experiments. Picture credits: 3S project

We used two boats during our experiments: the source boat which towed the sonar source, and the tracking boat from which we visually tracked the focal whale. The source boat positioned itself 7-8 km in front or to the side of the tagged whale. It started transmitting sonar signals while approaching the focal whale at 7-8 knots (so that it would reach it after 30 minutes of full power sonar transmission). The tracking team communicated the focal whale's positions to the source boat, so that it may adjust its approach course. The source vessel fixed its heading once it reached 1000 meters from the focal whale, and continued transmitting for five minutes after crossing its path (Figure 1C). We transmitted no sounds for around one hour between successive experiments to allow the whale to return to normal behaviour, and for the source boat to get back into position. In addition to the approach by the source boat, we used a ramp up procedure so that the received level of sonar signals would gradually increase for the focal whale. The source level of sonar pings was regularly increased over 10 minutes. Sonar transmissions lasted 40 minutes in our design (10 min ramp up and 30 minutes to reach the focal whale), so the ideal timeline for sonar exposure experiments started with 40 minutes of pre-exposure period and ended with 40 minutes of post-exposure period (Figure 1A). As for playback experiments, logistical constraints resulted in this timeline not being always respected. We observed a mitigation procedure to shut down the sonar source if animals moved too close to the source (100 m threshold, conservative equivalent to a 200 dB re 1 μPa received sound pressure level), showed pathological reactions, of approached the shore or confined areas. We used silent vessel approaches, following the same course as sonar exposure trials, as negative controls. All experimental procedures were permitted by the Norwegian Animal Research Authority, with ethical approval form the Animal Welfare Ethics committee of the University of St Andrews.

Individual ID	Focal	Exposure 1	Exposure 2	Exposure 3	Exposure 4	Exposure 5	Exposure 6
mn11_157a	Yes	OOS SONAR	MEKW	CTRL-			
mn11_160a	Yes	OOS SONAR	MEKW	CTRL-			
mn11_165e	Yes	OOS SONAR	MEKW	CTRL-			
mn12_161a	Yes	OOS SONAR	CTRL-	MEKW			
mn12_164b	Yes	OOS SONAR	CTRL-	MEKW			
mn12_170a	Yes	OOS SONAR	CTRL-	MEKW			
mn12_171a	Yes	OOS SONAR	MEKW	CTRL-			
mn12_180a	Yes	OOS SONAR	CTRL-	MEKW			
mn16_018a	Yes	HFKW	CTRL-				
mn16_020a	Yes	MEKW	HFKW				
mn16_023a	Yes	HFKW	MEKW				
mn16_024a	Yes	CTRL-	HFKW				
mn17_024a	Yes	MEKW	HFKW				
mn17_026a	Yes	HFKW	MEKW				
gm08_150c	Yes	MFAS	LFAS				
gm08_154d	Yes	LFAS	MFAS				
gm08_159a	Yes	SILENT	LFAS	MFAS	HFKW	HFKW	
gm09_138a	No	LFAS	MFAS	SILENT	LFASDS		
gm09_138b	Yes	LFAS	MFAS	SILENT	LFASDS	HFKW	HFKW
gm09_156b	Yes	SILENT	LFAS	MFAS	LFASDS	HFKW	HFKW
gm10_157b	Yes	CTRL-	CTRL-				
gm10_158d	Yes	CTRL-	HFKW	CTRL-	HFKW		
gm13_137a	Yes	OOS PB	MEKW				
gm13_149a	Yes	CTRL+	MEKW				
gm13_169a	Yes	MEKW	CTRL+	CTRL-			
gm13_169b	No	MEKW	CTRL+	CTRL-			
gm14_180a	Yes	CTRL+	MEKW				
gm14_180b	No	CTRL+	MEKW				

Table 1: Overview of sound exposure experiments on humpback whales and long-finned pilot whales. Each tagged individual is identified with an eight-symbol Dtag code: the initials of the species scientific name (mn: humpback whales, gm: long-finned pilot whales), the last two digits of the experiment year, the date in the Julian calendar, and the number of the tag deployment for this day (from a to z). MEKW: playback of mammal-eating killer whale sounds; HFKW: playback of herring-feeding KW sounds; CTRL-: playback of broadband noise; CTRL+: playback of artificial frequency-modulated sounds; LFAS: controlled exposure to low frequency active sonar; MFAS: controlled exposure to medium frequency AS; LFASDS: controlled exposure to

LFAS, down sweep pings; SILENT: silent vessel approach; OOS SONAR: out-of-study sonar; OOS PB: out-of-study playback.

3: CHAPTER 1 – BEHAVIOURAL RESPONSES TO THE SOUNDS OF HETEROSPECIFICS ARE INFLUENCED BY TROPHIC RELATIONSHIPS AND ECOLOGICAL CONTEXT

(submitted to Animal Behaviour)

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3.1: Abstract

The reception of acoustic signals not intended for oneself, or eavesdropping, has many ecological implications, such as the detection of predators, prey, or competitors, which can be crucial fitness-enhancing information. The marine environment is a particularly favourable medium for receiving information through acoustic cues. The cosmopolitan killer whale *Orcinus orca* has diverged into several morphotypes and ecotypes, which vary in both prey type and vocal behaviour, making acoustics a potentially reliable sensory modality for eavesdroppers to discriminate between ecotypes and to respond adaptively. We tested how humpback whales *Megaptera novaeangliae* in the northeast Atlantic responded to the sounds of familiar herring-feeding killer whales (HFKW, which mostly consume herring like humpback whales) during winter, inshore and of unfamiliar mammal-eating killer whales (MEKW, potential predators) during winter, inshore and summer, offshore. We used animal-borne tags and surface visual observations to record responses before, during, and after playback experiments. As expected, humpback whales clearly approached HFKW sound source, indicating a dinner-bell effect. Random Forest analysis showed that this consistent response to HFKW sounds differed from how humpbacks responded to MEKW sounds. MEKW sounds elicited typical flight responses in most cases with stronger and more consistent avoidance responses offshore compared to inshore. In summer offshore areas, the humpback whales were in poorer body condition, in a more exposed environment, and with less killer whale presence than during winter within the fjords – all factors that may increase the likelihood of anti-predator responses. Our results indicated that humpbacks are able to discriminate between killer whale ecotypes based upon their acoustic characteristics. However, the consistency of their response to a given ecotype sounds may depend upon the detailed context in which the sounds were heard.

Keywords: humpback whales (*Megaptera novaeangliae*), killer whales (*Orcinus orca*), playback experiment, ecotypes, anti-predator response, dinner-bell effect, ecological context.

3.2: Introduction

In the ocean, the ability to eavesdrop on acoustic cues or displays, that is the detection of the sounds produced or exchanged between individuals of the same or another species and not intended to oneself, can affect animals' fitness (McGregor, 1993). Gathering information through acoustic eavesdropping is likely to be particularly beneficial within predator-prey, competition, and cooperation systems. Eavesdropping on species sharing similar food type may be an indirect way to locate food patches (*Noctilio spp*. bats: Übernickel et al., 2013; ant-following birds: Pollock et al., 2017), or to avoid areas of high-intensity competition (drywood termites *Cryptotermes secundus*: Evans et al., 2009). Individuals of prey species may thwart predation attempts if they are able to detect and identify sounds informing them about predator presence and to adopt appropriate behaviours to reduce the risk of predation, such as avoidance (gray whales *Eschrichtius robustus*: Cummings and Thompson, 1971; passerines: Emmering and Schmidt, 2011), stealth (tropical dolphins: Rankin et al., 2013), or mobbing (long-finned pilot whales *Globicephala melas*: Curé et al., 2012). Individuals from predatory species may in turn improve their foraging efficiency if they were to reduce sound emissions that could be used by prey to detect them (killer whales *Orcinus orca*: Barrett-Lennard et al., 1996). Another way to reduce predation risk can be the detection and use of alarm calls released by other species within the prey community (white-bellied copper-striped skinks *Emoia cyanura*: Fuong et al., 2014; superb fairy-wrens *Malurus cyaneus*: Magrath et al., 2015).

In practice, the appropriate behaviour to adopt upon receiving a signal also integrates contextual information, which encompasses receiver-, sender-, and environment-related cues. Indeed, a decision may depend on the receiver's body condition (dwarf mongooses *Helogale parvula*: Kern et al., 2017), its prior experience (crayfish *Faxonius spp*.: Beattie and Moore, 2018), or the behavioural activity it is engaged in (blue whales *Balaenoptera musculus*: Goldbogen et al., 2013). Behavioural responses can also be influenced by sender-related cues, such as the sender's species (Canids: Kershenbaum et al., 2016), size (hamadryas baboons *Papio hamadryas*: Pfefferle and Fischer, 2006), group size and composition (elephants *Loxodonta africana*: Payne et al., 2003), reliability (dwarf mongooses: Kern et al., 2017; African herbivores: Palmer and Gross, 2018), or current behaviour (killer whales: Filatova et al., 2013). Moreover, cues related to the receiver's environment may also be important in shaping its responses, such as topography (Gunnison's prairie dogs *Cynomis gunnisoni*: Perla and Slobodchikoff, 2002; dwarf mongooses: Kern et al., 2017), or the size and composition of the receiver's social group (Tibetan macaques *Macaca thibetana*: Rowe et al., 2018).

Sound is the primary information medium in the marine environment; light quickly fades with depth, whereas sounds travel about five times faster than in the air and with little absorption. Marine mammals rely on sounds for foraging (killer whales: Barrett-

Lennard et al., 1996; sperm whales *Physeter macrocephalus*: Miller et al., 2004), breeding (humpback whales: Smith et al., 2008; Herman, 2017), and social coordination (killer whales: Nousek et al., 2006; short-finned pilot whales *Globicephala macrorhynchus*: Jensen et al., 2011; sperm whales: Gero et al., 2016; bottlenose dolphins *Tursiops truncatus*: King et al., 2018). Their hearing sensitivity allows them to hear outside of the frequency range of the sounds produced by their own species, enabling them to hear in the frequency ranges of many other species in their environment, such as potential prey, predators, or competitor species. This makes marine mammals particularly suitable for the study of interspecific acoustic eavesdropping. Yet, there have been far fewer studies on acoustic communication and eavesdropping in marine than in terrestrial systems, likely because of the intrinsic challenges in monitoring the behaviour of aquatic animals that spend most of their time underwater. The recent development of animal-borne multi-sensor tags, which enable the tracking of marine mammals and the recording of their behaviour (for example, dtags: Johnson and Tyack, 2003), made it possible to conduct such acoustic studies on wild marine mammals, for instance using playback experiments. Playback experiments, i.e. broadcasting sound stimuli and monitoring the behavioural responses of exposed animals, is a classic method to probe into the potential functions of animal vocalisations or to investigate sound discrimination in particular contexts (reviewed in Deecke, 2006).

Playback of killer whale sounds to wild marine mammals has demonstrated anti-predator responses in numerous species: avoidance (beluga whales *Delphinapterus leucas*: Fish and Vania, 1971; harbour seals *Phoca vitulina*: Deecke et al., 2002; sperm whales: Curé et al., 2013; humpback whales: Curé et al., 2015; Risso's dolphins *Grampus griseus*: Bowers et al., 2018), and apparent mobbing (pilot whales: Curé et al., 2012; Bowers et al., 2018; Curé et al., 2019). Killer whales are cosmopolitan apex predators known to prey upon members of most families of marine mammals (Jefferson et al., 1991). However, there exist distinct ecotypes and morphotypes of killer whales, which have different physical features and exhibit different behaviours, including distinct diets and vocal productions (reviewed in de Bruyn et al., 2013). Thus, killer whale sounds can potentially convey a wide range of ecological meanings to marine mammal eavesdroppers.

The plurality of the ecological significance of killer whale sounds to unintended recipients has been demonstrated in one species of pinnipeds (harbour seals: Deecke et al., 2002) and one species of toothed whales (long-finned pilot whales: Curé et al., 2019). Harbour seals avoided the source of transient killer whale sounds (local marine mammal predators) and unfamiliar fish-eating killer whale sounds, but did not react to resident killer whale sounds (local fish specialists that do not prey on seals). Long-finned pilot whales showed more severe anti-predator responses to unfamiliar marine mammal-eating killer whales sounds than to familiar fish-eating killer whale sounds.

Harbour seals and long-finned pilot whales seem to have selectively habituated to the sounds of familiar, low predation risk killer whales, while maintaining anti-predator responses to familiar predatory killer whales or unfamiliar killer whales.

Migratory cetaceans such as most baleen whale species cover much larger areas than other non-migratory marine mammal species, and may therefore encounter more killer whale ecotypes in a higher diversity of contexts. For instance, humpback whales in the northern hemisphere spend winter on tropical or subtropical breeding grounds, summer on high-latitude feeding grounds, and generally migrate annually between these areas (Clapham and Mead, 1999). We hypothesised that killer whale sounds could assume a particularly wide breadth of ecological significance for humpback whales, and that they would show different types or degrees of responses in accordance with the ecotype of killer whale involved and the overall context of the encounter (location, season, behavioural activity, etc.).

Here, we report the behavioural responses of humpback whales to playbacks of killer whale sounds conducted in Norway, with particular focus on whether and how these responses varied according to the killer whale ecotype and the ecological context within which the sounds were presented to the humpback whales. In the northeast Atlantic, humpback whales feed from early summer to early winter around Spitzbergen, Bear Island, and coastal Norway before migrating to lower latitude areas to breed. We broadcasted the feeding sounds of two killer whale ecotypes: herring-feeding killer whales from Norway, representing a familiar and low-risk population, and mammal-eating killer whales from the northeast Pacific, simulating a potential predation threat. We presented the sounds of mammal-eating killer whales to humpback whales in two different contexts: inside the fjords in January (in Kaldfjord and Vestfjord) and offshore in June (off Spitzbergen).

Killer whales in the northeast Atlantic have been shown to produce a wide range of social and feeding sounds when they feed upon herring *Clupea harengus* (Simon et al., 2007; Samarra and Miller, 2015). During winter, humpback whales and herring-feeding killer whales both exploit the herring stock which overwinters in the Norwegian fjords. Mixed-species feeding aggregations are commonplace and are most often initiated by killer whales (Jourdain and Vongraven, 2017). We hypothesised that the feeding sounds of herring-feeding killer whales could signal the presence of a food patch to eavesdropping humpback whales. We expected that humpback whales would approach the source of herring-feeding killer whale sounds and would explore the water layer around the source through deeper dives and a more tortuous route.

Marine mammal-eating killer whales appear to exert a strong predation on humpback whales around the world (reviewed in Jefferson et al., 1991; South Pacific: Florez-Gonzalez et al., 1994; Australia: Naessig and Lanyon, 2004, Pitman et al., 2015; North Atlantic: McCordic et al., 2014). Marine mammal-eating killer whales from the northeast Pacific (de Bruyn et al., 2013) prey mostly upon pinnipeds, but occasionally take larger cetaceans and are a known predator of humpback whales (Saulitis et al., 2015). Even if Norwegian humpback whales are unlikely to be familiar with the northeast Pacific killer whale population, we expected humpback whales to perceive these unfamiliar marine mammal-eating killer whales as a threat (Deecke et al., 2002; Curé et al., 2019). We hypothesised that humpback whales would respond to unfamiliar marine mammal-eating killer whale sounds by adopting typical anti-predator behaviours. Due to their large flippers and robust body size, humpback whales appear to be fight strategist (Ford and Reeves, 2008), which is seemingly confirmed worldwide by observations of humpback whales approaching and harassing marine mammal-eating killer whales (reviewed in Pitman et al., 2017). However, no case of harassment of killer whales by humpback whales has been reported in Norway (Pitman et al., 2017), and playback experiments showed that humpback whales in Norway strongly avoided northeast Pacific mammal-eating killer whale sounds (Curé et al., 2015). We thus expected humpback whales to avoid – horizontally or vertically – the source of mammal-eating killer whale sounds, or to exhibit stealth behaviours, either deep diving or staying in shallow waters and reducing the strength of blows.

We predicted that the responses of humpback whales to mammal-eating killer whale sounds would vary with the specific ecological context in which they were heard. Inside the fjords during winter, humpback whales have been feeding for the entire season and are on the verge of starting their southward migration. Within the fjords, humpback whales also regularly hear killer whales of the herring-feeding ecotype in a non-predatory context, presumably since the superabundance of herring constitutes a much more profitable and easily accessible food source to killer whales. Offshore during early summer, humpback whales are in much poorer body condition: they have not fed during the breeding season and during the roundtrip migrations, and must therefore replenish their resources. Moreover, the offshore environment may not provide any cover or possible hiding place compared to the shallower, narrower fjords. During early summer humpback whales are thus under stronger pressure to feed, but are also more vulnerable to killer whale attacks. The two contexts of presentation correspond to different balances along the trade-off between foraging and escaping predation risk, and we predicted that these conditions could modulate how humpback whales respond to unfamiliar mammal-eating killer whale sounds.

3.3: Material and methods

3.3.1: Study site and population

In summer 2011 and 2012, we performed N = 8 playback experiments with transient killer whale sounds on summer feeding grounds off Spitzbergen and Bear Island, Norway (Table 2). During the last decade, a substantial portion of the humpback whale population has fed upon herring during winter in the Norwegian fjords, prior to continuing their migration south. In winter 2016 and 2017, we conducted playback experiments with herring-feeding (N = 6) and mammal-eating (N = 4) killer whale sounds in the fjords around Vengsøya, Norway (Table 2). The 2011 and 2012 focal whales were exposed to naval sonar prior to the killer whale playbacks as part of another research project. The 2011 and 2012 focal whales, as well as mn16_018a and mn16_024a, were also exposed to a broadband noise control playback (data not shown). The 2011 and 2012 experiments were used in a previous work to describe the responses of humpback whales to playback of mammal-eating killer whale sounds (Curé et al., 2015).

3.3.2: Data collection

We combined data from tag deployments and visual observations of the tagged whale at the surface to record the behaviour and movements of humpback whales before, during, and after playbacks of killer whale sounds. During each experiment, one humpback whale was tagged, then identified as the focal individual (Altmann, 1974). In 2011, 2012, and 2016, we deployed Dtags (Johnson and Tyack, 2003). Dtags contain a suite of sensors (250 Hz 3-axis accelerometer, 250 Hz 3-axis magnetometer, 50 Hz pressure sensor) and two hydrophones (sampling frequency: 96 kHz, sampling width: 12 bits). In 2017, we used 'mixed-tags', custom-made tags combining all the sensors of Dtags with a GPS logger (FastLoc™, SirTrack: Wildlife Tracking Solutions, Havelock North, New Zealand).

Individual ID	Study location	Ecological context	Sound stimulus type	Version
mn11_157a	Spitzbergen	Offshore summer	MEKW	v1
mn11_160a	Spitzbergen	Offshore summer	MEKW	v2
mn11_165e	Spitzbergen	Offshore summer	MEKW	v3
mn12_161a	Spitzbergen	Offshore summer	MEKW	v1
mn12_164b	Spitzbergen	Offshore summer	MEKW	v2
mn12_170a	Spitzbergen	Offshore summer	MEKW	v3
mn12_171a	Spitzbergen	Offshore summer	MEKW	v1
mn12_180a	Spitzbergen	Offshore summer	MEKW	v2
mn16_018a	Vengsøya	Inshore winter	HFKW	v2
mn16_020a	Vengsøya	Inshore winter	MEKW	v1
		Inshore winter	HFKW	v3
mn16_023a	Vengsøya	Inshore winter	HFKW	v3
		Inshore winter	MEKW	v1
mn16_024a	Vengsøya	Inshore winter	HFKW	v1
mn17_024a	Vengsøya	Inshore winter	MEKW	v2
		Inshore winter	HFKW	v2
mn17_026a	Vengsøya	Inshore winter	HFKW	v1
		Inshore winter	MEKW	v3

Table 2: Overview of the collected data showing the focal subject (Individual ID), the study location, the ecological context (Offshore summer or Inshore winter), and the specifications of the sound stimulus used (killer whale ecotype and stimulus version). Each focal individual was given an eight-symbol identifier, which takes the form aaBB_CCCd: aa is the first initials of the species' scientific name, BB is the last two digits of the experiment year, CCC is the Julian date of the experiment, and d is the number of the tag deployment within the day, from a to z. For two individuals (mn11_160a and mn16_020a), the tag came off prematurely, and the post-exposure observation phase of the second experiment was not completed. In one case (mn16_018a), we were not able to retrieve the tag after the experiments, which restricted our data to the visual tracking information for this individual. MEKW: unfamiliar mammal-eating killer whale; HFKW: familiar herring-feeding killer whale.

We attached all tags to the animals temporarily with suction cups. We deployed tags with a long pole or a pneumatic launching system (ARTS™, LKARTS, Bodø, Norway). Humpback whales only showed short-term reactions – flinches and submersions – to tag deployments. All tags were equipped with a VHF beacon which allowed the visual tracking of the focal whale and tag recovery after detachment from the whale.

We started the visual tracking of the focal whale immediately after tagging. We recorded the position (based upon range and bearing from the observation vessel) and heading of the focal whale when the focal whale was at the surface. We made an average of one observation every 4.89 +/- 1.86 min (mean +/- standard-deviation; range 2.81 – 11.25 min). We made all visual tracking records in Logger 2010 (courtesy of the International Fund for Animal Welfare, Yarmouth, Massachusetts, US).

3.3.3: Playback procedure

The stimuli we used for playback experiments were natural sound sequences of feeding wild killer whales, recorded with Dtags in previous studies. We used two stimulus types: herring-feeding killer whales (HFKW) recorded in Norway from killer whales feeding on herring, and marine mammal-eating killer whales (MEKW) recorded in South-East Alaska. Noisy sound sections, such as flow noise from the whale's movements, bubbling, and surfacing noise, were removed from the stimuli. The resulting files were looped to 15 minutes and amplified to reach an average of 140-155 dB re 1 µPa @ 1 m for killer whale calls (similar to natural source levels: Miller, 2006). We prepared three versions of each stimulus type from different recordings to reduce pseudoreplication (Table 2). Example spectrograms for herring-feeding and mammal-eating killer whale sounds are presented in appendix (Figure 7).

We presented mammal-eating killer whale sounds in two different contexts, offshore during early summer (beginning of the feeding season), and inshore during winter (end of the feeding season). Herring-feeding killer whale sounds were only presented inshore during winter. We therefore had three combinations of stimulus type and context of presentation: mammal-eating killer whale sounds presented offshore (OMEKW: offshore MEKW) and inshore (IMEKW: inshore MEKW), and herring-feeding killer whale sounds presented inshore (IHFKW: inshore HFKW). In 2016 and 2017, we exposed four humpback whales to both herring-feeding and mammal-eating killer whale sounds (Table 2).

Each playback experiment consisted in three 15-minute-long phases: the pre-exposure observation period (PRE), the exposure period during which the stimulus was presented (EXP), and the post-exposure observation period (POST). When we performed two playbacks to a focal whale, the order was alternated (Table 2). The average duration between successive experiments was 16 min 37 s, which means that the time between the start of successive broadcasts was 46 min 37 s in average (range: 29 min 16 s –

1 h 6 min 29 s). On two occasions, the tag came off prematurely and the post-exposure observation phase of the second experiment was incomplete (Table 2).

We used two boats during playback experiments: one was devoted to tracking and observing the focal whale (the tracking boat), and the second boat was used for sound playbacks (the playback boat). In 2016 and 2017, we waited on average 1 h 34 min 37 s +/- 25 min 26 s (range 1 h 9 min 22 s – 2 h 27 min 3 s) from the tag deployment to the first playback. In 2011 and 2012, the crew performed naval sonar exposure experiments before the killer whale playbacks (details can be found in Kvadsheim et al., 2015). An average recovery period of 2 h 3 min 12 s +/- 1 h 10 min 2 s (range 39 min – 3 h 39 min) separated sonar exposures and playback experiments. The recovery period between the tag deployment or sonar exposure and the killer whale playback aimed to ensure that the whales' behaviour had returned to normal before starting the playback experiment. The tracking boat continued to track the focal whale consistently irrespective of the playback experimental phase, and sightings locations of the tagged focal whale were used to position the playback boat. We aimed to place the sound source ahead of the whale, on the side of its path, so that either attraction or avoidance reactions could be clearly identified. The average distance between the focal whale and the sound source at the onset of the playbacks was 851 +/- 567 m (range 231 – 2915 m).

The playback chain consisted of a player (2011, 2012: M-Audio Micro Track II recorder; 2016, 2017: DR40-Tascam recorder), a resistor, an amplifier (2011, 2012: Cadence Z8000, 2016, 2017: Sony XM-N502), and a loudspeaker (2011, 2012: Lubell LL9642T, frequency range 0.2-20 kHz; 2016, 2017: Lubell LL9162T, frequency range 0.2-20 kHz). The playback boat got into position before the pre-exposure period ended, turned its engine off, and lowered the loudspeaker 8 m underwater.

3.3.4: Data treatment and response variables

We computed the dive profile and the horizontal track of the focal whale during the experiment. We calibrated the tags' pressure sensor data to compute the dive profiles of the focal whales. We followed the method described by Wensveen and colleagues (2015) to construct a horizontal track of the focal whale, which consists of a dead-reckoning track anchored to visual (and GPS, when available) positions. We had no tag data for whale mn16_018a (Table 2), so we constructed the horizontal track of this whale with a linear interpolation between visual surfacing positions and times. We measured nine response variables to describe the responses of humpback whales to killer whale sounds: for the horizontal component of the response, we calculated a horizontal reaction score (HRS), an approach index (AI), and a linearity index (LI); for the vertical component of the responses, we focused on the maximum dive depth (MDdepth) and duration (MDdur) reached during each experimental phase. We used maxima for dive depth and dive duration as they are efficient in detecting outlier response dives.

The $HRS_t = \frac{Extrapolated\ distance_t - Real\ distance_t}{Initial\ distance}$ measures the difference, relative to the sound source, between the actual position of each whale and its extrapolated position based upon its movement patterns during the pre-exposure phase. *Extrapolated distance$_t$* is the distance between the extrapolated position of the whale and the sound source at time *t*, *Real distance$_t$* is the distance between the whale and the sound source at time i, and *Initial distance* is distance between the whale and the sound source at the onset of the playback.

To calculate the extrapolated distance, we first converted the latitude and longitude of the whale to UTM coordinates and then made a linear regression between the whale's northing and easting during the pre-exposure phase to get the whale's global heading. Next, we projected the positions of the whale at the start and at the end of the pre-exposure phase on the regression axis to obtain the global distance (and thus the global speed) travelled along the regression axis during the pre-exposure phase. We used the global heading and speed of the whale during the pre-exposure phase to extrapolate the whale's position if it had kept the same movement patterns as during the pre-exposure phase. The Extrapolated distance is measured between the extrapolated position of the whale and the position of the sound source. HRS are positive values if Real distance was smaller than Extrapolated distance, which means that the whale approached the sound source relative to its prior movement trajectory, and are negative values if the focal whale avoided the sound source relative to its prior movement trajectory. We measured

HRS at 15 minutes (end of the broadcast) to measure the whale's response during the playback and at 30 minutes (end of the post-exposure phase) to quantify whether the whale's responses extended after the end of the playback (Figure 4).

The $AI = \frac{Closest\ distance\ to\ sound\ source}{Initial\ distance\ to\ sound\ source}$ measures the closest approach of the whale to the sound source during the exposure. AI values fall between 0 and 1, with 0 meaning the whale came into contact with the source (strong approach) and 1 meaning the initial distance to the source was also the smallest (immediate avoidance). The AI compliments the HRS value, as it quantifies the maximum approach observed over the entire exposure period.

The $LI = \frac{Distance\ between\ start\ and\ end\ of\ experimental\ phase}{Total\ distance\ travelled}$ measures the directedness of the whale's course (as in Jahoda et al., 2003; Scheidat et al., 2004; Williams et al., 2006). LI values range from 1 if the whale travelled in a straight line to 0 if it turned in a circle.

We defined a dive as any duration spent deeper than 5 m (corresponding roughly to the body height of humpback whales). We measured the dive depth and dive duration from each dive profile, and used the maximum observed during the exposure period (MDdepth: maximum dive depth; MDdur: maximum dive duration). We only took into account dives performed entirely within an experimental phase, in order to avoid that long and deep dives overlapping experimental phases would drive the values of the variables.

We calculated differences in LI, MDdur, and MDdepth between experimental phases: between the playback period and the pre-exposure phase to identify the responses of the whale during the stimulus presentation (noted VARIABLEexp-pre); and between the post- and pre-exposure phases to determine whether the responses extended after the end of the broadcast (noted VARIABLEpost-pre).

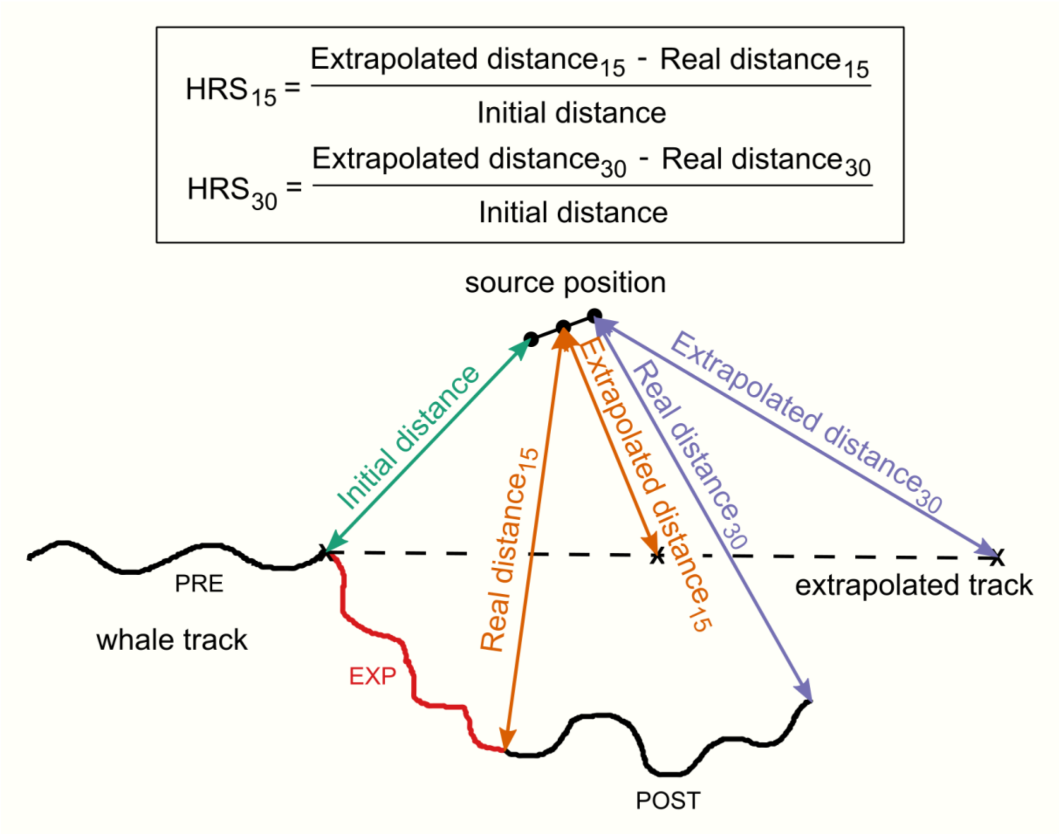

Figure 4: Horizontal reaction score (HRS) calculation. The HRS measures the difference in the distance between the whale and the sound source and the distance there would be between the whale and the sound source if the whale kept the same behaviour as right before the playback. We used the speed and heading of the whale during the pre-exposure phase to extrapolate its movement trajectory.

3.3.5: Statistical analysis

In order to determine whether humpback whales exhibited ecotype- and context-dependent reactions to the sounds of killer whales, we tested whether a classifier could assign the correct experiment type – inshore herring-feeding killer whale sounds (IHFKW), inshore mammal-eating killer whale sounds (IMEKW), or offshore mammal-eating killer whale sounds (OMEKW) – to a playback solely from the response variable data. We used the Random Forest procedure (Breiman, 2001), because it has been shown to be particularly efficient on small or unbalanced datasets (Gündüz and Fokoué, 2015). The Random Forest combines the output of multiple tree classifiers, each of which is trained on roughly two thirds of the data and classifies the last third. Our data set consisted of six IHFKW experiments, four IMEKW experiments, and eight OMEKW experiments. We trained each tree on a random subset of four IHFKW, three IMEKW, and five OMEKW playbacks, to ensure that all training sets contained approximately two thirds of the playbacks of each type. We filled missing values with the variable medians for the whale with missing tag data and incomplete experiments (Table 2). In addition to classification, the Random Forest assesses the importance of each variable in the decision process, by computing the reduction of classification accuracy resulting from the random permutation of a given variable values. We centred and scaled all variables before running the Random Forest in order to avoid size effects in the classification or the calculation of variable importance (Strobl et al., 2008).

The accuracy of the fitted Random Forest depends on two parameters: the higher the number of trees used (ntree) and the lower the number of variables selected to split each node during training (mtry), the more accurate the classification. We chose an arbitrarily large ntree (100,000) because our low sample size made computational costs negligible. Our selection of mtry was guided by our total number of variables, but reduced compared to standard formulas (eg: Latinne et al., 2001; Cutler et al., 2007) in order to increase accuracy (as advised in Breiman, 2001). We ran a first Random Forest (ntree = 100,000; mtry = 3) with all response variables, and a second one (ntree = 100,000; mtry = 1) with only the three most important variables from the first Random Forest, referred to as key variables. The second Random Forest allowed a graphical representation of the results in three dimensions, and determined whether a reduced number of key variables were sufficient for accurate classification.

We used Matlab (Matlab R2017a, the Mathworks Inc., Natick, Massachusetts, US) to calibrate tag data, compute dive profiles and horizontal tracks, and draw the three dimension plot. We used R (R Core Team, 2017) to run Random Forests with the "randomForest" package (Liaw and Wiener, 2002).

3.3.6: Ethical note

Tagging activities were licenced under permits issued by the Norwegian Animal Research Authority (2011-2012, permit n° S-2011/38782) and the Norwegian Food Health Authority (2016-2017, permit ID 8165). The research protocol was approved by the Animal Welfare Ethics Committee of the University of Saint-Andrews.

3.4: Results

Humpback whales were strongly attracted by the sounds of herring-feeding killer whales (HRS15, AI: Figure **5**A and B). This attraction was temporary and was typically reduced during the post-exposure period (HRS30, Figure 5A). Humpback whales dove more deeply during IHFKW playbacks. This diving behaviour ceased as soon as the playback stopped (LI, MDdepth, MDdur: Figure 5C, D, and E). By comparison, humpback whales avoided the source of mammal-eating killer whale sounds (HRS15, AI, LI: Figure 5A, B, and C), with the exception of two whales. Some avoidance responses extended into the post-exposure period, but not all (HRS30, LI: Figure 5A, and C).

		Classification outcome			Error rate
		IHFKW	IMEKW	OMEKW	
Playback type	IHFKW	6	0	0	0 %
	IMEKW	1	2	1	50 %
	OMEKW	2	1	5	37.5 %
				Overall	27.8 %

Table 3: Classification results for the first Random Forest, using all response variables.

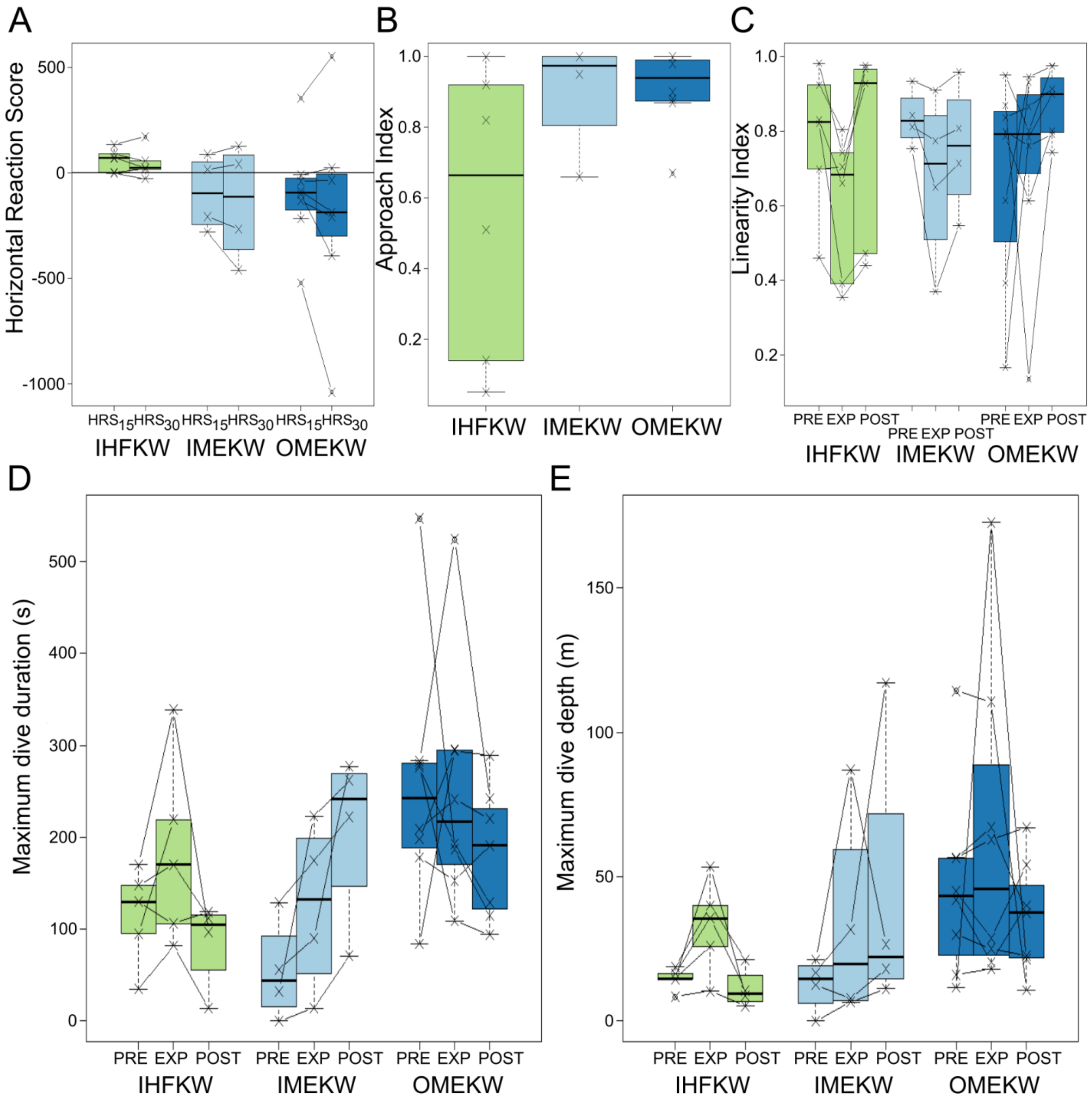

Figure 5: Behavioural responses of humpback whales to killer whale sounds (IHFKW in green, IMEKW in light blue, and OMEKW in dark blue) **A)** Horizontal reaction scores (HRS) at 15 and 30 minutes. The black lines correspond to individual playback sessions **B)** Approach Index (AI) **C)** Linearity Index (LI) **D)** Maximum dive duration (MDdur) during each experimental phase for each experiment type **E)** Maximum dive depth (MDdepth) during each experimental phase for each experiment type

Humpback whales showed strong, consistent avoidance away from the source of mammal-eating killer whale sounds offshore. However, this avoidance response was mixed in the inshore setting, with two strong avoidances and two mild approaches (HRS, AI: Figure 5A and B). Humpback whales showed no change in directedness during or after OMEKW playbacks, but followed less direct routes during and shortly after IMEKW playbacks (LI, Figure 5C).

Humpback whales tended to make shallower dives during the OMEKW playbacks ($\text{MDdepth}_{\text{exp-pre}}$, Figure 5E) and to reduce dive duration when the playbacks ended ($\text{MDdur}_{\text{post-pre}}$, Figure 5D). During IMEKW playbacks, humpback whales dove deeper and for longer durations. This increase in dive depth and duration continued into the post exposure period (MDdur, Figure 5D; MDepth, Figure 5E). Numeric values of response variables for each playback experiment are listed in appendix (Table 5).

The Random Forest using all response variables correctly classified 72.2 % of experiments overall: 100 % of inshore herring-feeding killer whale playbacks (IHFKW), 50 % of inshore mammal-eating killer whale playbacks (IMEKW), and 62.5 % of offshore mammal-eating killer whale playbacks (OMEKW) (Table 3). The three most important variables were (in decreasing order of importance): HRS15, $\text{MDdur}_{\text{post-pre}}$, and $\text{MDdepth}_{\text{post-pre}}$ (Figure 6A). Indeed, HRS15 covered different ranges for each experiment type: mostly positive for IHFKW experiments, mostly negative for OMEKW experiments, and variable for IMEKW experiments (Figure 5A). The other important variables ($MDdur_{post-pre}$ and $MDdepth_{post-pre}$) were different between some experiment types: $MDdur_{post-pre}$ was generally positive for IMEKW experiments and slightly negative for IHFKW and OMEKW experiments (Figure 5D), while $MDdepth_{post-pre}$ was negative for IHFKW experiments and positive for IMEKW experiments (Figure 5E). The other variables provided less distinct information and were less important for the classification process: HRS30 (Figure 5A), LI (Figure 5C), $MDdur_{exp-pre}$ (Figure 5D) and $MDdepth_{exp-pre}$ (Figure 5E) were spread over large ranges regardless of experiment type, and while some humpback whales exhibited particularly small AI in response to IHFKW playbacks, large AI were reported for all three experiment types (Figure 5B).

The second Random Forest confirmed that the three key variables were sufficient to sort experiments by type (Figure 6B). It classified correctly 83.3 % of playbacks, among which 100 % of IHFKW and IMEKW, and 62.5 % of OMEKW (Table 4).

		Classification outcome			Error rate
		IHFKW	IMEKW	OMEKW	
Playback type	IHFKW	6	0	0	0 %
	IMEKW	0	4	0	0 %
	OMEKW	2	1	5	37.5 %
				Overall	16.7 %

Table 4: Classification results for the second Random Forest, using the three most important response variables (HRS15, $MDdur_{post-pre}$, and $MDdepth_{post-pre}$).

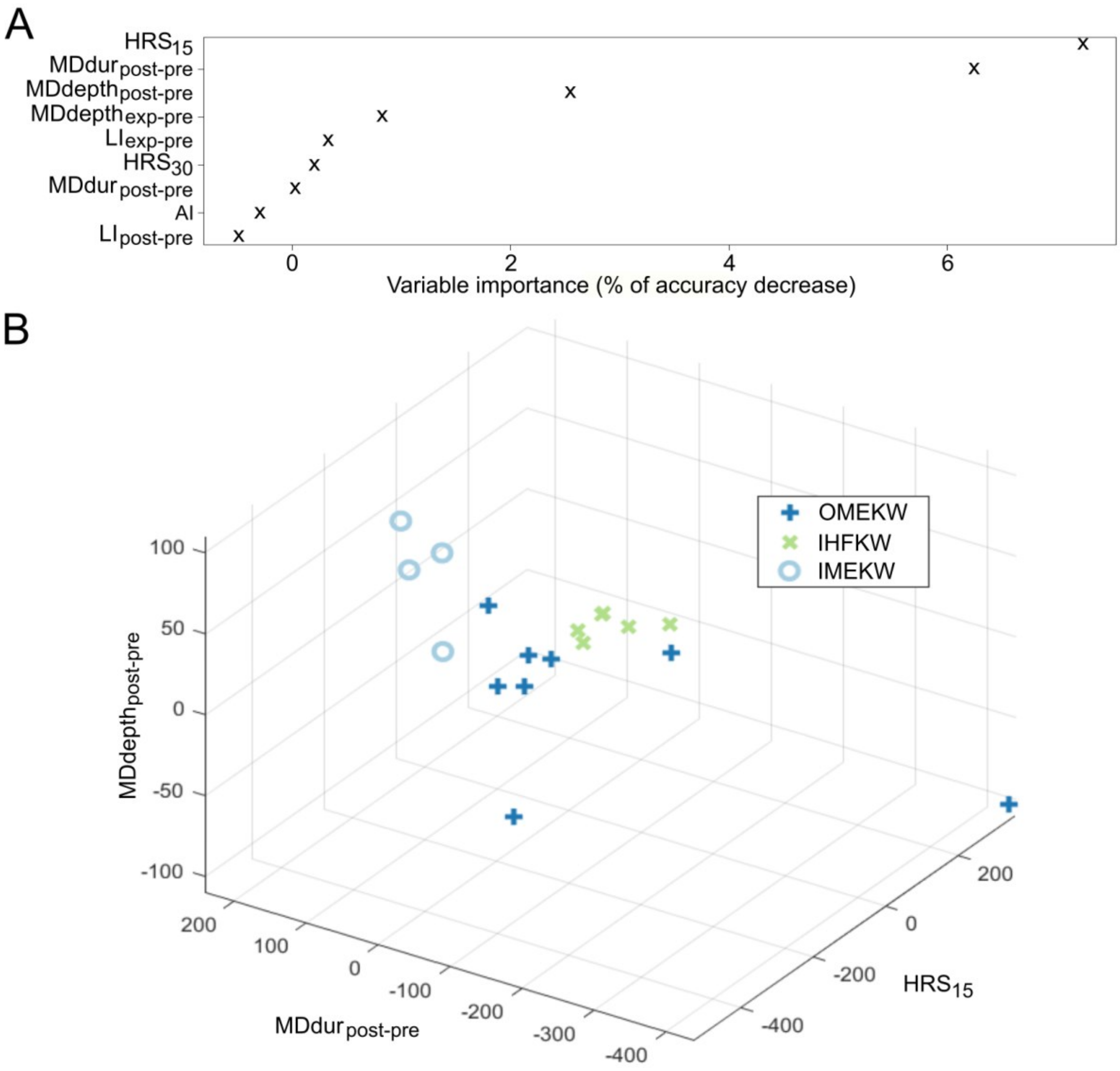

Figure 6: Random Forest results **A)** The importance of each variable in the Random Forest is computed as the mean decrease in classification accuracy resulting from the random permutation of this variable. The three most important variables were HRS15, $\text{MDdur}_{\text{post-pre}}$, and $\text{MDdepth}_{\text{post-pre}}$, with associated decreases in accuracy of 7.2 %, 6.2 % and 2.5 %, respectively **B)** Visualisation of the responses to each stimulus in the space of the three most important variables (IHFKW as green x crosses, IMEKW as light blue circles, OMEKW as dark blue + crosses)

3.5: Discussion

Random Forest analyses demonstrated that humpback whales responded differently to the sounds of two killer whale ecotypes, which means that they were able to discriminate between these two stimuli. Specifically, humpback whales approached the source broadcasting the sounds of familiar herring-feeding killer whales and dove deeper around it, whereas they avoided the source of unfamiliar mammal-eating killer whale sounds. Moreover, our results showed that the response of humpback whales to mammal-eating killer whale sounds was influenced by the context of presentation: humpback whales exhibited strong and consistent horizontal avoidance responses offshore during summer at the beginning of feeding season whereas avoidance responses were less clear inshore during winter at the end of the feeding season.

Previous studies showed that harbour seals, a pinniped species commonly preyed upon by killer whales, and long-finned pilot whales, a toothed whale at a low risk of predation by killer whales, react differently to the sounds of familiar fish-eating and familiar and/or unfamiliar mammal-eating killer whales (Deecke et al., 2002; Curé et al., 2019). Our results confirmed this ability to discriminate between the sounds of killer whale ecotypes in a baleen whale species particularly vulnerable to predation by killer whales, the humpback whale (McCordic et al. 2014). We exposed some of the focal whales to a broadband noise as a control and they barely reacted to it (2011-2012 dataset, N = 8: see Curé et al., 2015; 2016-2017 dataset, N = 2: data not shown), which indicates that humpback whales responded to killer whale sounds and not to unspecific cues produced by the playback system.

Humpback whales were consistently attracted towards the source broadcasting herring-feeding killer whales sounds and initiated deeper diving, likely as exploration behaviour, upon detecting them. These results are consistent with observations of mixed-species groups between herring-feeding killer whales and humpback whales in the study area, where both species feed on herring patches (Jourdain and Vongraven, 2017). We interpreted these responses to herring-feeding killer whale sounds as a dinner-bell effect; the feeding sounds of a neighbouring species sharing the same food source as humpback whales may signal the presence of a food patch to eavesdroppers. In contrast, mammal-eating killer whale sounds generally repelled humpback whales. Whereas some cetacean species exhibit fight strategies when confronted with a predator, physically defending themselves or mobbing the attacker, other species adopt flight responses to avoid detection by predators or to prevent predator encounters (Ford and Reeves, 2008). Humpback whales clearly avoided the source of mammal-eating killer whale sounds, which is in line with the typical anti-predator-like responses described in several other marine mammal species while interacting with killer whales (reviewed in Jefferson et al., 1991) or while exposed to the playback of mammal-eating killer whale sounds (Deecke et al., 2002; Curé et al., 2013; Bowers et al., 2018). These results indicate that humpback whales likely perceived mammal-eating killer whale sounds as a predation threat.

While the responses to herring-feeding killer whale sounds only lasted throughout the playback, the response to mammal-eating killer whale sounds continued beyond the end of playback despite the cessation of the sounds.. The sounds produced by mammal-eating killer whales while consuming a prey may signal the presence of a predator not actively hunting, as mammal-eating killer whales are mostly silent when hunting until the attack is launched (Guinet et al., 2000; Deecke et al., 2005; Jourdain et al., 2017). The cessation of the mammal-eating killer whale sounds at the end of the playback period could indicate to prey species that nearby predators have started an active hunt, thus enticing humpback whales to pursue their anti-predator behaviour. Curé and colleagues (2015) noted that five out of eight humpback whales off Spitzbergen (2011 and 2012 experiments in this dataset) increased their swimming speed during transient killer whale playbacks, and further increased it when the playbacks ended.

The response of humpback whales to herring-feeding killer whale sounds was more easily correctly classified (0/12 misclassifications) than the response to mammal-eating killer whale sounds (8/24 misclassifications overall: 2/8 for IMEKW, 6/12 for OMEKW). Indeed, the “approach and explore” response to herring-feeding killer whale sounds was clearly identifiable: it consisted of approaching the sound source and increasing dive depth and duration likely to explore the environment.

Anti-predator response strategies may vary according to various ecological factors: avoidance may be vertical, horizontal, cryptic, or any combination of the aforementioned strategies (Ford and Reeves, 2008). Here, we found that responses to unfamiliar mammal-eating killer whale sounds simulating a potential predation risk were influenced by the ecological context, which may explain why they were less easily recognised by Random Forests than responses to herring-feeding killer whale sounds. Specifically, humpback whales showed strong avoidance responses offshore (as previously reported by Curé et al., 2015), while only half of the humpback whales avoided mammal-eating killer whale sounds inshore. In addition, humpback whales made deeper and longer dives during and after mammal-eating killer whale playbacks inshore, whereas they made shallower dives during and shorter dives after these playbacks offshore. The context of presentation not only varied in topography (inshore and offshore settings), but also corresponded to different functional seasons for the whales. We performed offshore experiments during early summer, at the beginning of the feeding season when humpback whales need to replenish their resources after a breeding season in tropical waters and a roundtrip migration without feeding. We conducted the inshore experiments during winter, at the end of the feeding season when the whales were presumably in optimal body condition and about to depart for the southward migration. Humpback whales may be more vulnerable to killer whale attacks during summer when they are in poorer condition and in the offshore settings that does not provide any potential refuge to hide from killer whales. These ecological constraints may explain that responses to mammal-eating killer whale sounds were stronger and more consistent for the experiments carried out offshore during summer.

An additional possible explanation is that both OMEKW and IMEKW situations correspond to different balances along the trade-off between foraging and escaping predation risk which could explain why responses to mammal-eating killer whale sounds depend on context. During summer, foraging is the main activity of humpback whales. In this context, avoiding mammal-eating killer whale sounds means evading the risk of injury or death but losing the benefits of the current behaviour (e.g. foraging), while not avoiding them implies an increased predation risk but ensures the completion of the current behaviour. The decision process depends on how vulnerable the humpback whale is and how beneficial is the current behaviour. Similar trade-offs between foraging and predation risk have been described in bats (Indiana bats *Myotis sodalis*: Arndt et al., 2018) and lizards (broad-headed skinks *Eumeces laticeps*: Cooper, 2000). In winter, humpback whales reach the end of the feeding season: there is both less pressure to forage and less risk associated with predator encounters.

Another possibility is that humpback whales could have failed to recognise the sounds of unfamiliar mammal-eating killer whales as a threat in the inshore setting, due to the abundance of cohabiting herring-feeding killer whales. Indeed, during winter both humpback whales and herring-feeding killer whales move into the fjords to feed on herring, resulting in large mixed-species feeding aggregations (Jourdain and Vongraven, 2017). In such conditions, it might be that humpback whales cohabiting with large numbers of herring-feeding killer whales have a reduced ability to recognise the killer whale sound playbacks as a threat in the midst of other non-threatening killer whale sounds.

This work had some limitations. We selected the first whale we could tag as a focal whale. As a result, the humpback whales we monitored during playback experiments could have been a biased subset of the population, those more likely to approach the experimental vessels and therefore easier to tag, or less adverse to perturbations. The methods we applied in this study required the prolonged presence of the tracking boat. Humpback whales generally avoid boats (Scheidat et al., 2004), but show variable responses – no reaction (Frankel and Clark, 2000), approach (Stamation et al., 2009), and even threaten (Au and Green, 2000) – according to the number of vessels, their speed, distance, and orientation (Scheidat et al., 2004; Stamation et al., 2009). In this study, the average distance between the tracking boat and the focal whale was 213.3 +/- 131.4 m (range 25 – 800 m), which is mostly larger than the 100 m threshold mentioned in several studies (Scheidat et al., 2004; Stamation et al., 2009): the tracking boat should not have greatly disturbed the focal whales. In the case of the inshore whales, they may well have been somewhat desensitized to vessel traffic by the time the study was conducted, at the end of a long winter feeding period in the presence of large numbers of fishing vessels and other boat traffic. Indeed, whales frequently seek out fishing vessels, presumably because they associate the acoustic cues of fishing vessels with prey availability. Pods with calves respond more to the presence of vessels (Stamation et al., 2009), and whales actively engaged in foraging are less sensitive to them (Scheidat et al., 2004). However, three focal whales were accompanied by calves and could possibly have been more disturbed by the boat presence. To ensure the boat presence was not responsible for the behavioural responses we observed, the tracking boat was present for the whole duration of the experiment and there could be no additive effect of the boat presence and the sound stimuli on the focal whale's behaviour. Finally, the initial distance between the sound source and the focal whale (851 +/- 567 m, range 231 – 2915 m) is closer than the likely distance over which humpback whales could have detected killer whale sounds. The sudden appearance of a nearby source might have influenced the responses of humpback whales to killer whale sounds.

We describe here the ability of humpback whales to discriminate between the sounds of unfamiliar killer whales representing potential predator and familiar killer whales feeding upon the same food source. The behavioural responses exhibited by humpback whales in response to KW sounds indicate that they are able to associate different ecological situations to the detected presence of each population of killer whales.

In this study, humpback whales were familiar with herring-feeding killer whale sounds, but likely unfamiliar with the mammal-eating killer whale sounds used. We cannot establish whether humpback whales identified each ecotype or if they simply distinguished unfamiliar from familiar killer whales sounds to which they habituated as non-threatening. In a similar study, Deecke and colleagues concluded that harbour seals habituated selectively to local, harmless-perceived killer whales (Deecke et al., 2002). We need to conduct additional experiments using sounds of unfamiliar fish-eating killer whales to reach such a definitive conclusion. In any case, our results indicate that the sounds of familiar herring-feeding killer whales and the sounds of unfamiliar mammal-eating killer whales were associated with different ecological significance for the humpback whales: the former with the presence of a known sympatric species consuming similar food which elicited an approach and exploratory response, and the latter with a potential predation threat which triggered an avoidance response. The ability to discriminate between familiar and unfamiliar heterospecifics has been demonstrated in many terrestrial taxa, for instance birds (carrion crows *Corvus corone*: Wascher et al., 2012) or primates (African forest monkeys: Candiotti et al., 2013). Moreover, the ability to associate discrete heterospecific calling behaviours with distinct ecological significance was also shown to be widespread in terrestrial animals (reptiles: Fuong et al., 2014; birds: Dawson Pell et al., 2018). Our results on a species of baleen whale, in association with results from Deecke and colleagues on a species of pinnipeds (2002) and Curé and colleagues on a species of toothed whales (2019), indicate that the abilities of fine-scale acoustic discrimination of heterospecific acoustic signals are also widespread among marine mammal taxa.

Our study used full acoustic recording of natural sequences, and hence was not designed to elucidate which sound features specifically enabled the humpback whales to discriminate between the two sound types. The major acoustic difference between herring-feeding and mammal-eating killer whales is that the former rely on echolocation clicks for foraging and display tail slap sounds as part of the herring-foraging strategy (Similä and Ugarte, 1993) whereas the latter produce much fewer clicks and no tail slaps. The presence of tail slaps or multiple echolocation clicks could signal to humpback whales if they are facing a group of herring-feeding or mammal-eating killer whales. It might also be that some specific parameters in mammal-eating killer whale sounds trigger anti-predator responses. Indeed, it was recently shown in other species exposed to playback of mammal-eating killer whale sounds that the presence of call types containing non-linear phenomena in the stimuli induced strong anti-predator responses (Bowers et al., 2018). Moreover, herring-feeding and mammal-eating killer whales also differ in the characteristics of their calls, such as complexity (number of inflection points: Deecke et al., 2005) or frequency (Filatova et al., 2015). Some parameters of the calling behaviour (e.g. call rate, overlapping calls) may be indicators of the size of the killer whale group, or of the behaviour they are engaged in. Vocalising mammal-eating killer whales, for instance, are likely to be feeding or socializing at the surface (Deecke et al., 2005). Thus, the level of vocal activity of a killer whale group may be related to the level of threat they represent to humpback whales (Lima and Dill, 1990). We could investigate differences across various acoustic parameters between the vocal productions of different killer whale ecotypes or of killer whales engaged in different activities, and to test whether these parameters convey the information which might help eavesdroppers, such as humpback whales, to decide on which behaviour to adopt. Further experiments are therefore needed to explore the acoustic cues that humpback whales use to discriminate between the sounds of different killer whale ecotypes, which carry different ecological significance to eavesdroppers.

3.6: Acknowledgment

This research was funded by the 3S (Sea mammal Sonar Safety) consortium partners: the United States Office of Naval Research, the Royal Norwegian Navy, the Norwegian Ministry of Defence, the Defence Research and Development Department of the Netherlands Ministry of Defence, and the French Ministry of Defence (DGA). We thank all members of the fieldwork crew for their effort over the years. We are grateful to Dr. Valerie Dufour for her critical reading of the manuscript.

3.7: Appendix

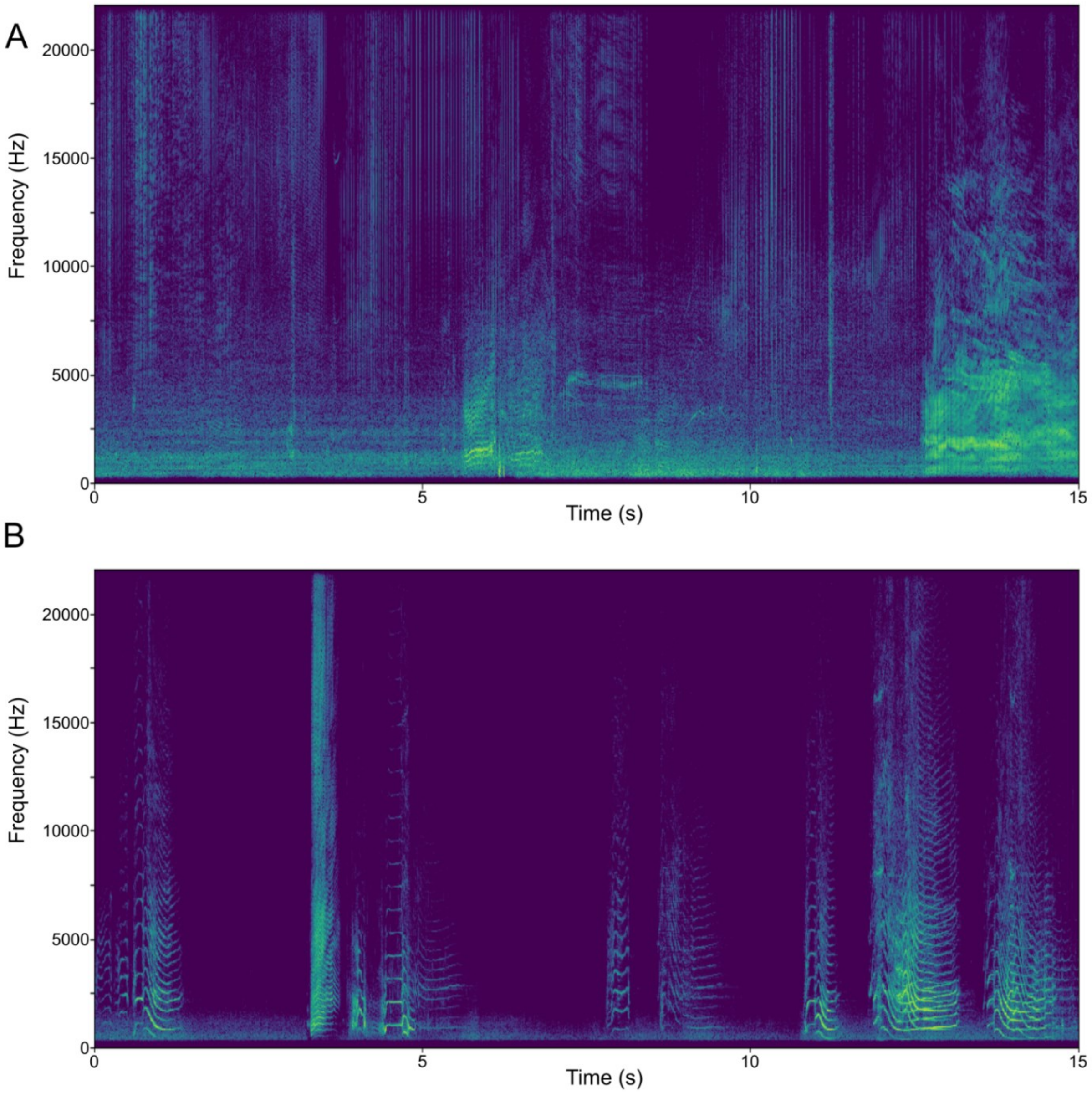

Figure 7: Spectrograms of the killer whale sounds stimuli used for the playback experiments **A)** Herring-feeding killer whale sounds (HFKW). Note the presence of echolocation clicks (vertical lines) **B)** Mammal-eating killer whale sounds (MEKW) containing much fewer clicks than HFKW sounds

		Response variables											
Individual ID	Stimulus type	HRS15	HRS30	AI	LI$_{pre}$	LI$_{exp}$	LI$_{post}$	MDdepth$_{pre}$	MDdepth$_{exp}$	MDdepth$_{post}$	MDdur$_{pre}$	MDdur$_{exp}$	MDdur$_{post}$
mn16_018a	IHFKW	1.6	17.1	0.92	0.70	0.71	0.93	N/A	N/A	N/A	N/A	N/A	N/A
mn16_020a		67.9	N/A	0.14	0.92	0.81	N/A	14.6	26	N/A	95	219	N/A
mn16_023a		133	171	1	0.82	0.39	0.47	16.4	35.6	10.6	170	339	97
mn16_024a		90.6	56.4	0.51	0.83	0.66	0.97	14.6	53.4	8.6	148	170	112
mn17_024a		-2.5	-27.6	0.82	0.46	0.36	0.44	8.4	10.4	5.2	35	82	14
mn17_026a		72.1	23.9	0.05	0.98	0.74	0.98	18.8	40	21.2	130	106	119
mn16_020a	IMEKW	88.5	126.7	0.66	0.84	0.65	0.71	12.5	7.9	18	56	90	277
mn16_023a		15.1	41.5	1	0.75	0.37	0.55	21.3	86.9	26.5	32	223	262
mn17_024a		-208.3	-266.5	1	0.81	0.77	0.81	0	6.6	11.2	0	14	71
mn17_026a		-280.7	-461.6	0.95	0.94	0.91	0.96	16.8	31.7	117.1	129	175	222
mn11_157a	OMEKW	-40.5	-35.1	0.88	0.80	0.76	0.79	56.4	62.8	67	198	294	289
mn11_160a		354.4	550.9	1	0.87	0.14	0.74	114.3	110.5	10.7	547	187	115
mn11_165e		-10.1	23.4	0.9	0.95	0.80	0.97	44.9	28.8	54	276	193	129
mn12_161a		-218.4	N/A	0.98	0.39	0.93	N/A	16	17.9	N/A	84	295	N/A
mn12_164b		-522.7	-1040.9	1	0.61	0.95	0.98	29.9	25	22.6	279	109	94
mn12_170a		-101.5	-394.1	0.87	0.17	0.78	0.90	56.5	67	37.5	209	241	220
mn12_171a		-88.4	-187.1	0.67	0.79	0.61	0.80	42	20.4	40.1	178	153	191
mn12_180a		-132.7	-208.5	0.98	0.84	0.87	0.91	11.6	172.6	21.4	283	524	242

Table 5: Numerical values of the response variables for all playback experiments. The individual identifiers are the same as in Table 2. IHFKW: inshore (winter) herring-feeding killer whale sounds, IMEKW: inshore (winter) mammal-eating killer whale sounds, OMEKW: offshore (summer) mammal-eating killer whale sounds

4: UNSUPERVISED CLASSIFICATION TO STUDY GRADATION IN ANIMAL VOCALISATIONS BASED ON FUZZY CLUSTERING AND MEL FREQUENCY CEPSTRAL COEFFICIENTS

(in prep. for submission to the Journal of the Acoustical Society of America)

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4.1: Abstract

This study presents an unsupervised procedure, based on Mel frequency cepstral coefficients and fuzzy clustering, for the classification of graded animal vocalizations. Cepstral coefficients compress information about the distribution of energy along the frequency spectrum in a reduced number of variables. The Mel scale corresponds to the perception of pitch by mammalian ears. Fuzzy clustering is a soft classification approach that accounts for the graded nature of vocalizations. The performance of the procedure is evaluated on a set of long-finned pilot whales (*Globicephala melas*) calls, and compared with the results obtained with a catalogue previously defined by audio-visual inspection of the calls by human experts. The procedure achieves lower classification precision than the catalogue approach (four fuzzy clusters vs. eight call types), but provides additional quantitative information about the graded nature of the vocalizations. Further applications of the procedure are discussed, to broaden its scope to other species and taxa, and to investigate the functions of call gradation.

Keywords: classification; unsupervised; Mel frequency cepstral coefficients; fuzzy clustering

4.2: Introduction

The description of vocal repertoires allows the characterization of differences in call types between species (cryptic species complexes: Braune et al., 2008), groups (regional dialects: Van Cise et al., 2018), individuals (individual-specific call types: King et al., 2018), and ecological contexts (functionally referential calls: Cunningham and Magrath, 2017). However, there is no consensus about the methods best suited for the construction of vocal repertoires, be it the procedure used for classification or the features used to categorize vocalizations.

Various classification schemes achieve a high degree of precision and accuracy when species produce stereotyped vocalizations (such as resident killer whales: Ford, 1989).

However, the sounds of many species do not form discrete categories, but rather vary along a continuum, rendering categorization challenging. Graded repertoires appear particularly common in mammalian species (terrestrial mammals: Garcia et al., 2016; non-human primates: Mandl et al., 2019; marine mammals: Murray et al., 1998), and are also found in other taxa (e.g. birds: Suzuki, 2014). This article presents an unsupervised classification algorithm, based on Mel frequency cepstral coefficients and fuzzy clustering, specifically designed to deal with graded animal vocalizations.

Historical classification methods rely on the audio-visual inspection of vocalizations by trained human operators and are still commonly used (e.g. Vester et al., 2017). They define subjective boundaries between categories based on operator perception, which makes them difficult to reproduce across studies. Moreover, the inspection process is time-consuming and therefore not adapted to large datasets. Supervised classification algorithms can speed up the classification: these algorithms (e.g. support vector machines: Van Cise et al., 2018) are trained on sorted datasets, and then generalize the classification rules to new vocalizations. They allow fast and reproducible classification of animal vocalizations, but still rely on subjective categorization by human operators and cannot recognize call types which are absent from their training data. Instead, unsupervised algorithm (e.g. neural networks: Deecke and Janik, 2006) derive classification rules from the data, which remove both the need for, and limitations from, prior classification. The classification procedure described in this article relies on an unsupervised algorithm.

The set of parameters used to describe the vocalizations can be another limiting factor for classification. Some studies select a reduced number of parameters in the time and frequency domains (e.g. Vergne et al., 2011). The selection targets parameters that are expected to be important for categorization: they vary with the experimenter, the study species, and the scope of the research project. The low number of parameters may limit the detection of subtle or localized differences between vocalizations (Deecke et al., 1999), which may be crucial in the study of animals' perception of sounds. On the contrary, other studies describe animal vocalizations with extensive sets of parameters, such as fine-scale acoustic features (Brown and Miller, 2007) or image descriptors (Shamir et al., 2014) extracted from spectrograms. Such large datasets incur high computational costs, and may require data reduction procedures (such as principal component analyses: Melendez et al., 2006). Some extensive sets of parameters even include dimension augmentation steps (e.g. feature learning: Stowell and Plumbley, 2014). The high number of parameters and their eventual transformation obscure the nature of the differences between classification categories and their perceptual significance to the study animals. The procedure described in this article relies on Mel frequency cepstral coefficients (MFCC) to describe vocalizations. MFCC represent an efficient technique to compress the information about the distribution of energy along the frequency spectrum. They have been widely used in speech segmentation and recognition, and are increasingly popular to study animal vocalizations (mammals: Clemins and Johnson, 2006; insects and anurans: Lee et al., 2006). MFCC can be defined for both harmonic and unvoiced sounds. They tend to be uncorrelated, and therefore suitable for classification algorithms. In addition, they integrate the logarithmic scale of pitch perception by mammalian species. Categories defined on the basis of MFCC differences should thus correspond to perceptual categories by mammalian study animals.

Most classification procedures attempt 'hard' categorization, that is to assign each vocalization to a single category (Wadewitz et al., 2015). The graded nature of vocalizations, which translates into an overlap between apparent categories, is problematic for 'hard' classification approaches. It increases the subjectivity and reduced the reproducibility of audio-visual categorization by human operators. Classification algorithms, which rely on geometrical rules to assign a call to a given call type, are also sensitive to gradation. For instance, the classification rules of support vector machines (see Van Cise et al., 2018) go through the computation of an hyperplane in the feature space which minimizes the number of misclassifications and maximizes the separation between categories. When the distribution of categories overlap, a unique optimal hyperplane may not exist or its overly complicated shape may not have any acoustical significance. Instead, the procedure presented in this article adopts a ‘soft’ classification approach, using the fuzzy clustering algorithm (as formulated in Wadewitz et al., 2015). The fuzzy clustering first defines the cluster centres as apparent stereotypes from the distribution of vocalization features in the dataset. Then, it quantifies the graded nature of the vocalisations as the positions of individual vocalisations in between these apparent stereotypes. Each vocalization is given a membership score to each fuzzy cluster. Membership scores correspond to the probability that a vocalization belongs to a fuzzy cluster. This algorithm has already been used successfully to classify primate calls (Wadewitz et al., 2015).

The performance of the fuzzy clustering- and MFCC-based classifier is evaluated on a set of long-finned pilot whale (*Globicephala melas*) calls, classified according to the latest vocal repertoire (based on audio-visual inspection: Vester et al., 2017) for comparison. Long-finned pilot whales are a delphinid species which lives in cohesive social groups all year long (Ottensmeyer and Whitehead, 2003) and present a high vocal activity in almost all behavioural contexts (Popov et al., 2017; Visser et al., 2017). Pilot whales produce a large variety of sounds: they produce of mix of tonal, broadband, and pulsed sounds, as well as intermediate forms containing portions of different acoustic nature or transitions from one sound type to another (Sayigh et al., 2013; Vester et al., 2017). Long-finned pilot whale calls can also be bi-phonated i.e. contain two independently modulated tonal components (Vester et al., 2017). A portion of their vocal repertoire consists of stereotyped tonal and pulsed call types. Audio-visual inspection of recordings described 173 call types in short-finned pilot whales (Sayigh et al., 2013) and 125 call types (with 29 further subtypes) in long-finned pilot whales (Vester et al., 2017). However, some long-finned pilot whale calls have no tonal component, and there is apparent gradation within and between call types(Nemiroff and Whitehead, 2009; Zwamborn and Whitehead, 2017b), which renders classification challenging.

4.3: Material and methods

4.3.1: Test dataset

We tested the fuzzy clustering- and MFCC-based classifier on a sample of long-finned pilot whale calls recorded from an hydrophone lowered from a small research vessel (details in Vester et al., 2017). The sounds used in this study have been recorded in northern Norway in summer 2003. The dataset contains 279 high quality calls, as evaluated by the visual inspection of spectrograms by trained operators. The long-finned pilot whale calls were sample at, or downsampled to, 48,000 kHz, and bandpass-filtered between 1000 and 22,000 Hz (4th order Butterworth filter). The samples in the dataset have already been classified according to an audio-visual inspection-based catalogue (Vester et al., 2017). They correspond to a small portion of the long-finned pilot whale vocal repertoire and were assigned to eight call types (and three subtypes) with at least ten samples of each call type in the dataset (Figure 8).

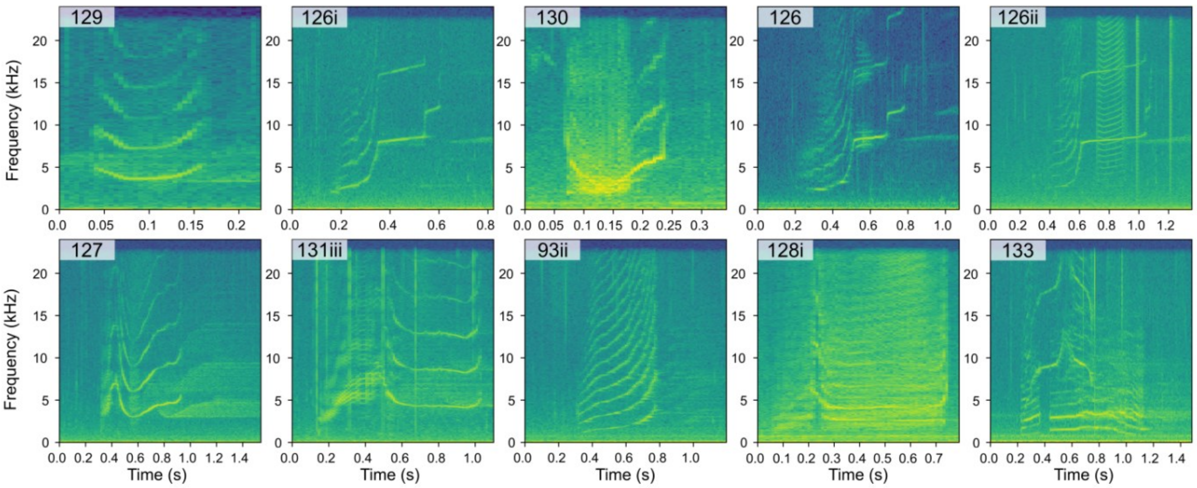


Figure 8: Example spectrograms of the eight catalogue call types present in the test dataset from the most abundant one (top left) to the least represented one (bottom right). The label in the top left of each spectrogram contains the custom name the call types are referred to as. Call types 126, 126i, and 126ii are subtypes of the same call. The distribution of call types and subtypes in the dataset is as follows: 129: n=76; 126i: n=46; 130: n=31; 126: n=24; 126ii: n= 24; 127: n=23; 131iii: n=16; 93ii: n=14; 128i: n=13; 133: n=12

4.3.2: Acoustic parameter extraction

We calculated Mel frequency cepstral coefficients (MFCC) to describe the calls (Figure 9). We created a bank of overlapping Mel-scaled triangular filters. We constructed 42 points between 1000 and 22,000 Hz, linearly spaced on the Mel scale, by using the Hz to Mel conversion equation: $mel = 2595\ x\ log(1 + {}^{f}/_{700})$, where *mel* is the frequency in Mels and f is the frequency in Hz. We designed 40 overlapping triangular filter which lower bound, centre frequency, and upper bound a succession of three of the previously constructed points. All filters shared the same maximum value at their centre frequency. We separated the calls into 1024 point segments with 50% overlap. We performed a Fourier transform on each of these segments to measure the distribution of energy along the frequency spectrum within the segments, and calculated the log of this energy. We summed the log energy of each call segment through the 40 Mel filters, and performed a one-dimension discrete cosine transform on the 40 Mel filter log energies to obtain 40 MFCC. We discarded the first MFCC, which corresponds to the average level of the call, and high-order ones, as they correspond to rapid changes in the energy distribution along the spectrum. To summarize the MFCC, we divided each call into equal time slices, and measured the mean and variance of each MFCC over these slices. We retained the average MFCC values for each slice, and calculated the square root of the summed variance measures as a single variability measure. Animals do not appear to be sensitive to slight variations of signal duration (Deecke and Janik, 2006); this dataset describes variation of energy distribution along the course of a call, irrelative of its total duration.

To investigate the trade-off between descriptive power and using a low number of acoustic features, we built nine different sets of parameters by keeping five, seven, or ten MFCC values summarized over five, seven, or ten time slices. This was motivated by the sensitivity of fuzzy clustering to high dimensionality (Winkler et al., 2011).

Indeed, in high dimensional spaces, fuzzy clustering tends to assign all samples to a single cluster, whose centre corresponds to the centre of gravity of the dataset.

We used the Python package "pylotwhale" (Vargas Noriega Romero, 2018) to extract the MFCC from the long-finned pilot whale calls.

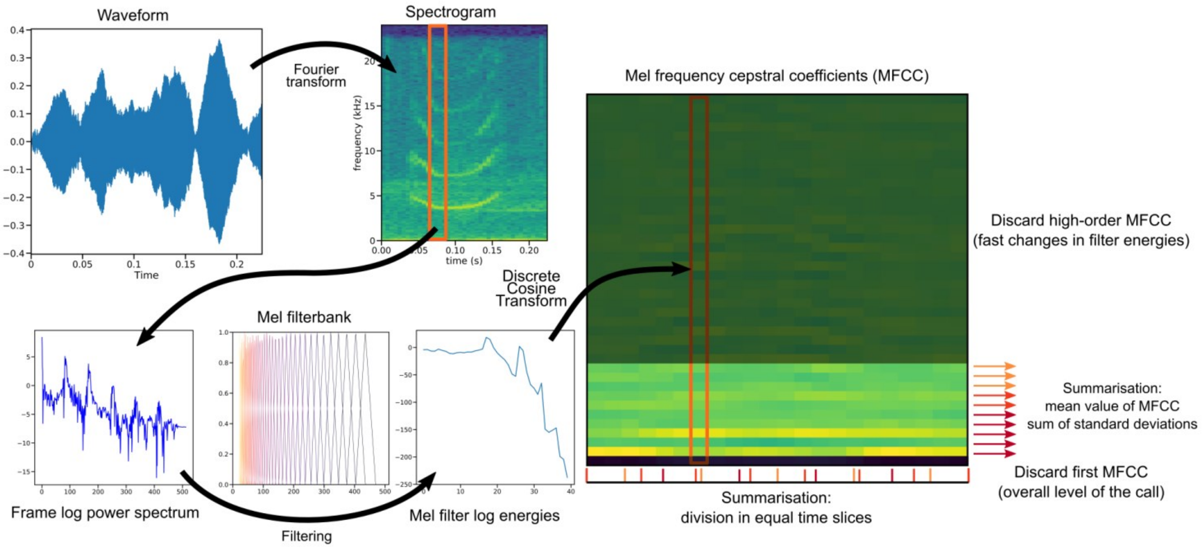


Figure 9: Successive steps for the calculation of Mel frequency cepstral coefficients-derived acoustic parameters.

4.3.3: Classification procedure

The fuzzy clustering defines the centres of fuzzy clusters based on the distribution of vocalizations features in the datasets. Then, it assigns each call a membership score between 0 and 1 to each cluster. Membership score correspond to the probability that a call belongs to a fuzzy cluster. The sum of all membership scores for a given call is equal to one. Fuzzy clusters correspond to apparent stereotypes in the dataset, and membership scores quantify the gradation of calls between these apparent stereotypes. We used the fuzzy c-means algorithm (as presented in Wadewitz et al., 2015), which is driven by two parameters: the fuzziness value μ and the number of initial clusters k. The fuzziness quantifies to what extent clusters are allowed to overlap. A fuzziness of 1 corresponds to no overlap between clusters and is equivalent to 'hard' clustering. The higher the fuzziness value, the more overlap there can be between clusters. For a given (μ, k) pair, the fuzzy c-means algorithm uses the following steps:

i) Initialize k random cluster centroids. We drew the centroid coordinates from uniform distributions over the feature ranges in the dataset.

ii) Iteratively calculate membership scores from the distance between data points and cluster centroids in the feature space and fuzziness (1), and update the positions of cluster centroid based on membership scores, data points, and fuzziness (2) until the convergence of an objective function, namely the sum of the squared distances between data points and cluster centroids weighted by membership scores and fuzziness (3). This objective function is also a measure of the compactness of the fuzzy clusters, and we used it as a measure of the quality of the clustering.

iii) After convergence of the objective function, fuse together close centroids. The threshold under which we fused centroids was the sum of 1% of the range of each feature in the dataset.

$$\frac{1}{m_{i,a}} = \sum_{c=1}^{k} \left(\frac{d_{i,a}}{d_{i,c}}\right)^{2/\mu-1} \quad (1)$$

$$c_a = \frac{\sum_{i=1}^{n\ calls} (m_{i,a})^{\mu} x\, f_i}{\sum_{i=1}^{n\ calls} (m_{i,a})^{\mu}} \quad (2)$$

$$F = \sum_{i=1}^{n\ calls} \sum_{c=1}^{k} (m_{i,c})^{\mu} x d_{i,c}{}^{2} \quad (3)$$

With:

- $m_{i,a}$ the membership score of call i to cluster a
- k the number of clusters
- $d_{i,c}$ the euclidian distance between call a and cluster centroid c
- μ the fuzziness value
- c_a the coordinates of centroid a in the feature set space
- f_i the coordinates of call i in the feature set space
- F the value of the objective function

Fuzzy c-means can be sensitive to local minima of the objective function. Therefore, we performed 100 realizations of the algorithm and kept the one with the lowest final value of the objective function.

The full classification procedure started with the selection of the maximal number of clusters allowed k_{max} and the initial value of fuzziness μ_{start}. k_{max} should be slightly larger than the number of expected clusters in the dataset, so as not to be a limiting factor for classification and not to incur additional computational costs. We chose 15, as there were ten catalogue call categories (types and subtypes) in the dataset. μ_{start} should be so that the fuzzy c-means results in a single fuzzy cluster, but not too high. We set $\mu_{start} = 2$ after initial tests. We then ran the fuzzy c-means algorithm for $\mu = \mu_{start}$ and $k = 1, \ldots, k_{max}$ and kept the best clustering solution (the one with the lowest objective function). We then decremented μ and started again, until $\mu = 1.01$. We used steps of 0.05 between $\mu = 2$ and $\mu = 1.3$, and steps of 0.01 between $\mu = 1.3$ and $\mu = 1.01$.

4.3.4: Fuzzy clustering analyses

The first step in the analysis of fuzzy clusters is the identification of stable clustering solutions. For the highest values of fuzziness, the algorithm results in a single fuzzy cluster. As the fuzziness decreases, clusters start to crystallize as the overlap allowed between them diminishes. Stable clustering solutions, which are optimal over large intervals of fuzziness, should represent prominent structures in the dataset. We plotted the optimal number of clusters according to fuzziness (Figure 10) and visually identified the stable clustering solutions, taking into account both the number of fuzziness values for which a solution was optimal as well as the presence of successive values of fuzziness for which the same solution was the best.

We then aimed to characterize the fuzzy clusters defined by the stable clustering solutions. We reconstructed the 'stereotypical call' for each fuzzy cluster, i.e. the call corresponding to each cluster centroid. We computed the Mel filter energies of the calls, as during the first steps of the MFCC calculation procedure, and averaged them over the same time slices as the MFCC (resulting in 10x40 matrices of Mel filter log energy averages: MFLE matrices). The 'stereotypical calls' were built as the element-wise average of the MFLE matrices, weighted by the membership scores to each cluster (a similar reconstruction method can be found in Clemins and Johnson, 2006).

The reconstruction of stereotypical calls only characterizes the centroids of the fuzzy clusters, but gives no indication as to where individual calls lie between these clusters. We measured the typicality of calls to visualize the gradation between fuzzy clusters, in order to develop a more complete view of the results. The typicality of a call is the difference between its two highest membership scores.

4.3.5: Comparison of the fuzzy clustering with the catalogue-based classification

In order to compare the fuzzy clusters with the call types defined in the catalogue, we constructed correspondence tables by sorting each call according to its catalogue call type and main fuzzy cluster (cluster with the highest membership score). We only took into account calls with a typicality higher than 2/3 (ensuring that they were at least twice closer to their main cluster than to other ones).

Correspondence tables only consider the most likely cluster, and thus do not take into account the gradation between fuzzy clusters. In order to visualize the distribution of catalogue call types around fuzzy cluster centroids, we performed a principal component analysis on the MFCC parameters. We then plotted, along the first two principal components, the calls coloured by catalogue call type, and the centroids of the fuzzy clusters.

We developed a Python package "fuzzyClustering" to run the fuzzy c-means and analyse the clustering results. Module "fcmeansAlgo" runs the fuzzy c-means classification and measures typicality, and module "visualTools" produces all the figures. We used the modules "preprocessing" and "decomposition" of Python package "sickit-learn" (Pedregosa et al., 2011) to scale the datasets and compute the principal components analyses.

4.4: Results

4.4.1: Identification of stable clusters

Stable clustering solutions with up to four fuzzy clusters were present for all feature sets, from the least descriptive one (five MFCC over five time slices) to the most precise one (ten MFCC over ten time slices). A five cluster solution appeared for two feature sets. For the three feature sets with the highest temporal resolution (ten time windows), there was a six cluster solution (Figure 10).

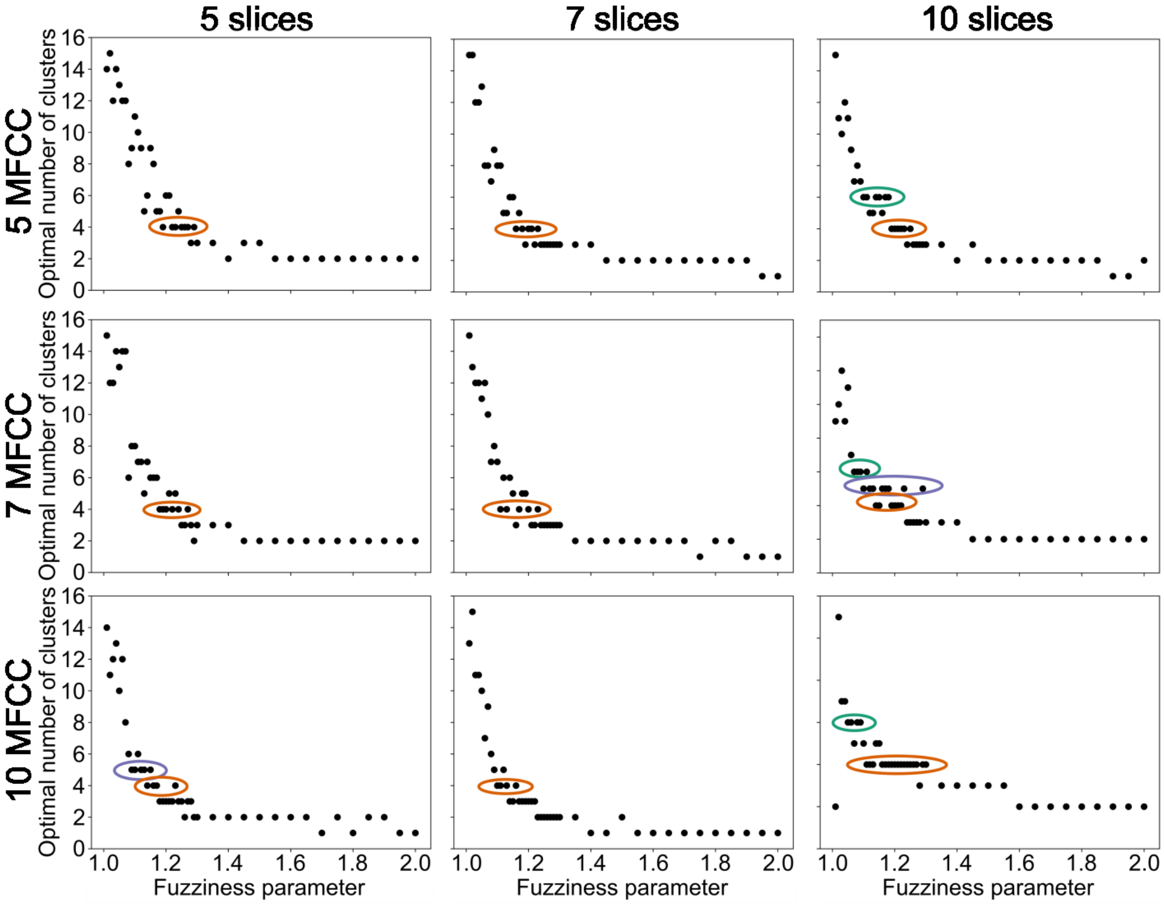


Figure 10: Optimal number of clusters relative to fuzziness for all nine sets of features. Stable four cluster solutions are highlighted by brown circles, five cluster solutions by purple circles, and six cluster solutions by green circles.

We selected both extrema of the four cluster solutions: the solution obtained with five MFCC over five time slices, to see how much we could extract from the smallest feature set; and the ten MFCC over ten time slices solution, because it was particularly stable. For ease of reading, we refer below to the four cluster solution obtained with the five

MFCC over five slices as the "5-5" solution, and to the four cluster solutions obtained with the ten MFCC over ten slices the "10-10" one.

4.4.2: Reconstruction of stereotypical calls

The reconstructed stereotypical calls shared similar structures across the different clustering solutions (Figure 11). We described stereotypical calls by the presence or absence, and characteristics of three recurring motifs: the initial rise motif (IR), the plateau-like motif (PL), and the high-frequency motif (HF). The IR corresponded to a steep rise in frequency at the beginning of the call. It contained most energy between the 15th and the 20th Mel filter (approximately the 5-7 kHz band), and usually covered the third to fifth time slices of the stereotypical calls. IR were most visible for the third cluster of the presented realisations of the 5-5 solution (Figure 11A and B), and the first cluster of the presented realisations of the 10-10 solution (Figure 11C and D). The PL was a long level or slightly U-shaped motif which covered the fourth to eight time slices of the stereotypical calls. It contained most energy between the 20th and 25th Mel filter (approximately the 7-9 kHz band). The second and fourth cluster of the 5-5 solution examples contained marked PL (Figure 11A and B). The second cluster of the first 10-10 example consisted in a single PL (Figure 11C). The HF contained most energy right below the 30th Mel filter (around 11 kHz), and extended from the 5th to the 8th time slice of the stereotypical calls. The first cluster of the 10-10 solution examples contained marked HF (Figure 11C and D). The 10-10 solutions sometimes provided less structured stereotypical calls for one cluster (Figure 11D, second cluster).

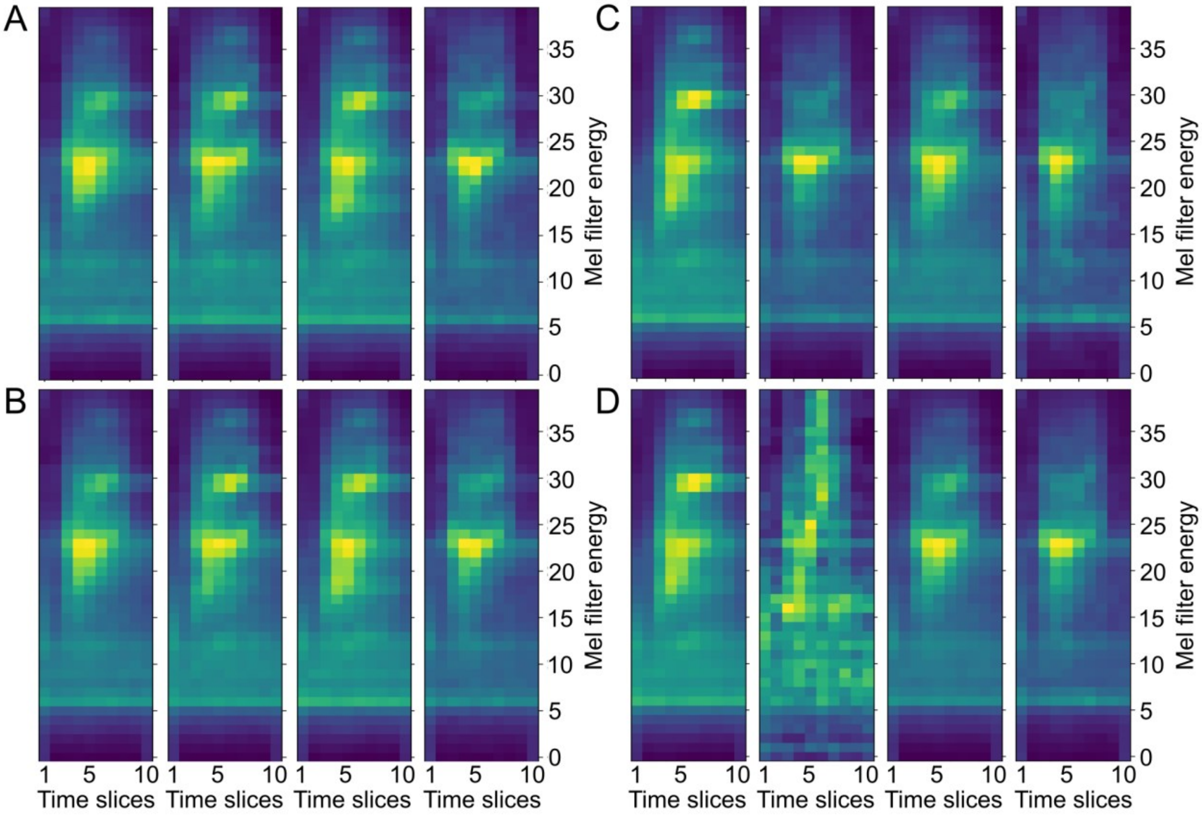


Figure 11: Reconstructed stereotypical calls for two realizations of the 5-5 clustering solution (A and B) and two solutions of the 10-10 clustering solution (C and D). The x-axis corresponds to the 10 time slices used for MFCC summarization. The y-axis corresponds to filters of the Mel filter bank **A)** 5-5 solution, μ = 1.23 **B)** 5-5 solution, μ = 1.27 **C)** 10-10 solution, μ = 1.17 **D)** 10-10 solution, μ =1.25

4.4.3: Typicality analysis

We recorded high values of typicality, indicating that some calls mostly fell into discrete categories. The distribution of typicality values was skewed toward high values for the 5-5 solution (Figure 12A and B), whereas the 10th decile (0.9-1.0) contained most calls for the 10-10 solution (Figure 12C and D). The skew towards high values of typicality was more marked for lower values of fuzziness (compare Figure 12A and B with Figure 12C and D).

In the 5-5 solution, we observed two kinds of distribution patterns: the typicality of some clusters was evenly distributed along the entire range (Figure 12A: blue and orange clusters; Figure 12B: red cluster); while some clusters contained mostly calls with a very high typicality (Figure 12A: green cluster; Figure 12B: blue cluster). For the 10-10 solution and some of the realisations of the 5-5 solution, clusters with high typicality corresponded to clusters which contained all motifs: IR, PL, and HF (Figure 11A, B, and C and Figure 12A, B, and C). A third kind of distribution appeared in the 10-10 solution: clusters with a low number of associated calls (Figure 12D: green). These low count clusters corresponded to the unstructured clusters of the 10-10 solution (Figure 12D: green cluster corresponds to Figure 11D: second cluster).

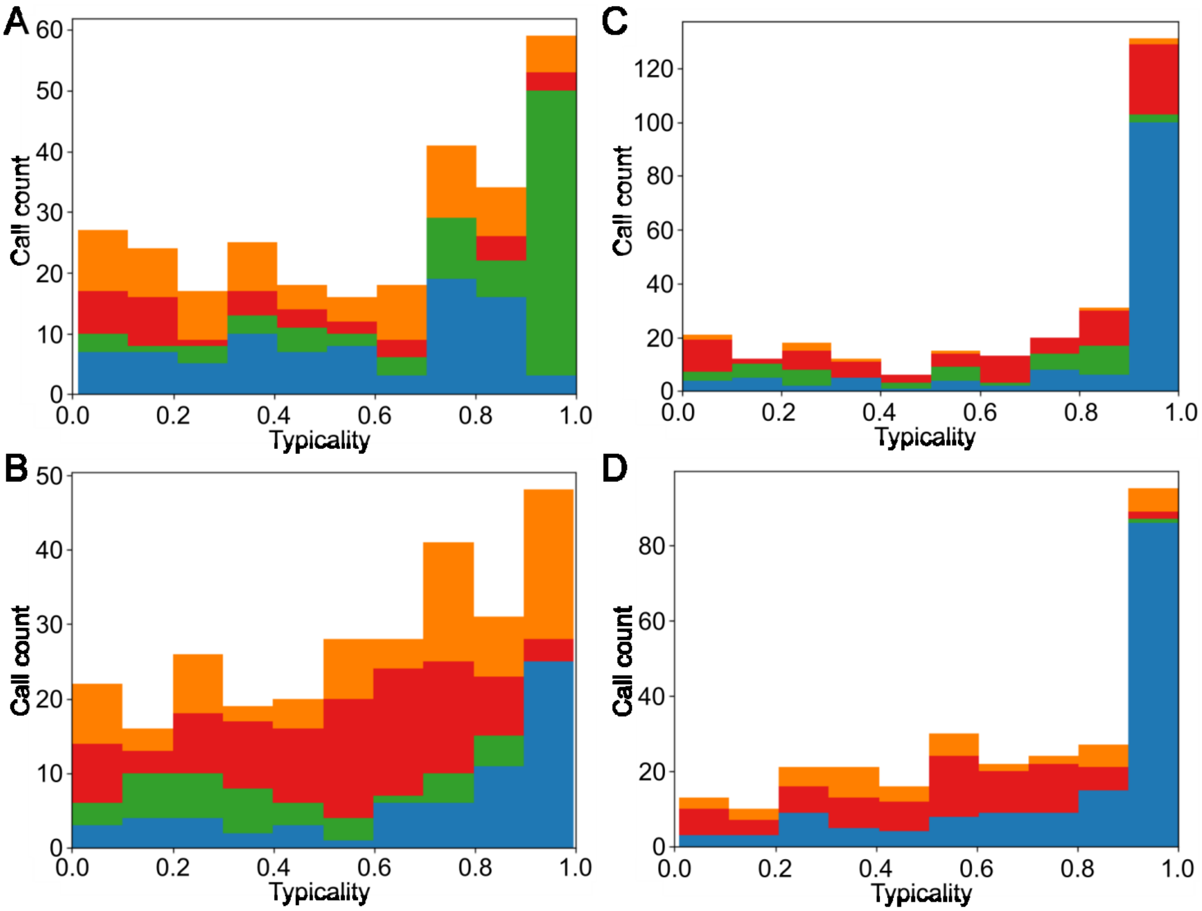


Figure 12: Typicality values coloured by main fuzzy cluster for two realizations of the 5-5 clustering solution and two realisations of the 10-10 clustering solution. The clustering solutions presented in this figure are the same as in Figure 11. The bottom-up colour order (blue, green, red, and orange) corresponds to the left-to-right order in Figure 4 **A)** 5-5 solution, μ = 1.23 **B)** 5-5 solution, μ = 1.27 **C)** 10-10 solution, μ = 1.17 **D)** 10-10 solution, μ = 1.25

4.4.4: Gradation between fuzzy clusters

It appeared that some clusters overlapped, some did not, and others overlapped several clusters which did not overlap each other. All pairs of clusters in the 5-5 solution overlapped to some extent, with the exception of the clusters 1 and 2 (Figure 13A). The gradation seemed to involve multiple clusters at once in most cases, as the points were mostly placed in the middle of the graphs (Figure 13A). Gradation between cluster 0 and 1 is more representative of gradation within a pair of clusters. In the 10-10 solution, cluster 0 overlapped cluster 2, and cluster 2 overlapped clusters 3, while there was no overlap between clusters 0 and 3 (Figure 13B). The overlaps in the 10-10 solution were almost exclusively within pairs of clusters, as many points were located along the diagonal of the triangular plots (Figure 13B).

Comparing the gradation between clusters (Figure 13) with the reconstruction of cluster stereotypical calls (Figure 11), it appeared that only clusters that shared structural similarities overlapped each other. In the 5-5 solutions, only cluster 1 and 2 did not overlap (Figure 13A): cluster 2 contained a PL and a HF, and cluster 2 contained an IF and a HF (Figure 11A). In the 10-10 solution, cluster 2 overlapped clusters 0 and 3, which did not overlap each other (Figure 13B). Cluster 0 was a complete call with IR, PL, and HF (Figure 11C). It shared a PL and faint IR and HF with cluster 2, but only shared a PL with cluster 3 (Figure 11C). Clusters 2 and 3 were both centred on a marked PL (Figure 11C).

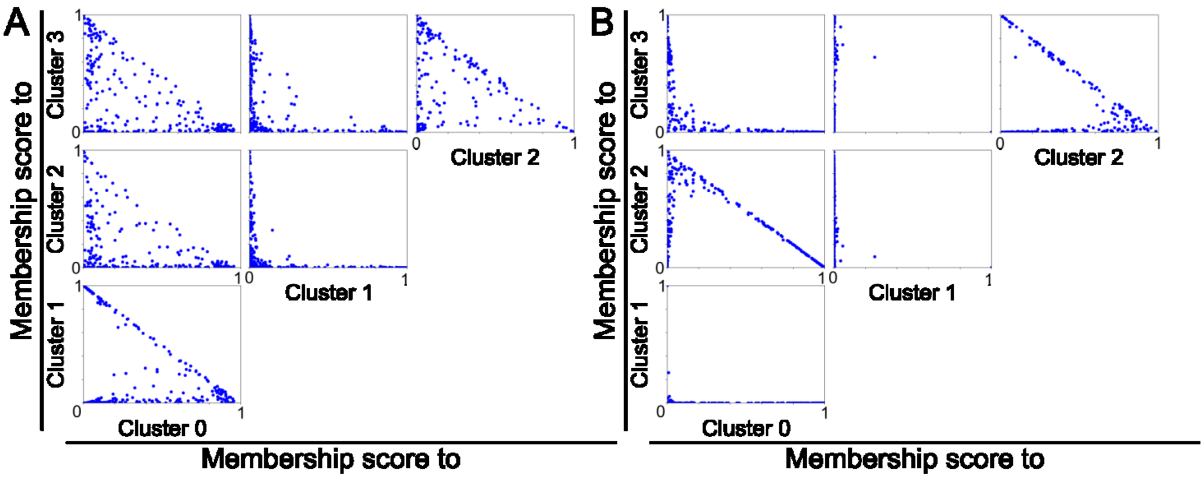


Figure 13: Gradation between fuzzy clusters for example realisations of the 5-5 and 10-10 clustering solutions. Each point corresponds to an individual call. Points along the diagonal of the plot correspond to calls that are graded exclusively between the two clusters represented by the axes. Points in the middle of the graph represent calls that are graded between multiple call types **A)** 5-5 solution, $\mu = 1.23$. There was overlap between all pairs of clusters with the exception of cluster 1 and 2 **B)** 10-10 solution, $\mu = 1.25$. There was clear gradation between cluster 0 and cluster 2, and between cluster 2 and cluster 3, but not between cluster 0 and 3

There was much more overlap between cluster in the 5-5 solution than in the 10-10 one. Moreover, the overlaps in the 5-5 solution mostly involved several clusters, while the overlaps in the 10-10 solution were typical of exclusively pairwise overlaps.

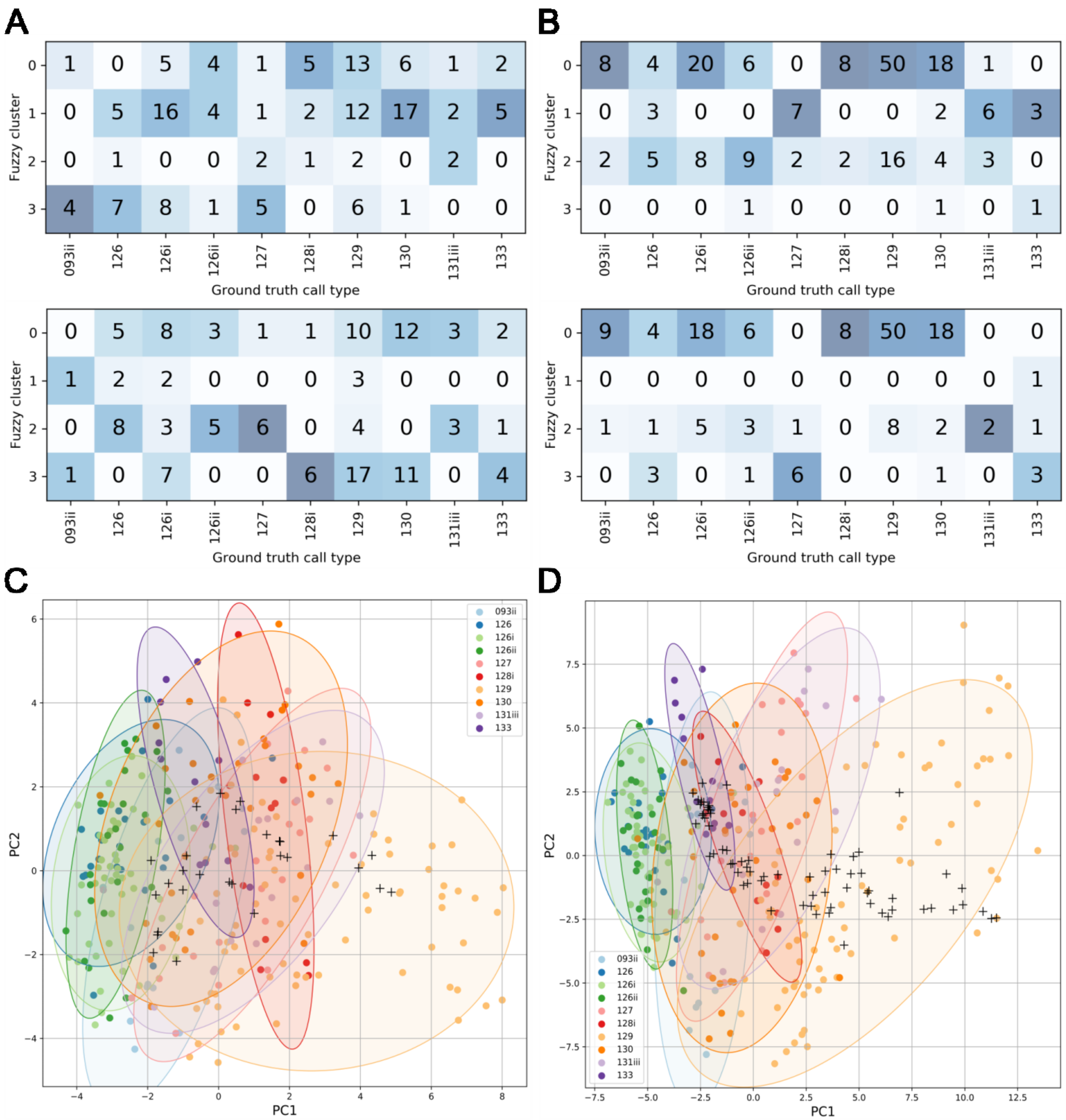
4.4.5: Correspondence between catalogue call types and fuzzy clusters

We obtained four fuzzy clusters, compared to eight catalogue call types (ten including subtypes). We did not replicate the results of the audio-visual inspection of recordings by human operators. Indeed, fuzzy clusters did not correspond to catalogued call types or sets thereof. Rather, calls from a given call type were mostly distributed over several fuzzy clusters (Figure 14A and B). This was consistent with large overlaps between the distribution of call types in the dataset (Figure 14C and D).

Some call types were associated within fuzzy clusters: their distribution across fuzzy clusters was consistent. In the 5-5 solutions, there were three prominent call type associations within clusters. Call types 126ii, 127, and 131iii; call types 126i, 130, and 133; and call types 128i, 129, 130, and 133 tended to be associated within fuzzy clusters (Figure 14A). In the 10-10 solution, the main associations of call types within cluster were call types 126, 127, 131iii, and 133; call types 093ii, 126i, 128i, 129, and 130; and call types 126ii, 128i, and 129 (Figure 14B). When comparing these associations, it appeared that call types 127 and 131iii, as well as call types 128i, 129, and 130, tended to be clustered together in both fuzzy clustering solutions. The distribution of call types 127 and 131iii was highly similar (Figure 14C and D). Call types 129 and 130 had the largest spreads in the dataset, and the distribution of call types 128i, 129, and 130 largely overlapped (Figure 14C and D). It was worth noting that, despite a smaller number of fuzzy clusters than catalogued call types, the three call subtypes (126, 126i, and 126ii) were not clustered together (Figure 14A and B).

The centroids of the fuzzy clusters were not distributed around a discrete number of positions (Figure 14C and D). Such modes in their distributions would have corresponded to stereotyped call types, between which the calls would have been graded. Instead, the positions of the fuzzy cluster centroids followed a curve from position *(-2,-2)* to position *(4,0)* in the 5-5 solution (Figure 14C) and between positions *(-2.5,2.5)* and *(12.5,-2.5)* in the 10-10 solution (Figure 14D). This distribution corresponded to a gradation following a directed continuum, without stereotypes.

The spread of the call type distributions was larger in the 5-5 solution than in the 10-10 solution (Figure 14C and D), which was consistent with the precision of both sets of acoustic features.



Fuzzy cluster	093ii	126	126i	126ii	127	128i	129	130	131iii	133
0	1	0	5	4	1	5	13	6	1	2
1	0	5	16	4	1	2	12	17	2	5
2	0	1	0	0	2	1	2	0	2	0
3	4	7	8	1	5	0	6	1	0	0

Fuzzy cluster	093ii	126	126i	126ii	127	128i	129	130	131iii	133
0	8	4	20	6	0	8	50	18	1	0
1	0	3	0	0	7	0	0	2	6	3
2	2	5	8	9	2	2	16	4	3	0
3	0	0	0	1	0	0	0	1	0	1

Fuzzy cluster	093ii	126	126i	126ii	127	128i	129	130	131iii	133
0	0	5	8	3	1	1	10	12	3	2
1	1	2	2	0	0	0	3	0	0	0
2	0	8	3	5	6	0	4	0	3	1
3	1	0	7	0	0	6	17	11	0	4

Fuzzy cluster	093ii	126	126i	126ii	127	128i	129	130	131iii	133
0	9	4	18	6	0	8	50	18	0	0
1	0	0	0	0	0	0	0	0	0	1
2	1	1	5	3	1	0	8	2	2	1
3	0	3	0	1	6	0	0	1	0	3

Figure 14: Comparison between fuzzy clusters and catalogue call types **A and B)** Correspondence tables between fuzzy clusters and catalogue call types. The numbers in the table corresponds to the number of times a call belonging to a given call type (column) had a given fuzzy cluster (row) as its main cluster **A)** 5-5 solution, μ = 1.23 (top), μ = 1.27 (bottom) **B)** 10-10 solution: μ = 1.17, μ = 1.25 **C and D)** Principal component analyses for the visualization of

the catalogue call type distribution in the MFCC feature space. Calls are coloured by catalogue call types. Black + crosses represent the position fuzzy cluster centroids **C)** 5-5 solution. The two components explained 40 % of the dataset variance **D)** 10-10 solution. The 2 components explained 30 % of the dataset variance

4.5: Discussion

We presented a method for the classification of graded animal vocalizations. The unsupervised algorithm we proposed relies on Mel frequency cepstral coefficients for call description and on fuzzy clustering for call categorization. The algorithm defined four fuzzy clusters in a set of 279 high quality calls of long-finned pilot whales, and provides tools for the quantification and the visualization of the gradation between clusters.

On the same dataset, a human expert was able to recognize eight call types (and three additional subtypes). Thus, our procedure did not achieve the same categorization precision as a human agent, nor did it replicate the findings of audio-visual inspection-based classification. However, some catalogue call types were associated within the fuzzy clusters, which indicated that a certain underlying structure in the dataset was consistently captured by both approaches. For instance, call types 127 and 131iii, which had similar frequency-modulation patterns and bandwidth, but different duration, were clustered together. Vester and colleagues (2017) defined five broad categories of calls using a 'hard' clustering approach on a set of long-finned pilot whales twice as large as the one used in the dataset (541 vs. 279 samples). Theirs categories corresponded to two groups of low-pitched calls, two groups of high-pitched calls, and one group of noisy calls. Our fuzzy clustering approach defined a similar number of clusters. However, differences between clusters corresponded to the presence or absence of three call-scale patterns of energy distribution (IR, PL, and HF). Therefore, they differed from the broad categories defined by Vester and colleagues (Vester et al., 2017). In the only other use of fuzzy clustering for animal vocalizations to our knowledge (Wadewitz et al., 2015), the study defined five clusters for primate calls.

The algorithm described in this article was fully unsupervised and saved time compared to manual classification schemes. The fuzzy clustering procedure runs in a few days, while the audio-visual inspection of calls could take several months. The dataset we used still involved human operators to extract the sounds from the recordings. Another step to accelerate the processing of animal calls would be to use automated call extraction algorithms (as in Leroy et al., 2018; Zhang et al., 2018). Another limitation of our procedure was related to the objective function of the fuzzy c-means algorithm: the current objective function is only a measure of cluster compactness, i.e. how close individual calls are from cluster centroids, and does not take into account cluster separation, i.e. the distance between fuzzy cluster centroids. Rawadesh and Ralescu (2012) proposed an adaptation of the silhouette measure of clustering validity to fuzzy clustering: the generalized intra-inter silhouette. While having the advantage of measuring both cluster compactness and cluster separation in a fuzzy framework, the generalized intra-inter silhouette is computationally highly expensive, and we could not include it in our procedure.

The distribution of the fuzzy cluster centroids was skewed toward call type 129 – the most represented and variable call type in the dataset – and away from call types 126, although the region around call type 129 contained sparse calls whereas the area around call 126 was much denser. As the fuzzy clustering algorithm attempted to minimize the sum of the distances between individual calls and fuzzy cluster centroids, it may be that particularly variable calls (here, call type 129 and 130) attracted fuzzy cluster centroids. An update of the objective function of the algorithm to include cluster separation may solve this issue. In any case, the framework we worked on was designed to be fully unsupervised and intended to be used on raw datasets, with no control on the contents of the datasets and no manual classification to guide it. Our method managed to define stable and consistent clusters in an unbalanced dataset, which made us confident in its ability to tackle raw datasets in the future. The fact that the fuzzy clustering algorithm discovered similar clusters independently from the feature set we used may be evidence that the revealed structure was prominent in the dataset.

In this article, we used sets of parameters derived from Mel frequency cepstral coefficients to sort long-finned pilot whale vocalizations. Cepstral coefficients represent an efficient method to compress information on the distribution of energy along the frequency spectrum. As such, they contain more information than sets of hand-picked call-scale parameters (e.g. Vergne et al., 2011) or frequency contours of fundamental frequency or pulse repetition rate (e.g. Deecke and Janik, 2006) commonly used in other studies. In addition, the Mel scale corresponds to the perception of pitch by mammalian ears. It was adapted to the study species, the long-finned pilot whales, which have a typical mammalian audiogram (Pacini et al., 2010). Some studies used species-specific frequency weighting functions (e.g. Clemins and Johnson, 2006). It could be possible to use knowledge about a species audiogram to adapt the feature set for vocalization description: varying the centre frequency and bandwidth of the filters to render the perception of frequency by the species, and the maximal value of the filters to represent its auditory sensitivity.

The procedure we developed aims specifically to describe the graded vocal repertoire of certain species. It can still be used on stereotyped vocalizations, as they are but a particular example of graded repertoires from a mathematical point of view. However, the principal advantages of our procedures are the tools it provides to quantify and visualise the gradation within and between vocalisation categories. Indeed, the description of vocal repertoires permits the investigation of certain aspects of vocal communication in animals. Beyond the definition of valid call types for graded vocal production, the graded nature of vocalizations can be functional and informative in itself. Graded variation within a call type may carry information about the context of call production or the state of the signaller. For instance, juvenile black caimans use graded variations of the same calls either to attract their mothers when under attack or to reunite with their siblings when they get isolated (Vergne et al., 2011). Graded vocalisations indicate the intensity of an aggressive display in great Himalayan spear-nosed bats (Sun et al., 2018). The gradation quantification and visualisation methods we presented can be used to investigate variations in the graded nature of vocalisations between behavioural or ecological contexts.

4.6: Conclusions

This article presents an unsupervised procedure for the classification of graded animal vocalizations. The procedure describes vocalisations with a set of MFCC-derived parameters, and classifies them with an implementation of the fuzzy c-means algorithm. We tested the performance of our method with a set of long-finned pilot whale calls and compared our results with those obtained with a previously defined call catalogue based on audio-visual inspection of recordings by trained operators. The algorithm defined four clusters, compared to eight call types (ten, including subtypes) with the catalogue approach. The time resolution of the call catalogue, sub-units with consistent frequency-modulation patterns, was more precise than the time resolution of the fuzzy clustering, equal time slices. Our approach defined apparent stereotypes based on the presence or absence of call-scale motifs of energy distribution. The call types described by the catalogue were based on associations of sub-units. It would be interesting to adopt the fuzzy clustering approach at the sub-unit level and include it in the definition of call types. Sub-units are more consistent in the time and frequency domains than entire calls, but show slight variations of duration and frequency content (H. Vester, pers. comm.). The manual classification of calls includes the subjective categorisation of variable sub-units. The fuzzy clustering approach has the potential to quantify and objectify this decision-making process.

5: CHAPTER 3 – VOCAL RESPONSES OF LONG-FINNED PILOT WHALES (*GLOBICEPHALA MELAS*) TO NAVAL SONARS AND PLAYBACKS OF KILLER WHALE (*ORCINUS ORCA*) SOUNDS

(in prep.)

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5.1: Abstract

Naval sonar is one of the most intense anthropogenic sound sources in the marine environment. Over the past decades, there has been growing concerns about its impacts on marine ecosystems, and on cetaceans in particular. Cetaceans incur risks of direct physical damage, of disturbance of activities, and of masking of acoustic communication and echolocation signals associated with naval sonar use. In this study, we combined animal-borne multi-sensor tags and visual observations from a research vessel to monitor the vocal behaviour of free-ranging long-finned pilot whales during controlled exposure experiments to naval sonar. We also performed playbacks of marine mammal-eating killer whale sounds to pilot whales, in order to interpret the

biological significance of their responses to naval sonar according to the risk disturbance hypothesis. Long-finned pilot whales have a large vocal repertoire which contains a mix of tonal, pulsed, and broadband sounds, and which includes both stereotyped and graded vocalisations. We used a previously developed procedure designed to describe graded vocal repertoire in a quantitative way to identify vocal responses of long-finned pilot whales to naval sonar and killer whale playbacks. We analysed the vocal activity, call type usage, and call typicality (i.e. stereotyped or graded nature) of long-finned pilot whales. We noted changes in vocal behaviour in response to naval sonar exposures, killer whale playbacks, and control experiments. We did not find call types used in response to general disturbance or to specific acoustic stimuli across tag deployments. However, we noted differences in the vocal responses of long-finned pilot whales to successive sound exposure experiments.

5.2: Introduction

The ongoing development of human activities amplifies their impacts on ecosystems. Animals can incur a direct risk of injury or death related to human presence. For instance, collisions with vehicles accounts for a non-negligible amount roe deer (*Capreolus capreolus*) mortality in Europe (Bruinderink and Hazebroek, 1996). Beyond being the cause of direct physical damage to animals, human activities can also disturb their behaviour through the modification of habitat size and structure, the disruption of physiological processes, and the production of visual, olfactory and auditory stimuli (reviewed in Tuomainen and Candolin, 2011). Behavioural changes caused by anthropogenic stimuli range from short-term, local effects to broad scale or long-term effects. For instance, anthropogenic light can affect the migratory route and habitat use of bird species (McLaren et al., 2018). Anthropogenic noise may have been responsible for the long-term displacement of humpback whales (Megaptera novaeangliae) away from the Hawaiian shores (Glockner-Ferrari and Ferrari, 1990).

In the marine environment, the impacts of anthropogenic noise on the ecosystem, and particularly on marine mammals, are a primary source of concern (reviewed in Williams et al., 2015). Human activities at sea, such as vessel traffic, seismic exploration, pile driving, fisheries, or naval sonar operation, often emit substantial low frequency sound energy (mostly below 1000 Hz: Richardson and Würsig, 1997). Sounds propagate much faster and further in sea water than in the air. Low frequency sounds in particular suffer little absorption in sea water: for illustration, Munk and colleagues were able to detect 57 Hz signals broadcasted at an intense source level of 221 dB re 1 μPa @ 1 m around 10,000 km away (Munk et al., 1994). Marine mammal species rely on acoustic signals for multiple biological functions, such as communication within social groups (bottlenose dolphins *Tursiops truncatus*: King et al., 2018) or in the context of reproduction (humpback whales: Herman, 2017), navigation (bottlenose dolphins: Jensen et al., 2009a), and foraging (sperm whales *Physeter macrocephalus*: Miller et al., 2004; short-finned pilot whales *Globicephala macrorhynchos*: Soto et al., 2008), which makes them particularly sensitive to acoustic disturbances. Therefore, in addition to disturbing the behaviour of marine mammals (Richardson and Würsig, 1997), anthropogenic noise can mask natural communication or echolocation signals (Parks et al., 2007; Jensen et al., 2009a). Other effects include risk of hearing loss when sounds are received at high intensities (reviewed in Finneran, 2015), and increased levels of stress in marine mammals (Richardson and Würsig, 1997).

Among the different sources of underwater anthropogenic sounds, naval sonars have received particular attention concerning their potential adverse effects on marine mammals (Parsons, 2017). Indeed, naval sonar exercises have been spatially and temporally correlated with the mass stranding of cetaceans species (especially beaked whales: Cox et al., 2006). Naval sonar signals are one of the most powerful anthropogenic sounds in the ocean, with source levels between 200 and 240 dB re 1 μPa @ 1 m (root-mean-square sound pressure levels: Cox et al., 2006). The frequency range of sonar signals extends higher than most other anthropogenic sounds and can overlap with sounds produced by odontocetes or toothed whales (Richardson and Würsig, 1997).

The inherent challenges in monitoring the behaviour of cetaceans, the scarcity of opportunistic observations, and the absence of control over the conditions of naval sonar exercises have made it unrealistic to empirically evaluate the behavioural responses of cetaceans to operational sonar use in actual conditions. Researchers instead exposed free-ranging cetaceans to naval sonar in controlled conditions. These experiments are referred to as behavioural responses studies (BRS; reviewed in Southall et al., 2016) which allowed a quantitative characterisation of the behavioural responses of cetaceans to naval sonar, albeit in conditions that differ in important ways from operational sonar usage.

Therefore, some difficulties remain in the interpretation of the biological significance of behavioural responses to sonar. Indeed, the controlled exposure conditions of behavioural response studies differ from what cetaceans may actually face: behavioural response studies use a single sonar source and sonar exposure is limited in duration to short duration of hours during which an individual whale can be monitored using a suction-cup attached tag (Southall et al., 2016), whereas actual naval sonar exercises may last for days or weeks, or may occur repetitively in certain areas.

Moreover, since anthropogenic sounds made a recent and sudden emergence in the environment (at the evolutionary scale), how they are perceived by animals remains unclear. One possible approach to evaluate the potential biological significance of behavioural responses to naval sonar it to is to compare them with behavioural responses to natural high-level disturbance stimuli of known ecological significance for the study species. Sounds from predators have been most commonly used. Indeed, the risk of predation is a strong ecological signal: failure to respond adaptively to predation risk may be fatal (Lima and Dill, 1990). The actual trade-offs between the costs and benefits of behavioural responses to the risk of predation and to anthropogenic disturbances may differ, but the theory does predict that the costs of response to anthropogenic sounds perceived as a threat will be shaped by the costs of how they respond to natural threats (risk disturbance hypothesis: Frid and Dill, 2002). For cetacean species, an effective sound used to signal the risk of predation is killer whale *Orcinus orca* sounds (e.g. Curé et al., 2016; Isojunno et al., 2016). Killer whales are known to hunt members of most marine mammal families (Jefferson et al., 1991).

However, some killer whale populations may contain sympatric ecotypes which display some extent of dietary specialisation: some killer whales specialise in hunting marine mammals, while others feed mostly on fish (de Bruyn et al., 2013). Marine mammals can discriminate between the sounds of different killer whale ecotypes (pinnipeds: Deecke et al., 2002; odontocetes: Curé et al., 2019; mysticetes: see chapter 1). Therefore, not all killer whale sounds may be perceived as threats, and therefore serve as effective candidates to trigger an anti-predator response template to analyse the significance of behavioural responses to sonar.

Behavioural responses of cetaceans to sonar have been found to be very variable (Southall et al., 2016). Cetacean species display different response sensitivities to sonar: killer whales responses to experimental sonar exposure were stronger and lasted longer than responses of sperm whales and long-finned pilot whales (Miller et al., 2012).

Moreover, within cetaceans species, behavioural responses to sonar fluctuate with the type of sonar signal and the behaviour in which individual are engaged at the onset of sonar transmission (Goldbogen et al., 2013; Harris et al., 2015). Commonly observed behavioural responses to naval sonar include avoidance and interruption of functional activities such as foraging or resting (reviewed in Southall et al., 2016). The duration of most behavioural responses do not exceed the duration of the exposure: for instance, sperm whales and long-finned pilot whales which interrupted foraging activities in response to sonar usually went back to foraging as soon as the transmission stops (Miller et al., 2012; Sivle et al., 2012). However, some behavioural responses to sonar continued after the transmission ended: northern bottlenose whales *Hyperoodon ampullatus* exhibited interruptions of foraging and avoidance in response to sonar that were prolonged for several hours after the exposure stopped (Miller et al., 2015; Wensveen et al., 2019).

Modifications of social and vocal behaviour have also been observed in response to naval sonar, and are particularly relevant to assess for highly social and vocal species (such as many odontocete species). However, the difficulty to assess those changes increases with the size and complexity of the species vocal repertoire. Here, we focused on long-finned pilot whales *Globicephala melas*, a highly social and vocal odontocete species. Long-finned pilot whales have been shown to reduce vocal activity in response to sonar (Miller et al., 2012) and to match the frequency-modulation pattern of sonar signals (Alves et al., 2014). The behavioural measures used to describe the vocal responses of long-finned pilot whales to naval sonar either focused on overall vocal activity (number of calls: Visser et al., 2016) or a specific detail of their vocal behaviour (similarity between calls and sonar signals: Alves et al., 2014). No study was conducted to quantify changes in call type usage in response to sonar in long-finned pilot whales because of the inherent difficulty of measuring their vocal behaviour and classifying their calls. Indeed, the vocal repertoire of long-finned pilot whales is large (125 call types identified by human operators: Vester et al., 2017) and include a mix of harmonic, pulsed, and broadband sounds (Vester et al., 2017). Some calls are stereotyped, but there is a large amount of gradation between calls (Taruski, 1979; Nemiroff and Whitehead, 2009).

In this study, we used a procedure specifically designed to quantify call gradation in non-discrete vocal repertoires (Chapter 2) to characterise the vocal responses of long-finned pilot whales to naval sonar, and to compare them to vocal responses to playback of killer whales sounds. Between 2008 and 2014, 14 long-finned pilot whales have been equipped with sound and movement recording tags (dtag: Johnson and Tyack, 2003) and exposed to naval sonar and killer whale playbacks by the 3S (sea mammal sonar safety) consortium. Other aspects of the behavioural responses of these long-finned pilot whales have been analysed in previous publications, such as horizontal movements, diving activity, or foraging (Miller et al., 2012; Sivle et al., 2012; Isojunno et al., 2017; Curé et al., 2019). Here, we focus on the evolution of three key aspects of the vocal behaviour of long-finned pilot whales in response to sonar exposures and killer whale playback: overall vocal activity at the social group and individual levels, call types, and call typicality (a quantitative measure of the stereotyped or graded nature of calls).

Based on the high group cohesion observed in this species, we hypothesised that long-finned pilot whales would display coordinated responses to threatening or disturbing stimuli. Therefore, we expected overall vocal activity to increase in response to naval sonar exposures and killer whale playbacks. We looked for call types produced specifically in response to acoustic disturbances, which could represent recruitment or general alarm calls. We assumed that long-finned pilot whales would produce more stereotyped calls (increase in call typicality) during sonar exposures to compress information and speed up information transfer between group members during coordinated responses. Alternatively, long-finned pilot whales may produce more graded calls (decrease in call typicality) during coordinated responses because they require the transfer of more, or subtler, information.

5.3: Material and methods

5.3.1: Study area and population

We performed sound exposure experiment to free-ranging long-finned pilot whales off northern Norway, between 66 and 70° north. In 2008 and 2009, pilot whales have been exposed to naval sonar in controlled conditions. In 2013 and 2014, they were exposed to playback of killer whale sounds (Table 6).

ID	Sound exposure experiments				Playback experiments		
	LFAS	MFAS	LFASDS	SILENT	MEKW	CTRL+	CTRL-
gm08_150c	2	1					
gm08_154d	1	2					
gm08_159a	2	3		1			
gm09_138a*	1	2	4	3			
gm09_138b	1	2	4	3			
gm09_156b	2	3	4	1			
gm10_157b							1, 2
gm10_158d							1, 3
gm13_137a					1		
gm13_149a					2	1	
gm13_169a*					1	2	3
gm13_169b					1	2	3
gm14_180a*					2	1	
gm14_180b					2	1	

Table 6: Overview of sound exposure experiments conducted during each tag deployment. Each tagged whale is identified by the 8-symbol dtag code: the initials of the scientific name of the species, the two digits year of the tag deployment, an underscore, the date of the deployment in the Julian calendar, and the number of the tag deployment within the day from a to z. In 2008 and 2009, tagged whales were exposed to naval sonar transmissions and control trials. In 2010, 2013, and 2014, whales were exposed to playback of killer whale sounds and

control broadcasts. On three occasions, noted in italic, two long-finned pilot whales of the same group were equipped with tags at the same time. Only one of these whales, identified with an *, was the focal individual. LFAS: low-frequency active sonar (1-2 kHz). MFAS: medium frequency active sonar (6-7 kHz). LFASDS: exposure to LFAS down sweeps (2-1 kHz). SILENT: silent vessel approach (negative control for sonar exposures). MEKW: mammal-eating killer whale sounds. CTRL+: broadcast of LFAS signals (positive control for killer whale playback). CTRL-: broadcast of broadband noise (negative control for killer whale playbacks)

5.3.2: Data collection

We used both multi-sensor animal-borne tags (dtags: Johnson and Tyack, 2003) and visual observations from the observation vessel to monitor the behaviour of long-finned pilot whales throughout the sound exposure experiments. We deployed dtags on one or two individuals prior to the sound exposure experiments. The first tagged whale was designated as the focal individual and serially exposed to several sound exposure experiments. The number of successive experiments for a single focal individual ranged from 1 to 6 (Table 6).

Dtags are attached temporarily to the animal with suction cups. We deployed dtags using a hand-help long pole or a pneumatic launching system (ARTS, LKARTS). Dtags contain a 50 Hz pressure sensor, a 250 Hz tri-axial accelerometer and magnetometer, and two hydrophones. The hydrophones recorded sounds at 192 kHz with a sampling width of 16 bits. Dtag recording have been annotated: through audio-visual inspection of sounds and spectrograms, trained operators noted the start and end times of all long-finned pilot whale signals and classified them as echolocation signals or social sounds, a broad category covering both whistles and pulsed calls.

Dtags also contain a VHF beacon which allows the identification and visual tracking of the focal whale at the surface. We defined the focal group based on the distances between individual. Within a 200 m radius around the focal whale, referred to as the focal area, the focal group was the set of individuals closer to each other and to the focal whale than to their other neighbours (see Visser et al., 2014 for a detailed description of the protocol). Visual observers noted the number of individuals in the focal group and their inter-individual spacing, as well as the presence and size of other groups in the focal area. All visual observations were recorded in Logger 2010 (IFAW).

5.3.3: Stimuli used and procedures of sound exposition

5.3.3.1: General procedure

All sound exposure experiments relied on two research vessels. One vessel followed the focal whale and was the platform for conducting visual tracking and group observations (observation vessel). The other vessel carried the sound source and was devoted to the broadcast of sound stimuli (source vessel). Visual tracking started immediately after tagging and continued throughout the experiments. The observation vessel communicated the position of the focal whale to the source vessel to coordinate sound exposure experiments.

Each sound exposure experiment consisted in three experimental phases: the pre-exposure observation period (PRE) right before the presentation of the stimulus, the stimulus presentation period (DUR), and the post-exposure observation period (POST) starting right after the presentation of the stimulus. Comparisons of the vocal behaviour of long-finned pilot whales between PRE and DUR allow the identification of the vocal responses during the stimulus transmission. Comparisons between PRE and POST can be used to determine whether vocal responses initiated during DUR continued after the end of the exposure or whether vocal responses were initiated after the exposure. The duration of PRE and POST was fixed as the designed duration of the exposure: 40 minutes for sonar experiments and 15 minutes for playback experiments (see below). Due to the logistical constraints of fieldwork, the designed experimental timeline was not always realised. This classification of the experimental phases of some successive experiments resulted in minor overlapping periods (Table 7). We assigned all overlaps between PRE and DUR and between DUR and POST to DUR, as the stimulus presentation was present. We discarded all overlaps between PRE and POST from further analyses. Using overlapping PRE as a reference to identify vocal responses to stimuli may be a problem if there are any lingering effects of the previous exposure. In addition, this avoided the repeated sampling of time intervals in successive experiments.

Focal whale	Stimulus	PRE		DUR		POST	
		Ideal start	Effective start	Start	End	Effective end	Ideal end
gm08_150c	**MFAS**	**15:32:00**		**16:12:00**	**16:50:21**	**17:25:00**	**17:30:21**
	LFAS	**17:25:00**	**17:30:21**	**18:05:00**	**18:36:00**		**19:16:00**
gm08_154d	**LFAS**	**00:35:00**		**01:15:00**	**02:35:21**	**02:55:00**	**03:15:21**
	MFAS	**02:55:00**	**03:15:21**	**03:35:00**	**04:00:21**		**04:40:21**
gm08_159a	**SILENT**	**22:27:00**		**23:07:00**	**23:37:41**	**23:53:00**	**00:17:41**
	LFAS	**23:53:00**	**00:17:41**	**00:33:00**	**01:08:21**	**01:30:00**	**01:48:21**
	MFAS	**01:30:00**	**01:48:21**	**02:10:00**	**02:46:21**		**03:26:21**
gm09_138a	LFAS	14:02:00		14:42:00	15:14:00		15:54:00
gm09_138b	MFAS	16:00:00		16:40:00	17:15:00		17:55:00
	SILENT	**18:00:00**		**18:40:00**	**19:14:00**	**19:52:00**	**19:54:00**
	LFASDS	**19:52:00**	**19:54:00**	**20:32:00**	**21:05:00**		**21:45:00**
gm09_156b	SILENT	22:50:00		23:30:00	00:02:00		00:42:00
	LFAS	**00:56:00**		**01:36:00**	**02:09:00**	**02:30:00**	**02:49:00**
	MFAS	**02:30:00**	**02:49:00**	**03:10:00**	**03:37:00**	**04:15:00**	**04:17:00**
	LFASDS	**04:15:00**	**04:17:00**	**04:55:00**	**05:25:00**		**06:05:00**
gm10_157b	**CTRL-**	**14:33:00**		**14:48:00**	**15:02:40**	**15:02:40**	**15:17:40**
	CTRL-	**14:58:00**	**15:13:00**	**15:13:00**	**15:28:00**		**15:43:00**
gm10_158d	**CTRL-***	**19:44:47**		**19:59:47**	**20:14:30**	**20:14:30**	**20:29:30**
	CTRL-*	**20:28:30**	**20:43:30**	**20:43:30**	**20:58:20**	**20:58:20**	**21:13:20**
gm13_137a	MEKW	18:49:00		19:04:00	19:19:00		19:34:00
gm13_149a	CTRL+	11:25:40		11:40:40	11:55:40		12:10:40
	MEKW	13:22:26		13:37:26	13:52:25		14:07:25
gm13_169a	MEKW	11:08:40		11:23:40	11:39:00		11:54:00
gm13_169b	CTRL+	12:11:25		12:26:25	12:41:25		12:56:25
	CTRL-	14:11:17		14:26:17	14:41:16		14:56:16
gm14_180a	CTRL+	13:12:58		13:27:58	13:44:00		13:59:00
gm14_180b	MEKW	15:01:00		15:16:00	15:31:00		15:46:00

Table 7: Experiment timeline and overlaps between successive experiments. PRE and POST periods should ideally last 40 minutes for sonar experiments and 15 minutes for playback experiments. Nevertheless, there was some overlap between these time periods for successive sound exposure experiments. We discarded overlapping periods, resulting in effective start times of PRE and effective end times of POST different from the ideal start and end times in experiment design. Such cases are marked in bold in the table. No effective time is given when

it was identical to the designed time. *: sound exposure experiments overlapping a playback not presented in this study

5.3.3.2: Controlled exposure experiments to naval sonar

We used a towable sonar source (SOCRATES, TNO, the Netherlands) for controlled exposure experiments. The source vessel approached the focal whale at constant speed over the course of the experiment, with the aim of reaching it after 30 minutes of full power exposure. Sonar transmission started when the source vessel was 6 to 8 km from the focal whale. The source vessel first adjusted its course to the successive positions of the focal individual, and then fixed its heading when it reached 1 km from the focal whale. Sonar transmission continued for 5 minutes after the source vessel crossed the path of the focal whale. The source level of sonar signals increased gradually over the first 5 minutes of the exposure, which is referred to as the ramp up procedure. The planned duration of a controlled exposure to sonar was therefore 40 minutes: 5 minutes of ramp up, 30 minutes of full power transmission to reach the focal individual, and 5 minutes of transmission after crossing the path of the focal whale. In practice, exposure duration was variable (Table 7). A mitigation procedure was set so that sonar transmission would be interrupted if the whale approached within 100 m of the source, showed pathological reactions, or approached confined and shallow areas.

The frequency band and modulation pattern of sonar signals is variable and depends on the range and precision sought after. We tested three kinds of sonar signals: low frequency active sonar (LFAS) – 1 to 2 kHz hyperbolic upsweeps; medium frequency active sonar (MFAS) – 6 to 7 kHz hyperbolic upsweeps; and LFAS down sweeps (LFASDS) – 2 to 1 kHz hyperbolic downs weeps. All signals followed the same transmission scheme: 1 s pings followed by 19 s of silence. The source level of LFAS and LFASDS signals increased from 152 to 214 dB re 1 μPa (root-mean-square), and the source level of MFAS signals increased from 158 to 199 dB re 1 μPa (root-mean-square). In addition to sonar exposure experiments, we also carried out silent approaches of the source vessel towing the sonar source but without sonar transmissions, using the same approach protocol as sonar exposure experiments. We refer to these no-sonar control approaches as SILENT in the rest of the article.

5.3.3.3: Playback of killer whale sounds

We broadcasted playback stimuli from a loudspeaker lowered 8 m underwater (details of the playback chain material can be found in Curé et al., 2019). The source vessel positioned itself ahead of the focal whale, but not directly in its path. This disposition does not force reactions by blocking the path of the focal whale and eases the detection of approach and avoidance responses (Chapter 1). Once in position, the source vessel switched off its engine and lowered the hydrophone before the start of the DUR. At the end of the DUR period, the playback material was brought back on board, and the source vessel transited to the next playback position.

We used the sounds of unfamiliar mammal-eating killer whale (MEKW), which should represent maximal threat to long-finned pilot whales. Mammal-eating killer whale sounds were recorded using dtags on groups of around five individuals harassing and feeding on marine mammals off Southeast Alaska. We removed all sounds not produced by killer whales from the recordings, such as bubble sounds or the sound of the tag breaking the water surface. We looped the resulting files so that all stimuli would last 15 minutes. Stimuli were amplified so that recorded calls would reach the natural range of source levels for killer whales (140-155 dB re 1 μPa root-mean-square: Miller, 2006). We used two additional signals. We selected portions of killer whale recordings without killer whale sounds, prepared them in the same way as killer whale stimuli and amplified them to reach the same average root-mean-square sound pressure level as killer whale stimuli. We refer to the playback of background noise stimuli as CTRL-. We also broadcasted artificial frequency-modulated signals (1-2 kHz hyperbolic upsweeps, same as LFAS signals) at the same average root-mean-square sound pressure levels as killer whale calls. We refer to these broadcasts of artificial signals as CTRL+. For all stimuli, except for artificial signals, we prepared several stimulus exemplars to reduce pseudoreplication.

5.3.4: Vocal behaviour measures

5.3.4.1: Vocal activity

We measured the root-mean-square sound pressure level signal to noise ratio of all annotated calls, using the 0.2 seconds right before the call as reference. We selected all annotated calls with signal to noise ratio higher than 3 dB to measure the vocal activity of long-finned pilot whales.

We used two measures of vocal activity: the number of annotated calling events and the cumulative duration of calling events. The number of calling events is a measure of the total number of calls, except that overlapping calls and calls closer than 0.2 s apart were annotated as single events. The cumulative duration of calling events is a measure of time spent calling, except that overlapping calls were counted only once and gaps smaller than 0.2 s between calling events were included.

We measured the number of calling events and their cumulative duration for all experimental phases (PRE, DUR, and POST). Since the duration of experimental phase was variable, we divided the two measures of vocal activity by the duration of each experimental phase. We obtained the rate of calling events and the proportion of time scored as calling during the PRE, DUR, and POST of each experiment.

Dtags do not only record the calls produced by the focal whale or the focal group, but the calls produced by all conspecifics present in the surrounding area. The selection of calls with signal over noise ratio higher than 3 dB presumably removed annotated calls produced by very distant individuals from the dataset. However, the rate of calling events and the proportion of time scored as calling are measures of focal group vocal activity.

We divided these measures of group vocal activity by the size of the focal group to obtain a proxy of individual vocal activity within the focal group. We estimated the average group size during each experimental phase based on visual observations of the focal group at the surface. Visual tracking of the focal whale was not consistent: long-finned pilot whales may dive for various durations or may be lost from sight. To take into account the irregularity of visual tracking, we assumed that group size remained the same from one observation to the next one and included the duration between observations as a weighting factor in the calculation of average group size AGS:

$$AGS = \frac{1}{total\ duration}\ x \sum_{i=0}^{n\ obs} (t_{i+1} - t_i) x\ group\ size_i$$

With:

- $n\ obs$ the number of observations of the focal group during the experimental phase
- t_i the time of i-th observation. t_0 is the start time of the experimental phase, $t_{n\ obs+1}$ is the end time of the experimental phase.

- $group\ size_i$ is the focal group size estimation at i-th observation. $group\ size_0$ is the last observed focal group size before the start of the experimental phase.

This group size calculation method asymptotically corresponds to the mean of focal group size estimations, but reduces the influence of observations clustered in time.

5.3.4.2: Call types and typicality

We selected annotated calls with signal to noise ratio higher than 6 dB. We then visually inspected spectrograms (1024 pts, Hanning window, 50 % overlap) and discarded all calls which were overlapped by other calls, loud echolocation clicks, and transient or fluctuating background noise. We downsampled tag recordings to 48 kHz and classified long-finned pilot whales using a Mel frequency cepstral coefficients- and fuzzy clustering-based unsupervised classifier (see chapter 2 for method details). We classified the calls from each tag deployment separately.

Fuzzy clustering detects apparent stereotypes in the dataset and quantifies the position of individual calls between these stereotypes. Each call is given a membership score to each fuzzy cluster, or apparent stereotype, which corresponds to the probability to belong to that cluster. The classification algorithm depends on the fuzziness parameter μ, which determines how much clusters can overlap, and the maximum number of clusters allowed nc_{max}. Several stable clustering solutions may exist for a single dataset

(Table 8). Each stable clustering solution consists of several fuzzy clustering classifications obtained with different values of fuzziness.

We divided each calls into 10 equal time slices and calculated 10 Mel frequency cepstral coefficients for each slice. We set the maximal fuzziness value at $\mu_{max} = 2$, the maximum number of clusters allowed as nc_{max} = *number of calls/10 + 5*, and decremented the fuzziness parameter by steps of 0.01.

We derived two measures of vocal activity from fuzzy clustering results: the change in average membership scores and the change in average typicality between experimental phases.

Using calls selected for the fuzzy clustering analysis that were produced during sound exposure experiments, we calculated the average membership score to each cluster during the PRE, DUR, and POST of an experiment. Then, we computed the change in average membership scores between PRE and DUR and between PRE and POST as:

$$M_{p,q} = {}^{1}/_{n\ cluster}\ x \sum_{c=1}^{n\ cluster} \left(mb_{p,c} - mb_{q,c}\right)^2$$

with:

- $M_{p,q}$ the change in average membership scores between experimental phases p and q
- *n cluster* the number of clusters in the fuzzy clustering solution.
- $mb_{p,c}$ the average membership score to cluster c during experimental phase p

Tag ID	Fuzziness values for solutions with:		
	two clusters	three clusters	four clusters
gm08_150c	1.62; 1.58; 1.38; 1.35; 1.33; 1.32; 1.31; 1.30; 1.29; 1.28; 1.27; 1.26; 1.24: 1.23; 1.22; 1.20; 1.19	1.25; 1.21; 1.18; 1.17; 1.16; 1.15; 1.13	1.14; 1.12; 1.11
gm08_154d	1.14; 1.09; 1.08; 1.07; 1.06		
gm08_159a	1.22; 1.21; 1.18; 1.15; 1.14; 1.13; 1.12; 1.11; 1.10; 1.09; 1.08; 1.07		
gm09_138a	1.10; 1.08; 1.07		
gm09_138b	1.17; 1.15; 1.13; 1.12; 1.11; 1.10	1.08: 1.06; 1.09	
gm09_156b	1.16; 1.14; 1.12; 1.11; 1.10; 1.09; 1.08	1.07; 1.06; 1.05	
gm10_157b	1.20; 1.19; 1.18; 1.17; 1.16; 1.15; 1.14; 1.13; 1.12; 1.11; 1.10		1.08; 1.07; 1.06; 1.05
gm10_158d	1.20; 1.18; 1.16; 1.15; 1.14; 1.13; 1.12; 1.11; 1.10; 1.09		
gm13_137a	1.46; 1.38; 1.35; 1.32; 1.29; 1.28; 1.27; 1.26; 1.25; 1.24; 1.23; 1.22; 1.21; 1.20; 1.19; 1.18; 1.17; 1.16; 1.15; 1.14; 1.13	1.12; 1.11; 1.10	
gm13_149a	1.13; 1.12; 1.11; 1.08		
gm13_169a	1.23; 1.20; 1.18; 1.17; 1.16; 1.15; 1.13	1.14; 1.12; 1.11	1.10; 1.09; 1.08
gm13_169b	1.37; 1.29; 1.28; 1.27; 1.26; 1.25; 1.24; 1.23; 1.22; 1.20; 1.21; 1.19; 1.18; 1.17; 1.16; 1.15; 1.14; 1.13; 1.12; 1.11; 1.10; 1.09		1.07; 1.06; 1.05; 1.04
gm14_180a	1.38; 1.36; 1.35; 1.33; 1.32; 1.31; 1.30; 1.29; 1.28; 1.27; 1.26; 1.25; 1.24; 1.23; 1.21; 1.20; 1.19; 1.16	1.18; 1.17; 1.15; 1.14	
gm14_180b	1.39; 1.36; 1.35; 1.33; 1.31; 1.30; 1.28; 1.27; 1.26; 1.25; 1.24; 1.23; 1.22; 1.21; 1.20; 1.19; 1.18; 1.17	1.16; 1.15; 1.14; 1.13; 1.12; 1.11	

Table 8: Fuzziness values over which solutions with two, three, and four clusters were stable for each tag deployment.

M is a measure of changes in call type usage from one experiment phase to the other. M is distributed between 0 and 1 irrespective of the number of clusters in the fuzzy clustering solutions. However, as the sum of all membership scores for a given call equals 1, the distribution of M may somewhat shift towards smaller values as the number of clusters increases.

The typicality is the difference between the two highest membership scores of a call. It is a measure of the stereotyped or graded nature of calls. Calls with high typicality are much closer from one apparent stereotype than from the others (stereotyped calls). Calls with low typicality lie in between stereotypes (graded calls). We measured the average typicality of calls during the PRE, DUR, and POST of each experiment, and compared the average typicality during the PRE with the average typicality during either the DUR or the POST. We refer to the change in average typicality between experimental phases *p* and *q* as $T_{p,q}$ in the rest of the article.

We selected tag deployments with at least two calls in the PRE and DUR to measure $M_{PRE,DUR}$ and $T_{PRE,DUR}$, and tag deployments with at least two calls during PRE and POST for $M_{PRE,POST}$ and $T_{PRE,POST}$ calculations. We then measured *M* and *T* for each stable fuzzy clustering solution and for each fuzziness value.

5.3.5: Statistical analysis

5.3.5.1: Vocal activity

In order to work with independent samples, we pooled the vocal activity measures of tags deployed the same day on individuals from the same group if both whales stayed together during the sound exposure experiments (gm09_138a and gm09_138b, and gm13_169a and gm13_169b). Else, we discarded the non-focal whale from the analysis (gm14_180b). We kept gm09_138b instead of gm09_138a, as tag a malfunctioned and both whales stayed together throughout the deployment.

5.3.5.2: Call types and typicality

We considered the different realisations of fuzzy clustering to be repeated measures of the same vocal behaviour for each tag deployment. We used tag deployment days as blocking units to pool pairs of whales tagged the same day, as they were exposed to the same signals in the exact same conditions. We ran generalised estimated equations (GEE) to determine the effect of signal type on the changes in average membership scores and typicality between experiment duration. Changes in average membership scores were modelled under a Gamma distribution and changes in average typicality under a Gaussian distribution, both with an identity link function. We used the jack-knife variance estimator. Since sonar exposure experiments and playback signals targeted different subsets of individuals in the dataset, we built separate models for each type of experiment. The sample size of certain exposure types (CTRL-, LFASDS) and clustering solution size (four clusters) was too low to take into account clustering solution size and order of presentation in the models. Therefore, we did not perform any model selection procedure, and the GEE results must be taken as descriptive.

We compared the effect sizes of signal types within model to determine how the whales reacted to different types of sonar signals or playback stimuli. We compared the effect sizes of sonar signals across models to determine whether the nature of the response towards naval sonar and killer whale sounds was identical.

We used the R software (R Core Team, 2017) and package ‘geepack’ (Halekoh et al., 2006) to run the GEE models. The threshold for statistical significance was set at 0.05. Since the populations exposed to naval sonars and killer whale playbacks were different, there was no repeated testing and no correction of the threshold for statistical significance was needed.

5.4: Results

5.4.1: Vocal activity

Vocal responses to silent vessel approaches were variable (Figure 15). Out of three experiments, group vocal activity increased during the silent vessel approach in one case, decreased in the second one, and remained stable in the last one (Figure 15A and C). Individual vocal activity (group activity weighted by group size) was lower in POST than in PRE and DUR in two out of three experiments (Figure 15B and D). Individual vocal activity followed the same trend as group vocal activity except for gm09_156b: group vocal activity remained at the same level during PRE and DUR, whereas individual vocal activity largely decreased in DUR, which means that group size was larger in DUR than in PRE.

Both group and individual vocal activity tended to increase in response to LFAS (Figure 16). In 4 out of 5 LFAS experiments, group (Figure 16A and C) and individual (Figure 16B and D) vocal activity were higher in PRE than in DUR, and higher in POST than in DUR. Group and individual vocal activity followed similar trends for all experiments.

Vocal responses to MFAS experiments were variable (Figure 17). Group vocal activity decreased in DUR compared to PRE in two cases, increased in two cases, and remained at the same level in one case. Similarly, it was higher in POST than in PRE in three cases, and lower in two cases (Figure 17A and C). Individual vocal activities followed the same trends as group vocal activity during DUR. During POST, individual vocal activity was lower than or equal to individual vocal activity in PRE (Figure 17B and D). For tag gm09_156b, group vocal activity remained at a similar level in DUR and POST, whereas individual vocal activity decreased in POST, which means that group size increased in POST.

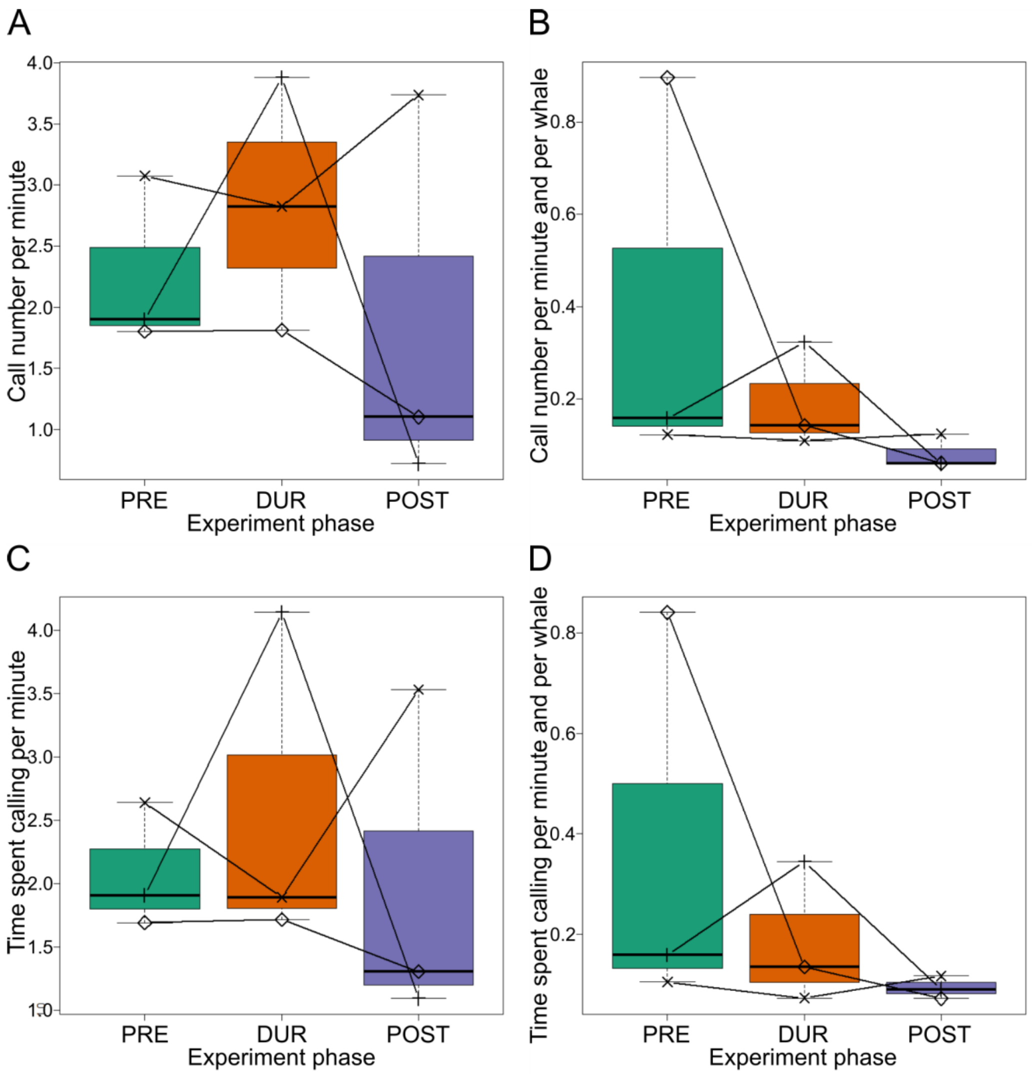

Figure 15: Vocal activity before, during, and after silent vessel approaches **A and B)** Number of annotated calling events **C and D)** Cumulative duration of annotated calling events. Left panels (A and C) were corrected for experiment phase duration. Right panels (B and D) were corrected for both experiment phase duration and average group size. Data for individual tag deployments is displayed as points and lines: + crosses – gm08_159a; x crosses – gm09_138b; diamonds – gm09_156b

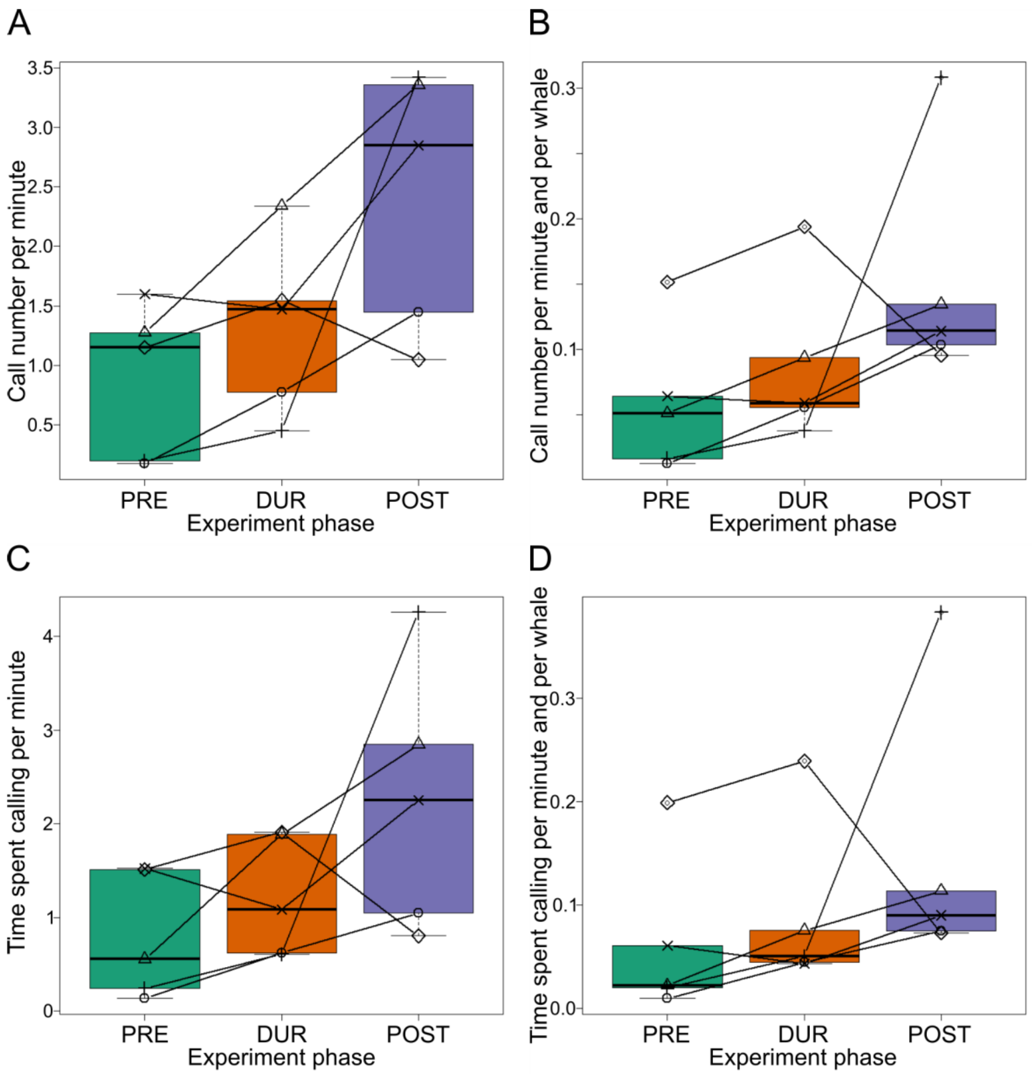

Figure 16: Vocal activity before, during, and after LFAS exposures **A and B)** Number of annotated calling events **C and D)** Cumulative duration of annotated calling events. Left panels (A and C) were corrected for experiment phase duration. Right panels (B and D) were corrected for both experiment phase duration and average group size. Circles – gm08_150c; triangles – gm08_154d; + crosses – gm08_159a; x crosses – gm09_138b; diamonds – gm09_156b

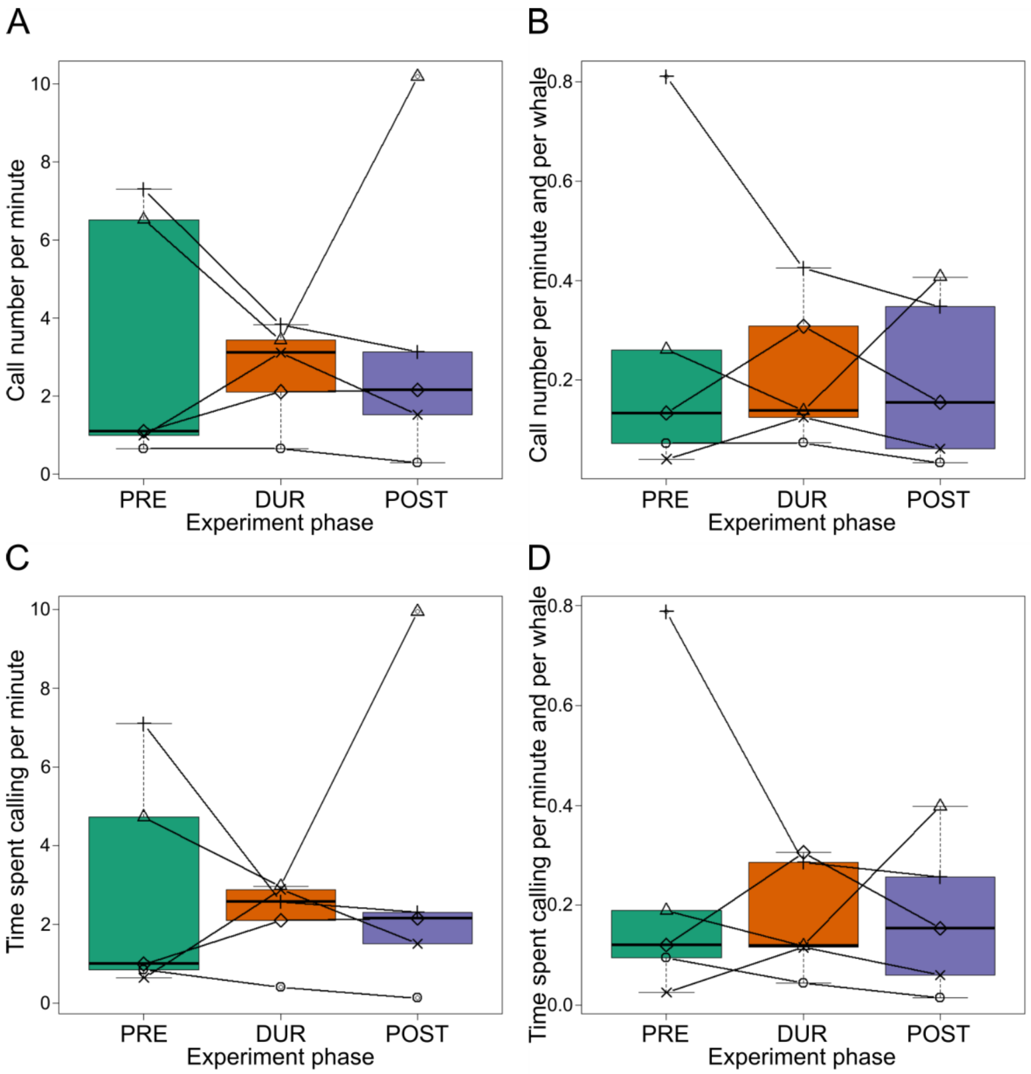

Figure 17: Vocal activity before, during, and after MFAS exposures **A and B)** Number of annotated calling events **C and D)** Cumulative duration of annotated calling events. Left panels (A and C) were corrected for experiment phase duration. Right panels (B and D) were corrected for both experiment phase duration and average group size. Circles – gm08_150c; triangles – gm08_154d; + crosses – gm08_159a; x crosses – gm09_138b; diamonds – gm09_156b

There were only two exposures to LFASDS, and the vocal responses recorded differed (Figure 18). Group level vocal activity either increased or decreased in DUR and in POST compared to PRE (Figure 18A and C). Individual vocal activity was lower in POST than in PRE in both cases (Figure 18B and D). For gm09_138b, the duration scored as calling increased whereas the number of calls decreased in DUR, which means that long-finned pilot whales produced longer calls in DUR than in PRE.

Group vocal activity either increased (3 cases) or decreased (3 cases) in response to MEKW experiments (Figure 19). When it increased, it was higher in POST than in PRE in all cases. In one case, vocal activity was increased in POST but not in DUR (Figure 19A and C). At the individual level, we observed two increases in vocal activity in response to MEKW, two decreases thereof, and an absence of modification in DUR (Figure 19B and D). In four out of five cases, individual vocal activity in POST was lower than or equal to individual vocal activity in PRE (Figure 19B and D). These results were mostly related to changes in group size. For instance, individual vocal activity remained the same throughout the MEKW playback for tag gm14_180a, but group vocal activity decreased in DUR and further decreased in POST.

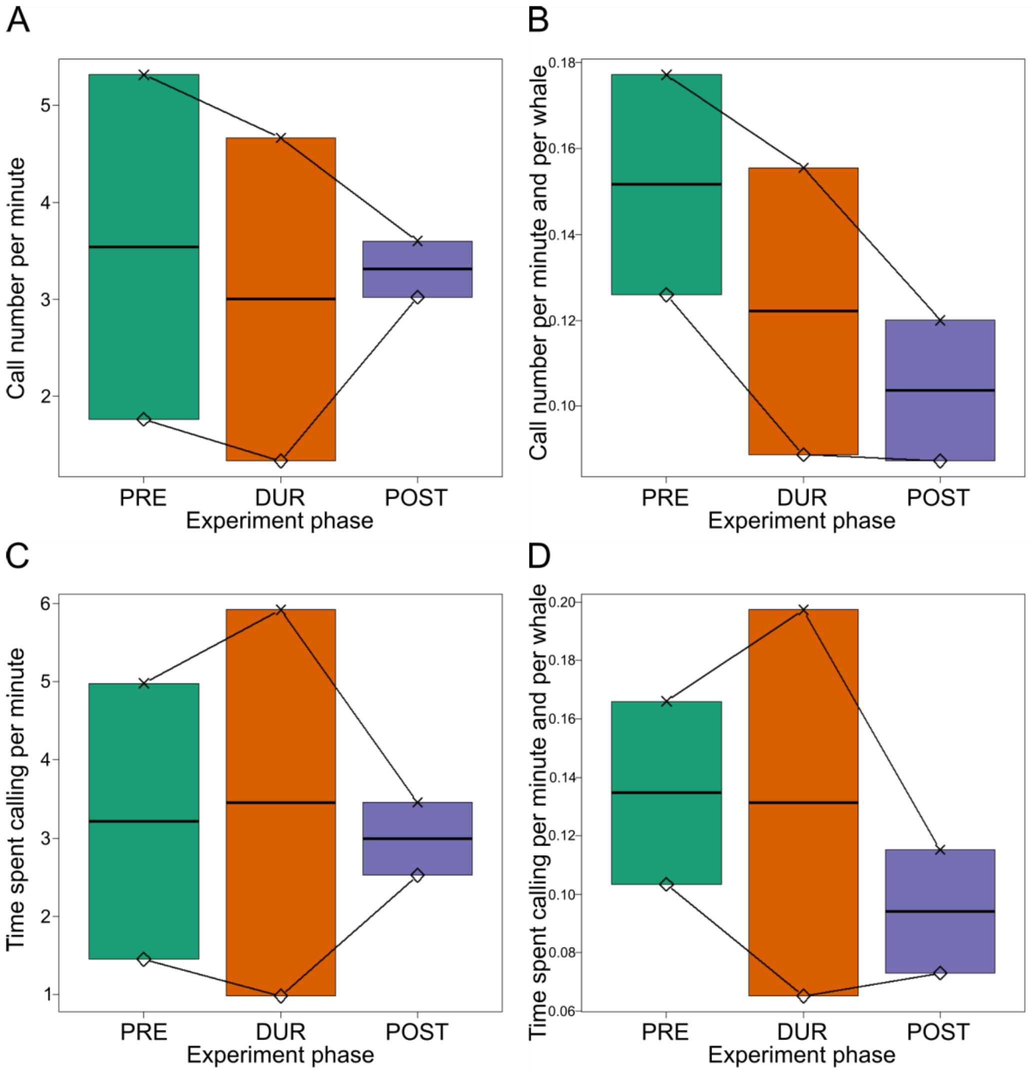

Figure 18: Vocal activity before, during, and after LFASDS exposures **A and B)** Number of annotated calling events **C and D)** Cumulative duration of annotated calling events. Left panels (A and C) were corrected for experiment phase duration. Right panels (B and D) were corrected for both experiment phase duration and average group size. X crosses – gm09_138b; diamonds – gm09_156b

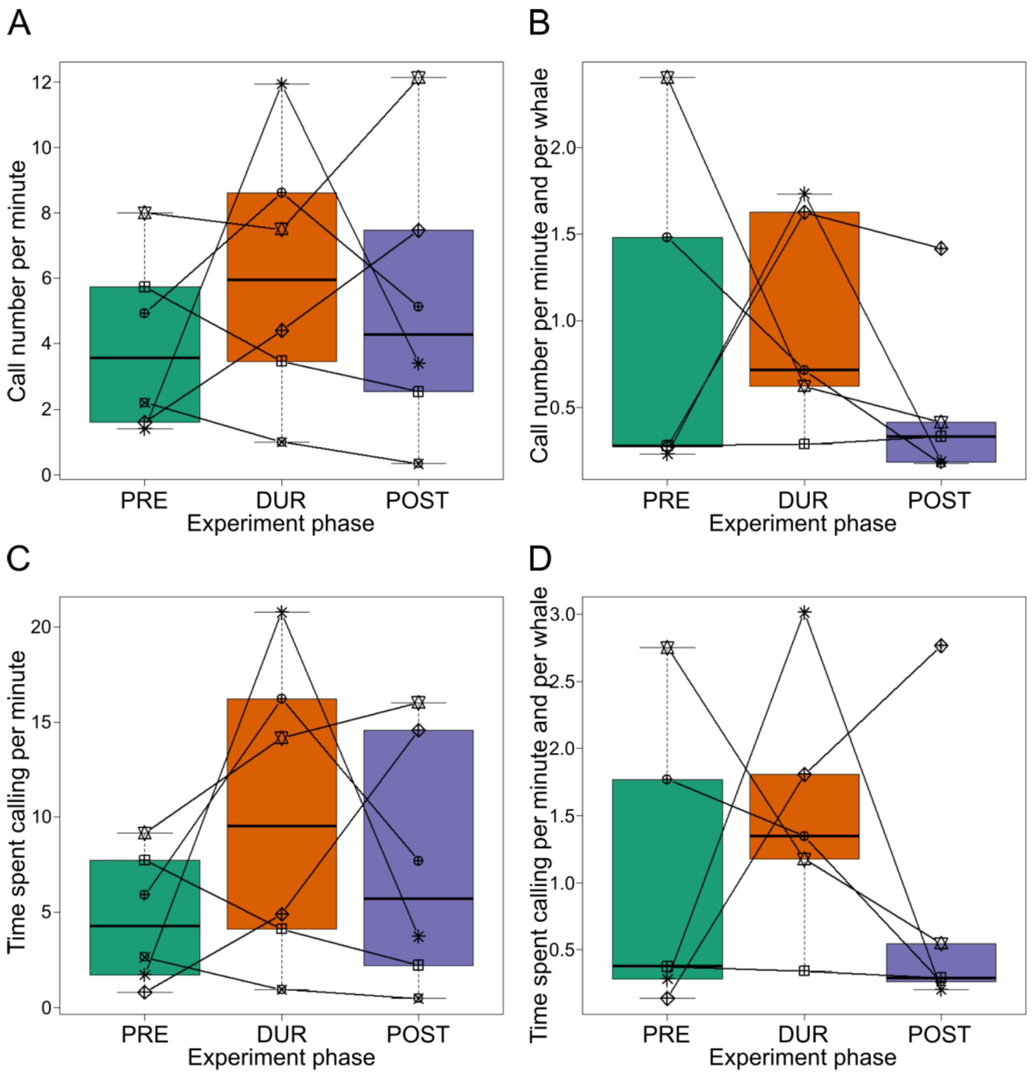

Figure 19: Vocal activity before, during, and after MEKW playbacks **A and B)** Number of annotated calling events **C and D)** Cumulative duration of annotated calling events. Left panels (A and C) were corrected for experiment phase duration. Right panels (B and D) were corrected for both experiment phase duration and average group size. Stars – gm13_137a; crossed diamonds – gm13_149a; + crossed circles – gm13_169a; double triangles – gm13_169b; crossed squares – gm14_180a; x crossed circles – gm14_180b

Group vocal activity increased during the DUR and POST of all five playbacks of CTRL+ compared to PRE (Figure 20A and C). Individual vocal activity increased in DUR, then decreased in POST to lower levels than in PRE for four out of five experiments (Figure 20B and D). For tag gm14_180a, individual vocal activity remained low throughout the experiment: the increase in group vocal activity observed in DUR corresponds to an increase in group size. Similarly, group vocal activity for tag gm13_149a remained at higher levels in POST than in PRE while individual vocal activity was lower in POST than in PRE: there was a prolonged increase in group size in response to CTRL+ playback.

Individual and group vocal activity followed the same trends for CTRL- playback (Figure 21). Vocal activity remained at the same level (two cases) or decreased (two cases) in DUR. In POST, group level vocal activity increase compared to DUR, and either remained lower than in PRE or increased to higher levels than in PRE (Figure 21A and C). Individual vocal activity in POST was higher than in PRE (Figure 21B and D).

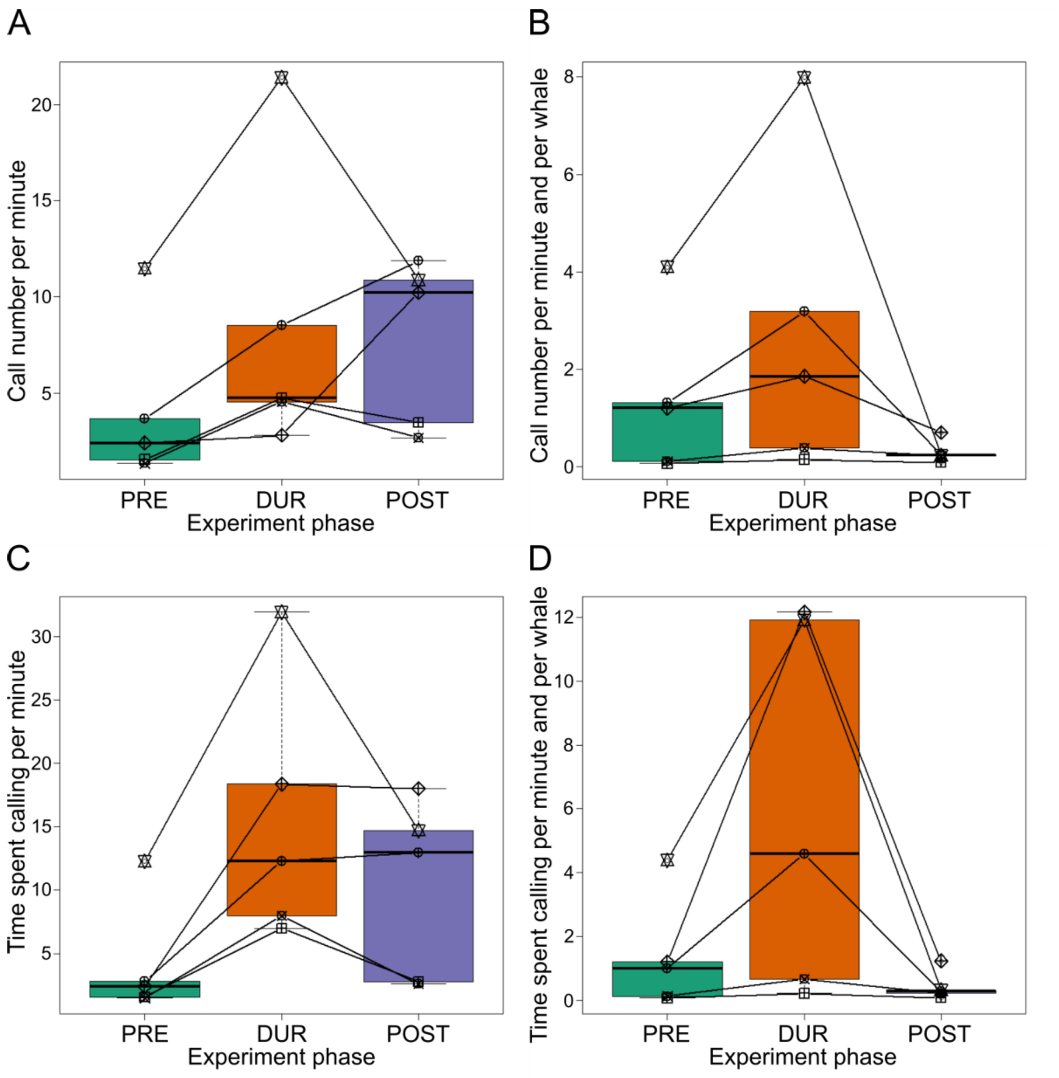

Figure 20: Vocal activity before, during, and after CTRL+ playbacks **A and B)** Number of annotated calling events **C and D)** Cumulative duration of annotated calling events. Left panels (A and C) were corrected for experiment phase duration. Right panels (B and D) were corrected for both experiment phase duration and average group size. Crossed diamonds – gm13_149a; + crossed circles – gm13_169a; double triangles – gm13_169b; crossed squares – gm14_180a; x crossed circles – gm14_180b

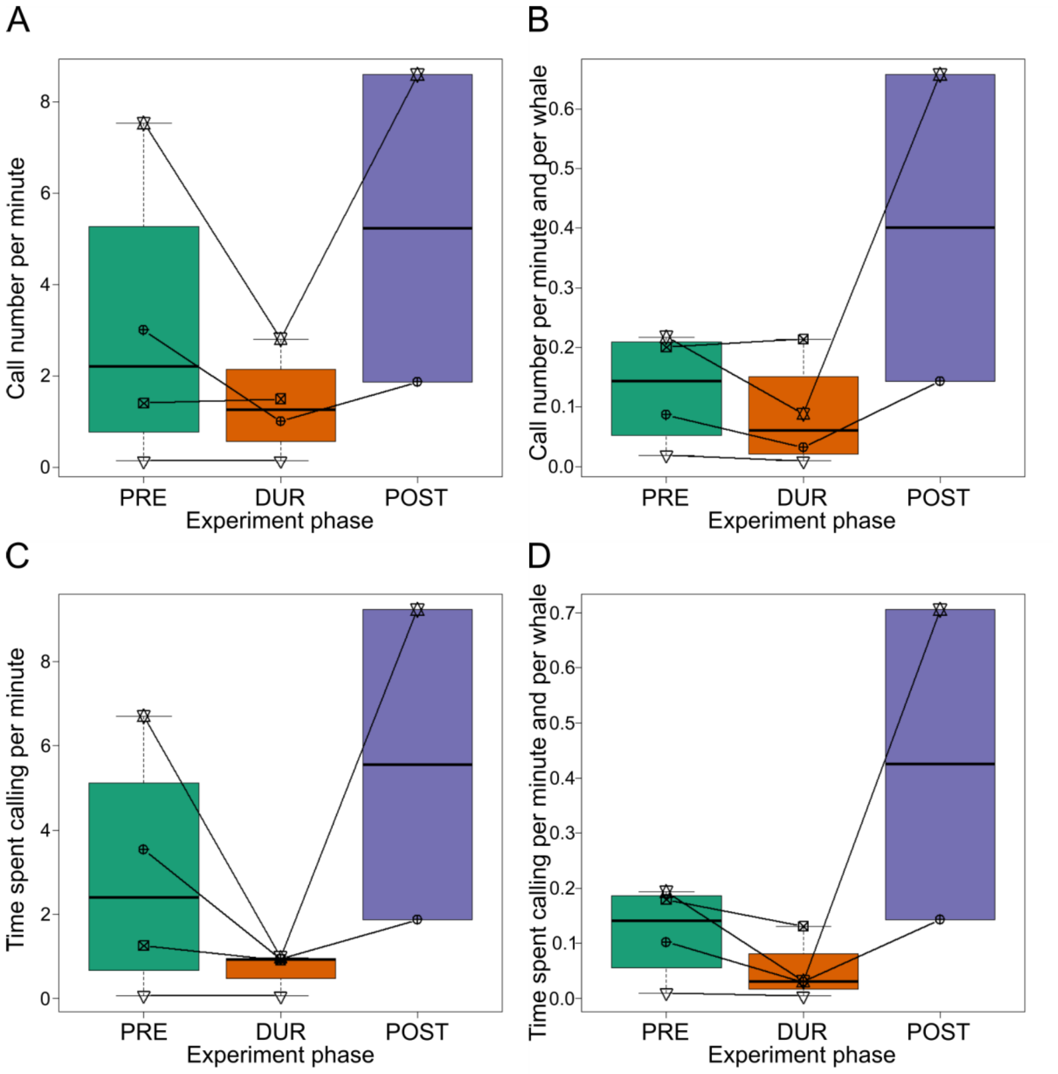

Figure 21: Vocal activity before, during, and after CTRL- playbacks **A and B)** Number of annotated calling events **C and D)** Cumulative duration of annotated calling events. Left panels (A and C) show data corrected for experiment phase duration. Right panels (B and D) show data corrected for both experiment phase duration and average group size. Inverted triangles – gm10_157b; x crossed squares – gm10_158d; + crossed circles – gm13_169a; double triangles – gm13_169b

5.4.2: Call types and typicality

The changes in call type usage during LFAS exposures were variable ($M_{PRE,DUR}$ = 0.170 +/- 0.158: Table 9). Changes in call type usage were also variable between the PRE and POST of LFAS experiments, but over a narrower range than differences between PRE and DUR ($M_{PRE,POST}$ = 0.047 +/- 0.039: Table 9).

In comparison, long-finned pilot whales used different call types in the PRE and DUR of exposures to MFAS ($M_{PRE,DUR}$ = 0.139 +/- 0.031: Table 9) and LFASDS ($M_{PRE,DUR}$ = 0.141 +/- 0.061: Table 9). These vocal responses to MFAS and LFAS stopped at the end of the exposure ($M_{PRE,POST}$ = 0.027 +/- 0.011 and $M_{PRE,POST}$ = 0.039 +/- 0.015, respectively, similar to responses observed between SILENT PRE and DUR: Table 9).

There was no change in call type usage between the PRE and DUR of silent vessel approaches ($M_{PRE,DUR}$ = 0.021 +/- 0.009: Table 9). Interestingly, we observed a large change in call type usage between the PRE and POST of SILENT exposures ($M_{PRE,POST}$ = 0.135 +/- 0.035, similar in magnitude to responses in DUR for MFAS and LFASDS: Table 9). There was no significant change in typicality during or after sonar exposures and silent vessel approaches (Table 10).

Changes in call type usage with no change in average typicality corresponded either to the long-finned pilot whales switching between stereotyped calls of one type to another (Figure 22A and B), or from shifts in the position of graded calls between stereotypes (Figure 22C). Some pilot whale barely responded to LFAS signals (Figure 23A), while other ones strongly altered their vocal behaviour (Figure 23B), which resulted in the large variation of responses observed.

Sound stimulus		Comparison PRE-DUR				Comparison PRE-POST			
		Mean	Std	Wald	p-value	Mean	Std	Wald	p-value
Sonar	**SILENT**	**0.021**	**0.009**	**4.76**	**0.029**	**0.135**	**0.035**	**14.60**	**<0.001**
	LFAS	0.170	0.158	1.16	0.281	0.047	0.039	1.43	0.231
	MFAS	**0.139**	**0.031**	**20.83**	**<0.001**	**0.027**	**0.011**	**6.11**	**0.014**
	LFASDS	**0.141**	**0.061**	**5.41**	**0.020**	**0.039**	**0.015**	**7.02**	**0.008**
Playback	**CTRL-**	**0.341**	**0.016**	**443.99**	**<0.001**				
	CTRL+	**0.060**	**0.005**	**156.80**	**<0.001**	**0.304**	**0.122**	**6.20**	**0.013**
	MEKW	**0.095**	**0.030**	**9.88**	**0.002**	**0.056**	**0.025**	**5.13**	**0.024**

Table 9: Results of the generalised estimated equation models to explain the variation of the change of average membership score between experiment phases by signal types. A different model was built to analyse responses to controlled exposure experiments and to playback experiments. Significant effects are indicated in bold.

Sound stimulus		Comparison PRE-DUR				Comparison PRE-POST			
		Mean	Std	Wald	p-value	Mean	Std	Wald	p-value
Sonar	SILENT	-0.033	0.059	0.32	0.57	-0.060	0.067	0.79	0.373
	LFAS	-0.073	0.180	0.16	0.69	-0.010	0.138	0.01	0.941
	MFAS	-0.007	0.028	0.06	0.80	-0.022	0.033	0.47	0.495
	LFASDS	-0.080	0.140	0.33	0.57	-0.022	0.012	3.11	0.078
Playback	CTRL-	-0.010	0.006	3.08	0.079				
	CTRL+	**-0.157**	**0.057**	**7.46**	**0.006**	-0.075	0.059	1.61	0.21
	MEKW	-0.018	0.04	0.19	0.664	0.018	0.067	0.07	0.79

Table 10: Results of the generalised estimated equation models to explain the variation of the change of average typicality between experiment phases by signal type. A different model was built to analyse responses to controlled exposure experiments and to playback experiments. Significant effects are indicated in bold.

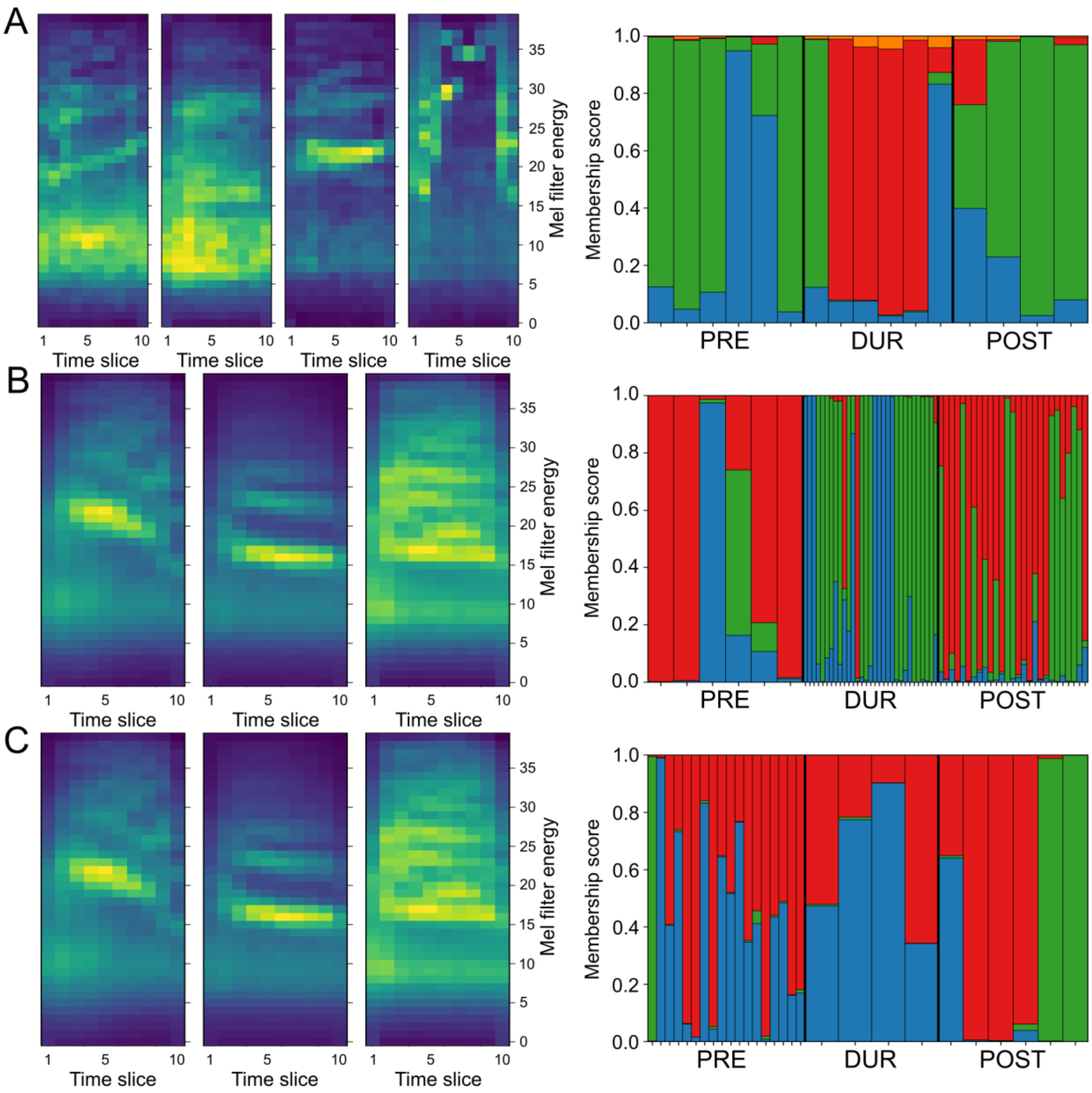

Figure 22: Examples of vocal responses of long-finned pilot whales to sonar signals. The left panels show reconstruction of the fuzzy cluster centroids. The right panels represent the membership scores of calls produced in PRE, DUR, and POST of the sound exposure experiment. The width of the histograms corresponds to the duration of the experiment phases. The left to right order of the left panels corresponds to the bottom to top order (blue, green, red, and orange) of the right panels **A)** Response of gm08_150c to MFAS (4 fuzzy clusters, fuzziness

= 1.14) **B)** Response of gm09_138b to LFASDS (3 fuzzy clusters, fuzziness = 1.09) **C)** Response of gm09_138b to SILENT (3 fuzzy clusters, fuzziness = 1.09)

Changes in call type usage were detected between the PRE and DUR of all three types of playback: MEKW, CTRL+, and CTRL- (Table 9). CTRL- had the largest response in call type usage ($M_{PRE,DUR}$ = 0.341 +/- 0.016: Table 9). Change in call type usage in response to MEKW was slightly larger than in response to CTRL+, which elicited the smallest change ($M_{PRE,DUR}$ = 0.090 +/- 0.030 vs. 0.065 +/- 0.005: Table 9).

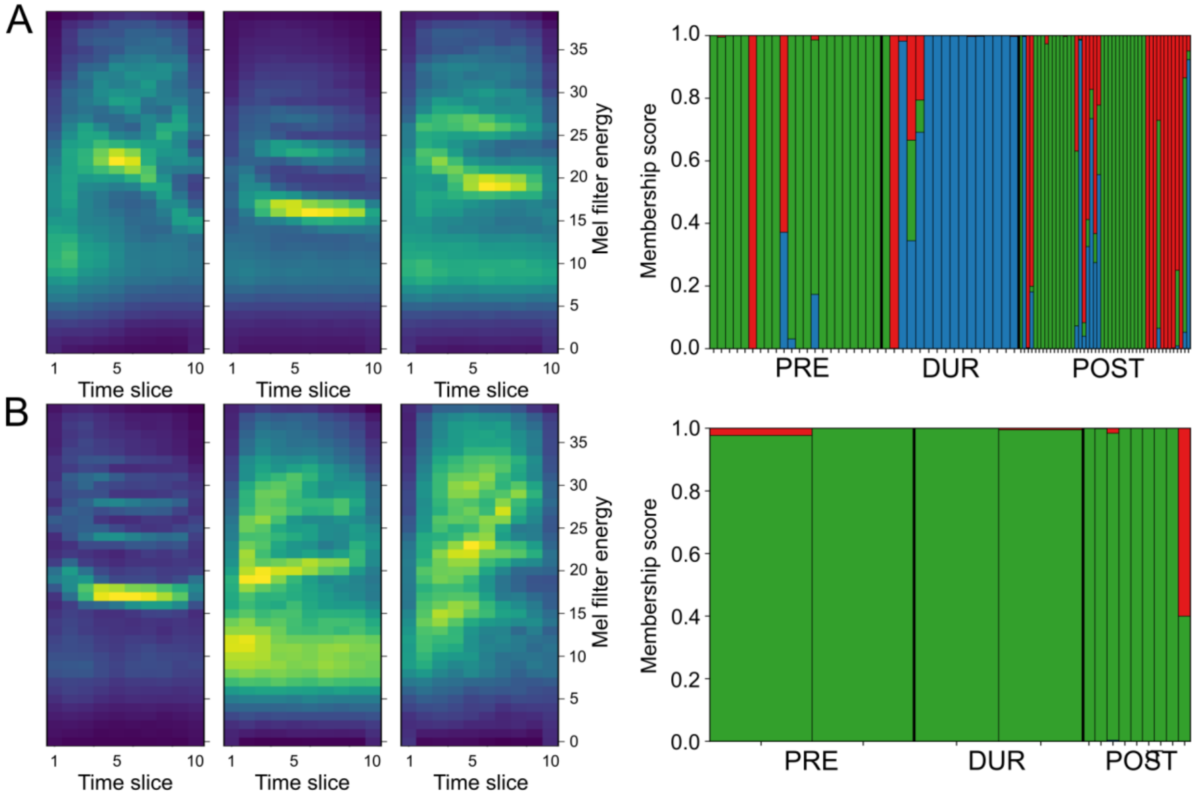

Figure 23: Examples of vocal responses of long-finned pilot whales to LFAS **A)** Strong response for gm09_138b (3 fuzzy clusters, fuzziness = 1.06) **B)** Absence of response for gm09_156b (3 fuzzy clusters, fuzziness 1.06)

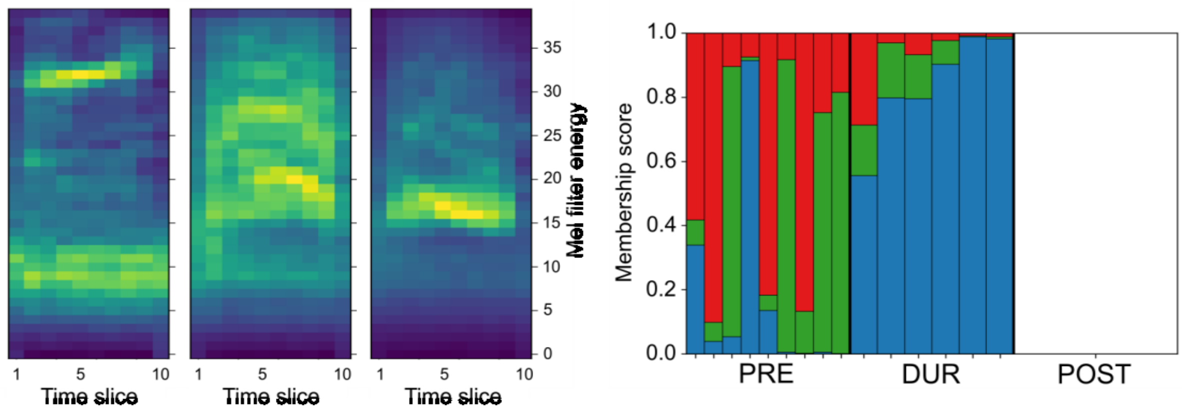

Figure 24: Example of vocal responses of long-finned pilot whales to CTRL- playbacks (gm13_169a, 3 fuzzy clusters, fuzziness = 1.12). The call type produced in DUR (left cluster, in blue) was higher in frequency that the call types used in PRE (centre and right cluster, in green and red)

We observed a large change in call type usage between the PRE and POST of CTRL+ experiments ($M_{PRE,POST}$ = 0.304 +/- 0.122, larger than the corresponding $M_{PRE,DUR}$: Table 9). Vocal behaviour did not return to PRE levels after the end of MEKW playbacks ($M_{PRE,POST}$ = 0.056 +/- 0.025, smaller than the corresponding $M_{PRE,DUR}$: Table 9).

We observed no change in typicality during or after MEKW playbacks ($T_{PRE,DUR}$ = -0.018 +/- 0.040, $T_{PRE,POST}$ = 0.018 +/-0.067: Table 10). Despite the large modification of call type usage, no change of typicality was recorded between the PRE and DUR of CTRL- experiments. Long-finned pilot whale switched between highly typical calls (Figure 24). They produced high frequency calls in response to CTRL- playbacks (Figure 24). The typicality of calls decreased in response to CTRL+ playback ($T_{PRE,POST}$ =-0.157 +/- 0.057:

Table 10). Long-finned pilot whale produced more graded calls during CTRL+ experiments (Figure 25).

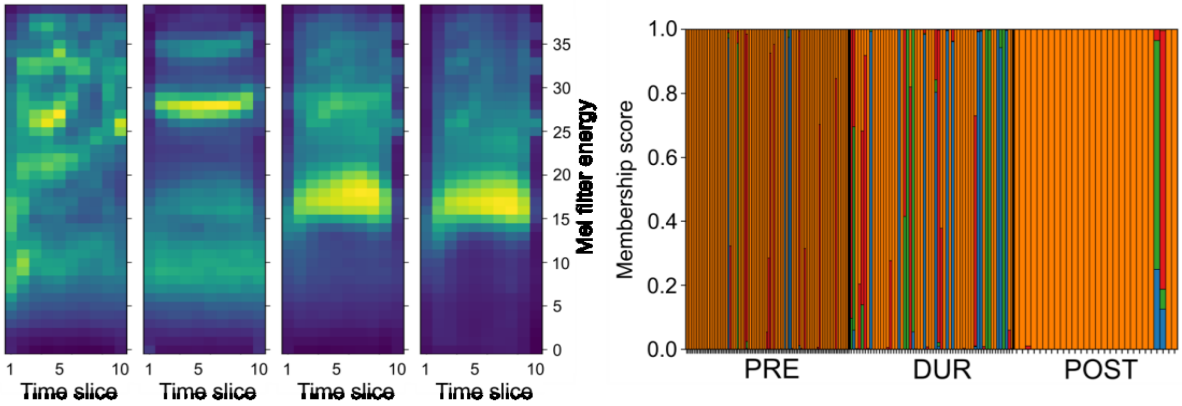

Figure 25: Example of vocal response of long-finned pilot whales to CTRL+ playbacks (gm13_169b, 4 fuzzy clusters, fuzziness = 1.07). Long-finned pilot whales produced more graded calls in DUR than in PRE and POST

5.4.3: Characterisation of call types used during sound exposure experiments

The call types used during exposure to LFAS was different from the call types used during exposure to MFAS (Figure 26A and B). In addition, for tag gm09_138b, the same call type was produced during exposure to both MFAS and LFASDS, and it was different from the call type produced during exposure to LFAS (Figure 26B).

The call types mainly used during MEKW and CTRL+ playbacks were the same for tag gm14_180a (Figure 27).

The call type used in the DUR of CTRL- playback for tag gm13_169a was higher in frequency than the other clusters of the deployment (Figure 24).

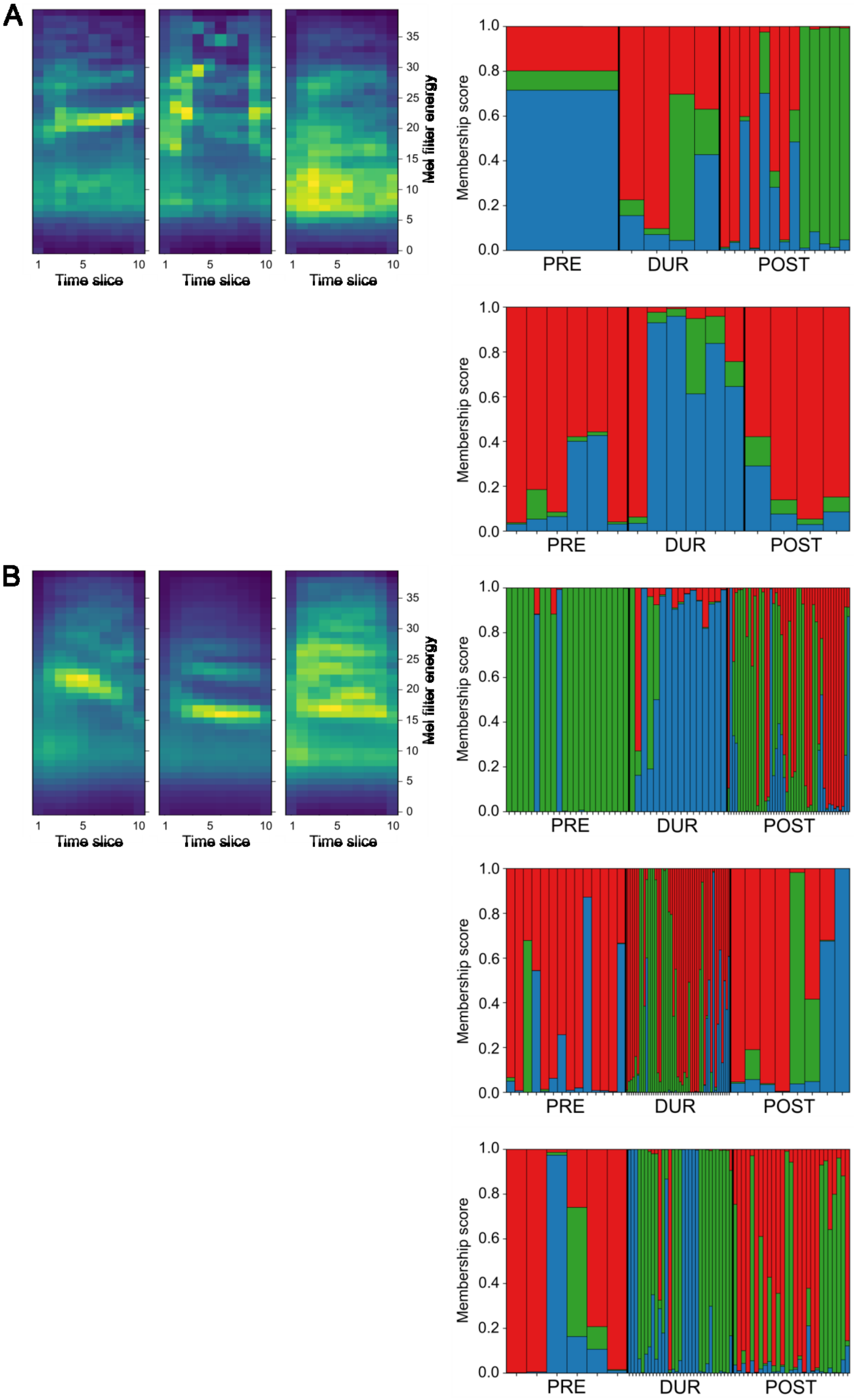
A
Time slice
Mel filter energy
Membership score
PRE
DUR
POST
B
Time slice
Mel filter energy
Membership score
PRE
DUR
POST

Figure 26: Examples of vocal responses of long-finned pilot whales to sonar signals. The left panels show apparent stereotypes. The right panels show memberships scores to each cluster. Left to right in left panels corresponds to bottom to top in right panels (blue, green, red) **A)** Responses of gm08_150c to LFAS (top) and MFAS (bottom); 3 fuzzy clusters, fuzziness = 1.17. The call type produced during exposure to LFAS (right cluster, in red) differed from the call type used during exposure to MFAS (left cluster, in blue) **B)** Responses of gm09_138b to LFAS (top), MFAS (middle), and LFADS (bottom); 3 fuzzy clusters, fuzziness = 1.09. The call type used during exposure to LFAS (left cluster, in blue) differed from the call type used during exposure to MFAS and LFASDS (centre cluster, in green)

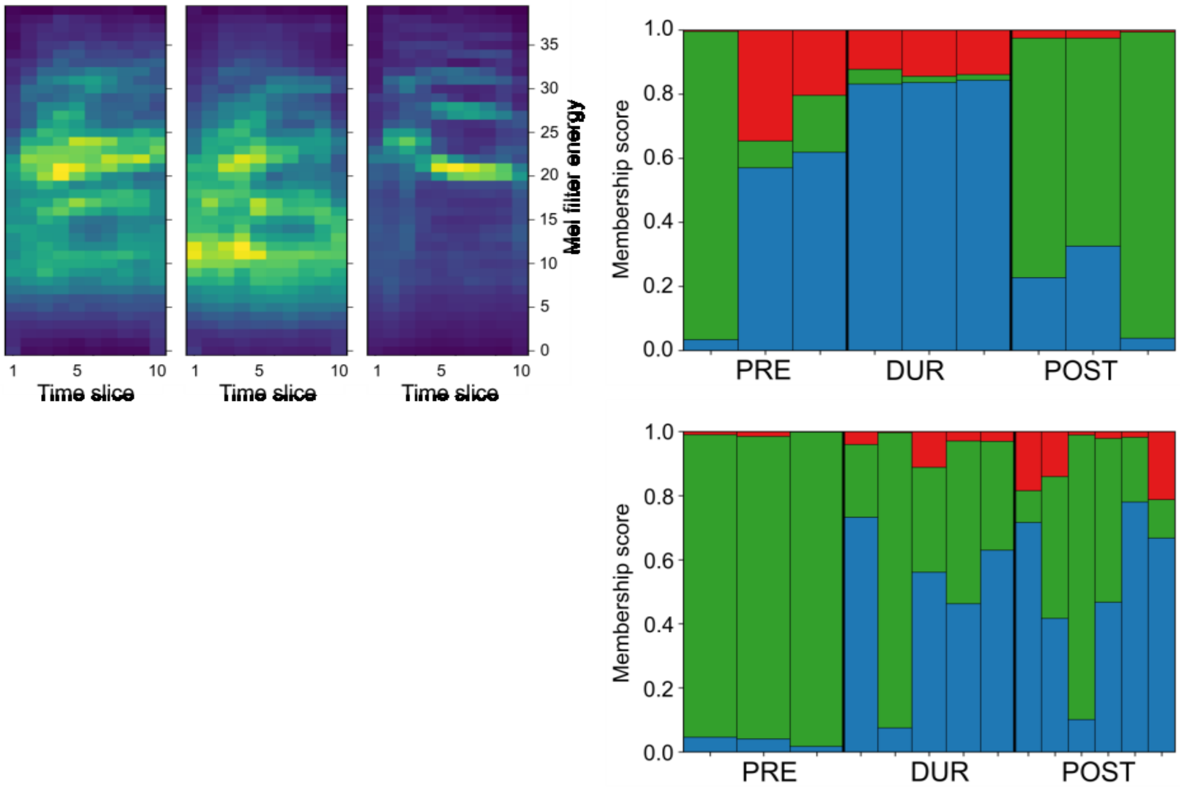

Figure 27: Vocal responses of tag gm14_180a to MEKW (top) and CTRL+ (bottom) playbacks. 3 fuzzy clusters, fuzziness = 1.18. The same call type (left cluster, in blue) was recorded during MEKW and CTRL+ playbacks

5.5: Discussion

By using an unsupervised classification procedure we developed in previous work (chapter 2), we aimed to quantify the changes in vocal activity (number of calls and time spent calling) at the group and the individual levels, as well as the changes in call type usage and call gradation of free-ranging long-finned pilot whales in response to naval sonar, playback of killer whale sounds, and respective control stimuli.

Overall, although responses were quite variable across individuals, our analyses showed evidence of changes in vocal behaviour in response to all stimulus types. Whales responded differently to sonar exposures, playback of killer whale sounds, and respective control stimuli. Figure 28 summarises the main outcomes of our study.

		LFAS		MFAS		LFASDS		SILENT		MEKW		CTRL+		CTRL-	
		PRE DUR	PRE POST	PRE DUR	PRE POST	PRE DUR	PRE POST	PRE DUR	PRE POST	PRE DUR	PRE POST	PRE DUR	PRE POST	PRE DUR	PRE POST
Vocal activity	Group	↑	↑	↑ ↓	↑ ↓	↓	↑ ↓	↑ ↓	↓	↑ ↓	↑ ↓	↑	↑	↓	↑ ↓
	Individual	↑	↑	↑ ↓	↑ ↓	↑ ↓	↓	↑ ↓	↓	↑ ↓	↓	↑	↓	↓	↑
Call type usage		↑ =	↑ =	↑	↑ =	↑	↑	↑ =	↑	↑ =	↑ =	↑ =	↑ =	↑	=
Call typicality		= ↓	= ↓	↑ = ↓	↑ = ↓	= ↓	= ↓	↑ = ↓	= ↓	↑ ↓	↑ ↓	↓	↑ = ↓	= ↓	↓

Figure 28: Summary of long-finned pilot whale vocal responses to sonar exposures, playback of killer whale sounds, and corresponding controls. Each cell can have three symbols: an arrow going up, an arrow going down, and an equal sign, which represent respectively an increase, a decrease, and the absence of directional change for the behavioural measure. When one type of change is consistent across individuals, only the corresponding symbol is represented. Therefore, the presence of several symbols means that vocal responses were variable between individuals. When the difference in magnitude between the vocal responses in DUR and in POST is consistent across individuals, the largest change is indicated with a larger arrow, and the smallest one with a smaller arrow

5.6.1: Vocal responses of long-finned pilot whales to naval sonars, playbacks of killer whale sounds, and control experiments

As predicted, long-finned pilot whales tended to increase their group and individual (group activity weighted by group size) vocal activity in response to sonar exposures, especially in response to LFAS exposures: in four out of five experiments, vocal activity was higher in PRE than in DUR, and further higher in POST than in DUR. They also increased vocal activity during CTRL+ playbacks and some replicates of MEKW playbacks. By contrast, we observed a tendency to decrease individual vocal activity during CTRL- playbacks and after silent vessel approaches (Figure 28).

Some call types were produced specifically during or after the exposure to acoustic stimuli. These call types could be triggered by the stimuli directly, or potentially used to coordinate the behavioural responses of group members in relation to the sound source. No single call type, such as general alarm or recruitment calls, appeared to be produced in response to acoustic disturbances across tag deployments. We did, however, observe similarities and differences in the call types produced in response to different stimuli within tag deployments. Long-finned pilot whales recorded by tag gm14_180a produced the same call type during MEKW and CTRL+ playbacks. For tag deployment gm08_150c, the call type produced during MFAS exposure was different from the call types recorded during LFAS exposure. For gm09_138b, the same call type was produced during exposure to MFAS and LFASDS, and another call type was produced during the LFAS exposure. Some call types were only produced during or after the end of sound exposures, and could underlie the behavioural responses of long-finned pilot whales to acoustic stimuli.

We observed no directional changes in typicality during sonar exposures (LFAS, MFAS, and LFASDS), silent vessel approaches, and MEKW playbacks (Figure 28). The only significant changes in the typicality of calls occurred during CTRL+ playbacks, with long-finned pilot whales producing more graded calls, and during the only POST of CTRL- playback (Figure 28). Therefore, behavioural responses to threatening or disturbing acoustic stimuli did not appear to include clear compression of information or increase in signal complexity.

Interestingly, we observed large changes in vocal behaviour during experiments designed as negative controls (SILENT for sonar exposures and CTRL- for playback experiments: Figure 28). Both kinds of experiment generated similar acoustic disturbances: continuous broadband noise with most energy below 10 kHz. Vocal responses to CTRL- and SILENT experiments could be compensatory mechanisms for masking. For instance, gm13_169a produced exclusively one call type during CTRL- playback, which was higher in frequency (most energy between the 30th and 35th Mel filters, which corresponds to 12-17 kHz) than both the other call types recorded by the tag and the frequency range with most energy in the CTRL- stimulus (below 10 kHz). An alternative explanation would be that CTRL- playbacks reduced the signal to noise ratio of low frequency calls, which results in only higher frequency calls being selected for the fuzzy clustering.

It seems that a passing vessel can elicit changes in vocal behaviour in long-finned pilot whales. Vocal responses to SILENT experiments occurred mostly during the POST phase. We did not observe similar changes in vocal behaviour in response to sonar exposures. Rather, the vocal behaviour of long-finned pilot whales during the POST of sonar exposures differed only slightly from their vocal behaviour during PRE. It could be that the presence of an intense acoustic stimulus (the sonar signals) elicited responses which overcame the responses to the passing vessel.

The low sample size of some experiment types makes our results likely to be driven by responses of single experiments. The confident generalisation of our conclusions will require additional experiments.

5.6.2: Integration of vocal responses into the set of behavioural responses

The most common behavioural responses of long-finned pilot whales to naval sonar were horizontal and vertical avoidance (Antunes et al., 2014; Wensveen et al., 2015a), and cessation of foraging (Miller et al., 2012; Sivle et al., 2012). More behavioural responses, with a higher probability to impact vital rates, were observed in response to LFAS than in response to MFAS (Miller et al., 2012). The results on vocal behaviour presented here showed that responses to LFAS exposure were very variable and that they can be larger than responses to MFAS and LFASDS. Vocal responses to MFAS and LFASDS were more consistent across individual than responses to LFAS. Miller and colleagues (2012) detected no behavioural response in horizontal movements, diving behaviour, and vocal activity to SILENT experiments. Our analysis showed that a change in vocal activity and the types of calls produced may occur in response to an approaching vessel (Figure 28).

Long-finned pilot whales were shown to match the frequency modulation pattern of sonar signals with their calls (Miller et al., 2012; Alves et al., 2014). Alves and colleagues (2014) observed sonar matching during exposure to MFAS and LFASDS. The call type produced by long-finned pilot whales during MFAS exposure in tag deployments gm08_150c and gm09_138b had narrower bandwidth and were closer in frequency range to MFAS signals than the other call types recorded by the tags (Figure 22A: call type increasing from the 20th to the 25th Mel filter, which corresponds to the 7-9 kHz band and Figure 22B: call type with most energy between the 15th and 20th Mel filter, which correspond to the 5-7 kHz band). The call type produced in response to LFASDS in tag gm09_138b matched the frequency-modulation pattern of LFASDS signals, but was in a higher frequency band (Figure 22B: decrease from the 20th to the 15th Mel filter, equivalent to a 7 to 5 kHz decrease).

Previous analyses revealed that long-finned pilot whales increased their group size, reduced inter-individual spacing, and approached the source broadcasting MEKW and

CTRL+ sounds, but that they barely responded to CTRL- playbacks (Curé et al., 2012, 2019). Here, we observed an increase in vocal activity during CTRL+ playbacks, as well as during some MEKW playbacks (although changes in vocal activity were more variable). Moreover, we found substantial vocal responses to CTRL-, with a reduction of vocal activity during the playbacks, and the production of higher frequency calls in one case (gm13_169a). No changes in additional behavioural metrics were reported for this individual (Curé et al., 2019).

5.6.3: Comparison of vocal responses to naval sonar and killer whale sounds

Overall, we reported larger changes in vocal behaviour in response to sonar signals than to MEKW sounds. However, the vocal changes observed during CTRL+ playbacks, for which acoustic signals had the same structure as LFAS signal (1-2 kHz hyperbolic upsweeps 1 s every 19s) but which were broadcasted at lower source levels (140-155 dB root-mean-square re 1 μPa for CTRL+, 152-214 dB root-mean-square re 1 μPa for LFAS), were smaller than responses observed during MEKW playbacks. Other responses of long-finned pilot whales differed between sonar exposures and killer whale playbacks: for instance, they avoided the source of sonar signals (Antunes et al., 2014), whereas they approached the source of MEKW and CTRL+ playbacks (Curé et al., 2019). It could be that differences in exposure conditions between sonar controlled exposure experiments and playback experiments influenced the behavioural responses of long-finned pilot whales.

During sonar exposures, the sound source was a large vessel which broadcasted intense sounds while approaching the focal whales from large distances. The source vessel could be perceived as a high-level threat, but the large initial distance between the source vessel and the focal whale would allow the use of evasive manoeuvres (Visser et al., 2016). Indeed, long-finned pilot whales did avoid the source vessel during sonar exposures (Antunes et al., 2014). During playback experiments, the source vessel is much smaller and stationary. Therefore, it could be perceived as a lower-risk threat than sonar source vessels (Visser et al., 2016). Moreover, the closer distance between the sound source and the focal whale may prevent the use of avoidance strategies. As a result, long-finned pilot whales may switch to close-range strategies toward threats such as the mobbing-like behaviour observed in response to playback (Curé et al., 2012, 2019).

Variations of the behavioural responses to different acoustic stimuli within each of these two contexts may reflect the level of threat perceived. For instance, MEKW sounds seem to be perceived as higher level threat than CTRL+ signals. Long-finned pilot whales stopped foraging and approached both the source of MEKW and CTRL+ broadcasts, however they increase group cohesion only in response to MEKW playbacks (Curé et al., 2019). Similarly, the changes in vocal behaviour we observed in during MEKW playbacks were larger than responses to CTRL+. A striking example is tagged whale gm14_180 which produced the same call type during MEKW and CTRL+ playback, but for which calls were more graded in response to CTRL+ than to MEKW.

Across the different types of sonar signals, we reported different vocal responses to LFAS than to MFAS and LFASDS. Vocal responses to LFAS were the largest, but also the most variable of responses to sonar signals. The call types used during LFAS also differed from the call types produced during MFAS and LFASDS. Miller and colleagues (2012) also reported that the responses to LFAS were stronger than the responses to MFAS. Therefore, LFAS seems therefore to be perceived as a particularly harmful stimulus, at least in some cases, compared to sonar signals in another frequency band (MFAS) or with a different frequency modulation pattern (LFASDS). It could be that LFAS signals resemble more typical MEKW calls. For gm14_180a, the call type produced during CTRL+ playback (playback of LFAS signals) was the same as the call type produced in response to MEKW playback.

The responses to sonar signals and killer whale sounds occurred mostly during sound exposures: during POST, vocal behaviour was mostly back to PRE levels (Figure 28). Such vocal responses could possibly be triggered by the acoustic stimulus itself. By contrast, responses to control experiments (SILENT, CTRL+, and CTRL-) induced vocal behaviour during POST (Figure 28).

5.6.4: Fuzzy-clustering-derived measures for the quantification of vocal behaviour.

The fuzzy clustering approach provides an advantageous method to quantify the variations of vocal behaviour across conditions within a graded framework compared to empirical operator-dependent classification methods (catalogues). The number of fuzzy clusters is lower than the number of call types that a human operator may define (Chapter 2). However, fuzzy clustering classification is much faster and objective than the audio-visual inspection of sounds by trained operators, and the quantitative information it yields can extend its classification into broad categories.

In some cases, the reduced number of clusters may preclude the detection of changes in vocal behaviour. For instance, the vast majority of the calls from gm13_169b were typical of one fuzzy cluster, and few changes in vocal behaviour were detected for this deployment.

The strict call selection procedure required to run the fuzzy clustering made it more suitable to study vocal responses to controlled exposures experiment than to playback experiments. Indeed, experiment phases were longer for controlled exposure experiments than for playbacks (40 vs. 15 minutes), which increases the number of call available to characterise vocal behaviour. In addition, sonar stimuli have a low duty cycle (1 s signals every 19 s), preventing too much overlap between the sound exposure and the emitted vocalisations by the exposed whales, whereas playback stimuli are much more continuous. As a result, we discarded more calls because of overlap with the experiment stimuli for playbacks than for controlled exposures, which further reduced the number of calls available to describe vocal behaviour during playbacks.

New generations of active sonar generating continuous signals (continuous active sonar, or CAS) are being developed to improve target detection. This raises further concerns about how CAS might affect the behaviour of cetaceans. In addition to the experiments presented in this study, we also exposed one group of long-finned pilot whales to continuous active sonar (CAS). CAS signals were 19-second-long 1 to 2 kHz hyperbolic upsweeps separated by 1 s silences. Due to its high duty cycle, CAS incurs a higher risk to mask biological signals than pulsed sonar (such as LFAS, MFAS, and LFASDS) and it would be particularly interesting to compare vocal responses to CAS and pulsed sonars. Preliminary analyses of this single conducted CAS exposure experiment indicated an increase in swimming speed and a possible switch of vocal production towards higher frequency calls during exposure to CAS (pers. obs.). The inclusion of continuous sonar in the fuzzy clustering framework will require some modifications of the procedure to accommodate the continuous nature of CAS which therefore overlaps all of the calls. Moreover, additional experiments would need to be conducted to be able to reach conclusions.

5.7: Aknowledgments

This study is part of the 3S (Sea mammal Sonar Safety) research project which was funded by: the United States Office of Naval Research, the Royal Norwegian Navy, the Norwegian Ministry of Defence, the Defence Research and Development Department of the Netherlands Ministry of Defence, and the French Ministry of Defence (DGA). We are grateful for the 3S scientific crew for their continuous efforts on the field and outside over the years. All experiments were conducted with permission from the Norwegian Animal Research Authority, and ethical approval from the University of Saint Andrews Animal Welfare and Ethics committee.

6: GENERAL DISCUSSION

My Ph.D. was centred on two research questions. First, how do cetaceans respond to heterospecific sounds? Second, how do responses to heterospecific sounds compare to how they respond to anthropogenic sounds?

With these questions in mind, I took part in an international effort within the 3S (Sea mammal Sonar Safety) consortium to equip free-ranging cetaceans, including humpback and long-finned pilot whales, in northern Norway with sound and movement recording tags, and to expose them to playbacks of killer whale sounds and to transmissions of naval sonar in controlled experimental conditions.

6.1: Responses of cetaceans to heterospecific sounds

To study the responses of cetaceans to heterospecific sounds, I focused on how humpback and long-finned pilot whales responded to playback of killer whale sounds. Killer whales are a cosmopolitan marine apex predator, which can prey upon a large variety of prey including most cetacean species. However not all interactions between killer whales and cetaceans are predatory (reviewed in Jefferson et al., 1991). Indeed, distinct killer whale ecotypes that exist in some populations have dietary specialisations: some prey upon marine mammals, while others feed on fish (reviewed in de Bruyn et al., 2013). These different killer whale ecotypes also have differences in production of sounds including vocal behaviour (Deecke et al., 2005; Foote and Nystuen, 2008; Deecke et al., 2011; Filatova et al., 2015a). Therefore, killer whale sounds may indicate a wide range of ecological consequences for other cetacean species. In the first part of my Ph.D., I investigated whether and how humpback whales discriminate between the sounds of different killer whale ecotypes.

Most cetacean species are reported to react strongly to playback of killer whale sounds. Behavioural responses include horizontal approach or avoidance, changes in diving activity, interruption of foraging and resting, and modifications of social and vocal behaviour (Table 11). The ability to discriminate acoustically between the sounds of killer whale ecotypes has been demonstrated in species from both suborders of cetaceans: the mysticetes, or baleen whales and the odontocetes, or toothed whales. Indeed, humpback whales (chapter 1 of this thesis) and long-finned pilot whales (Curé et al., 2019) showed different behavioural responses to playback of the sounds of familiar killer whales from a non-predatory ecotype and of unfamiliar killer whales of a potentially predatory ecotype. The same ability was demonstrated in harbour seals (pinnipeds): individuals avoided the source of familiar mammal-eating killer whale and unfamiliar fish-eating killer whale sounds, but not the source of familiar fish-eating killer whales (Deecke et al., 2002). Although the ability to discriminate between the sounds of killer whale ecotypes is present in widespread families of marine mammals, some species respond to killer whale sounds in a generic manner. Belugas and grey whales showed strong aversive responses to playback of unfamiliar fish-eating killer whales (Table 11). Such findings support Deecke's (2002) conclusion that non-familiar killer whales are perceived as a threat by potential prey, but that prey can learn that the specific sounds produced by non-threatening killer whales do not pose a threat.

In my Ph.D. work, I found that humpback whales responded differently to the sounds of herring-feeding killer whales, a familiar food competitor, and the sounds of marine mammal-eating killer whales, an unfamiliar potential predator, demonstrating that they were able to discriminate between the two types of killer whale stimuli (chapter 1). Humpback whales consistently approached the sound source and dove deeper during playback of herring-feeding killer whale sounds, while they tended to avoid, often strongly, the source of mammal-eating killer whale sounds. The responses of humpback whales to mammal-eating killer whale sounds were further influenced by the context of the playback presentation: avoidance responses were strongest during summer in an offshore area, while they were mitigated during winter in the Norwegian fjords, and the vertical diving aspect of the responses differed between these two contexts. I posited two possible explanations for this difference in behavioural response to mammal-eating killer whale sounds between presentation contexts. First, the lipid-store body condition of humpback whales during summer, after one breeding season and two migrations without foraging, is worse than during winter, at the end of the feeding season. Therefore, humpback whales in summer are both more vulnerable to killer whale attacks and under a stronger pressure to feed than in winter, which could affect their decision-making process. Alternatively, the presence of herring-feeding killer whales in large numbers during winter in the fjords may reduce the ability of humpback whales to consistently recognise mammal-eating killer whales as a threat.

6.2: Responses of cetaceans to anthropogenic sounds

To study the behavioural responses of cetaceans to anthropogenic sounds, I focused in the second part of my Ph.D. on how long-finned pilot whales responded to naval sonar signals. Naval sonar signals have been of particularly concern because they are generated at high source levels and have been associated with a wide range of pathological and behavioural impacts on cetaceans(reviewed in Southall et al., 2016).

Cetaceans exhibit a wide range of behavioural responses to sonar. Avoidance and interruption of activity appear to be the most common responses, but changes in social and vocal behaviour are also frequent (Table 11). The type and severity of behavioural responses to sonar vary between cetacean species. Some species, such as beaked whales, are very sensitive to sonar and display severe behavioural responses even at moderate received levels. Beaked whales avoid the source of naval sonar for tens of kilometres and may not return to the ensonified areas for several days (Miller et al., 2015). They stop foraging and vocalising in response to controlled sonar exposure experiments, and this response continues for several hours after the end of sonar exposures (Southall et al., 2016; Wensveen et al., 2019). Other species appear to be much less sensitive to sonar.

For instance, humpback whales and long-finned pilot whales exhibit shorter behavioural responses which initiate at higher received levels (Miller et al., 2012; Sivle et al., 2015).

Within species, the type and severity of behavioural responses to sonar vary according to various factors including signal type, behavioural context, and exposure conditions (Table 11). The influence of signal type on behavioural response differs between species (Harris et al., 2015). For instance, sperm whales ceased foraging in response to 1-2 kHz sonar but not during 6-7 kHz sonar transmissions (Miller et al., 2012). Behavioural responses also vary according to the behavioural state of cetaceans. For instance, blue whales were more responsive to 2.5-4 kHz sonar when foraging at depth than when foraging at the surface or not foraging (Goldbogen et al., 2013). The specific conditions of exposure to naval sonar also influence the behavioural responses of cetaceans. Humpback whales were more responsive to the first sonar exposure than to subsequent ones (Sivle et al., 2015), and humpback groups with calves were more likely to avoid sonars (Wensveen et al., 2017). The most severe behavioural response to sonar was observed in killer whales, the separation of a calf from its group, and it occurred during an 6-7 kHz sonar exposure which started closer to the animals than usual and took place in a particularly narrow fjord (Miller et al., 2012).

In my Ph.D. work, I identified and compared the vocal responses of long-finned pilot whales to naval sonar exposures and playback of killer whale sounds. Long-finned pilot whales are group-living cetaceans which are vocally active in almost all behavioural contexts (Visser et al., 2017). They produce a large variety of tonal, pulsed, and noisy sounds, as well as intermediate sounds between these categories, which are associated within vocalisations. Their large vocal repertoire contains some stereotyped calls, but most calls are of a graded nature which renders classification difficult. The first step of the analysis of long-finned pilot whale vocal behaviour in this thesis was the development of an unsupervised classification algorithm, based upon fuzzy clustering of Mel frequency cepstral coefficients. Fuzzy clustering provides a mechanism to account for the graded nature of long-finned pilot whale calls (chapter 2 of this thesis). In chapter 3, this algorithm was then used to describe the vocal responses of long-finned pilot whales to naval sonar exposures and playback of marine mammal-eating killer whale sounds. I observed diverse changes in the vocal behaviour of long-finned pilot whales in response to all sound stimuli (Figure 28). Vocal activity increased during and after exposure to 1 to 2 kHz low frequency active sonar, and decreased after silent vessel approaches. In addition, the vocal responses to 1 to 2 kHz naval sonar differed from the responses to 2 to 1 and 6 to 7 kHz pulsed active sonars (5% duty cycle), and were similar between playbacks of mammal-eating killer whale sounds and playbacks of 1 to 2 kHz hyperbolic upsweep signals. I did not detect specific response signals such as general alarm or recruitment calls, nor stimulus-specific call types, across experiment replicates.

6.3: Comparison of responses to heterospecific and anthropogenic sounds

One hypothetical framework to analyse the biological relevance of behavioural responses to sonar relies on the principle that costly behavioural responses to a risk-related stimulus are adaptive if the long-term benefits of the response exceed its short-term costs: the cost of the response itself and the loss of the fitness-enhancing benefits of the interrupted behaviour (Lima and Dill, 1990). Thus, the intensity of behavioural responses scales with the perceived risk associated to a given stimulus. For instance, costly behavioural responses to stimuli which indicate a heightened risk of predation have evolved because the long-term benefits of surviving overcome the costs of the responses. Therefore, comparing the behavioural responses to anthropogenic sounds, such as naval sonar, with the behavioural responses to natural threatening stimuli which indicate a heightened risk of predation, such as killer whale sounds for cetaceans, provides a framework to interpret the biological significance of animals' behavioural responses to anthropogenic sounds to animals (Frid and Dill, 2002).

Behavioural responses to naval sonar and killer whale sounds do have some similarities (Table 11). Humpback whales showed horizontal avoidance responses and cessation of foraging in response to both acoustic stimuli (chapter 1; Curé et al., 2015; Sivle et al., 2015). The responses of sperm whales to 1-2 kHz naval sonar and killer whale sounds were also similar: horizontal avoidance, cessation of foraging, and increase in the production of social sounds (Curé et al., 2016; Isojunno et al., 2016). The consistency and intensity of behavioural responses to killer whale sounds are generally higher than to naval sonar. Humpback whales avoided the sound source in seven out of eight playbacks of killer whale sounds, whereas they avoided the source of naval sonar in just 25-50 % of exposures (Curé et al., 2015; Sivle et al., 2015; Wensveen et al., 2017). In sperm whales, only playback of killer whale sounds elicited social grouping responses (Curé et al., 2016), and responses to killer whale sounds extended for longer after the end of the stimulus presentation than responses to naval sonar (Isojunno et al., 2016). The responses of long-finned pilot whales to playback of naval sonar signals were intermediate between the response to familiar fish-eating killer whales, a potential competitor for habitat use, and unfamiliar marine mammal-eating killer whales, a potential predator (Curé et al., 2019). They included joining with other subgroups (as in response to fish-eating killer whale sounds) and cessation of foraging (as in response to marine mammal-eating killer whale sounds). From these results, it appears that naval sonar is perceived as a threat by cetaceans, but that the level of threat perceived is less acute than the heightened risk of predation associated with the reception of potentially predatory killer whale sounds.

Some parts of the behavioural responses match between sonar exposure and predation risk indicators; however, there is not a strict concordance. Both killer whale sounds and naval sonar exposure provoke some specific behavioural responses. For instance, long-finned pilot whales approached the source of killer whale sounds and playback of naval sonar signals transmitted from a drifting boat, but avoided sonar sources transmitted from a moving vessel during controlled exposure experiments (Miller et al., 2012; Curé et al., 2019). Long-finned pilot whales gradually switched call types in response to both naval sonar exposure and killer whale playback, but the magnitude of the change in call type usage was greater in response to naval sonar than in response to playback of killer whale sounds (chapter 3). Long-finned pilot whale increase group size and cohesion in response to naval sonar exposure, tagging procedures, and killer whale playbacks; however they had disturbance-specific social responses (Visser et al., 2016). They increased vocal rate and approached the source of killer whale sounds; they increased surface resting and avoided the source of naval sonar; and they reduced surface logging and decrease vocal activity after tagging attempts (Visser et al., 2016). Playback stimuli were broadcasted by a small drifting vessel at medium range (around 800 m), naval sonar were transmitted by a large vessel which approached from large initial ranges, and tagging attempts involved repeated close-range approaches by a small vessel (Visser et al., 2016). The conditions of stimulus presentation, such as the source size and movement patterns, or the source levels of the broadcast, are relevant in the decision-making of responding individuals, and need to be included in the interpretation of the biological significance of behavioural responses to anthropogenic stimuli.

6.4: Methodological considerations

Overall, I had to work with datasets containing limited sample sizes during my Ph.D.: 4, 6, and 8 playbacks of killer whale sounds in Chapter 1 and between 2 and 5 replicates of each sound stimulus in Chapter 3. Gathering data is a global challenge in the study of the behaviour of free-ranging marine mammals. Over the course of my Ph.D., I took part in three fieldwork campaigns. The first one, in January 2017, was successful: over two weeks, we deployed two tags on humpback whales and performed four sound exposure experiments. In January 2018, the distribution of the study species had changes and we had to relocate the fieldwork site: over two weeks, and though we managed to deploy one tag on a humpback whale but could not perform any sound exposure experiment. In summer 2017, over five weeks of fieldwork, we tagged a single long-finned pilot whale and the tag came off before we could do any sound exposure experiment (although we did tag sperm whales and exposed them to naval sonar). As a result, I had to work on low sample sizes with partially dependent samples, due to imperfect replication schemes, and finding adapted statistical approaches to support my results has been a fundamental challenge in this thesis research.

However, marine mammal science is also an especially satisfying area of research. Every successful experiment is the result of team hard work and cooperation in successive steps: location of cetaceans, tag deployment, visual tracking, sound exposure experiment, and tag recovery. The datasets combining the record of the multiple sensors of the tags and visual observations from the deck of the research vessel swarm with details to look at to get insight into how cetaceans perceive their environment and interact with each other. Each fieldwork campaign builds on the successes and failures of the previous ones, as well as on the rapid development of tags and data processing and analysis methods (e.g. Wensveen et al., 2015a; von Benda-Beckmann et al., 2016; Cade et al., 2018).

Species		Responses to heterospecific sounds (killer whale sounds)	Responses to anthropogenic sounds (naval sonars)
Mysticetes	**Humpback whale** ***Megaptera novaeangliae***	**Approach (familiar FEKW)** **Deeper dives (familiar FEKW)** **Avoidance responses (unfamiliar MEKW)**[9] **Responses influenced by context of presentation**	Avoidance (1-2 and 6-7 kHz)[11] Cessation of foraging(1-2 and 6-7 kHz)[11] Lengthening of songs (150-320 Hz)[14] Habituation over successive exposures[11]
	Blue whale *Balaenoptera musculus*		Directional movement away from source (2.5-4 kHz)[14] Alteration of diving behaviour[14] Responses influenced by behavioural state[14]
	Grey whale *Eschrichtius robustus*	Avoidance (unfamiliar FEKW)[1]	Localised avoidance[14]
Odontocetes	Beaked whales		Prolonged avoidance[10,14,19] (Approaches at low received levels)[19] Prolonged cessation of foraging and vocal activity[10,14,19] Long ascent phases[10,14,19] Longest and deepest dive recorded for northern bottlenose whales *Hyperoodon ampullatus* (1-2 kHz)[10,14]
	Long-finned pilot whale ***Globicephala melas***	Approach (all killer whale sounds)[6,18] Join other groups (familiar FEKW)[6,15,18] Cessation of foraging (unfamiliar MEKW)[18] Increase in group cohesion (unfamiliar MEKW)[15,18] **Changes in call type usage (unfamiliar MEKW)**	Avoidance (1-2 kHz, 6-7 kHz)[4,8,12,14] Increase in group size and cohesion (1-2 kHz, 6-7 kHz)[4,15] Variations of vocal activity (1-2 kHz, 6-7 kHz)[4,8,15] Matching of sonar signals (1-2 kHz, 6-7 kHz)[4,8] **Changes in call type usage (1-2 kHz, 6-7 kHz)** Cessation of foraging (1-2 kHz)[4,5,14] Return to normal behaviour after exposure[4,8]
	Sperm whale *Physeter microcephalus*	Horizontal avoidance (unfamiliar MEKW)[13] Cessation of foraging (unfamiliar MEKW)[13,16] Cessation of resting (unfamiliar MEKW)[13,16] Increase in social sound production (unfamiliar MEKW)[13]	Horizontal avoidance (1-2, 6-7 kHz)[13,14] Increase in social sound production (1-2, 6-7 kHz)[13] Cessation of foraging (1-2 kHz)[5,14,16] Cessation of resting (1-2 kHz)[5,14,16]

		Grouping behaviour (unfamiliar MEKW)[13] Responses prolonged after end of playback[13]	
	Short-finned pilot whales *Globicephala macrorhychos*	Approach (unfamiliar MEKW)[17] Stronger responses to calls containing non-linear phenomena[17]	
	Risso's dophins *Grampus griseus*	Avoidance (unfamiliar MEKW)[17] Stronger responses to calls containing non-linear phenomena[17]	
	Killer whale *Orcinus orca*	No response (familiar FEKW conspecifics)[5]	Avoidance responses (1-2, 6-7 kHz)[5,14] Increase in call rate (1-2, 6-7 kHz)[5] Shift to high frequency whistles (1-2, 6-7 kHz)[5] Increase in group cohesion (1-2, 6-7 kHz)[5] Interruption of foraging (6-7 kHz)[5,14] Separation of one calf from its group (6-7 kHz)[5,14]
	Beluga whale *Delphinapterus leucas*	Avoidance (FEKW)[2] Silencing (FEKW)[2]	
Pinnipeds	Harbour seal *Phoca vitulina*	Avoidance (unfamiliar MEKW)[3] Avoidance (unfamiliar FEKW)[3] No response (familiar FEKW)[3]	

Table 11: Responses of marine mammals to heterospecific sounds (killer whale sounds) and anthropogenic sounds (naval sonars). FEKW: fish-eating killer whale sounds; MEKW: marine mammal-eating killer whale sounds. Results for this Ph.D. are shown in bold. Sources: 1: Cummings and Thompson, 1971; 2: Fish and Vania, 1971; 3: Deecke et al., 2002; 4: Miller et al., 2012; 5: Sivle et al., 2012; 6: Curé et al., 2013; 7: Alves et al., 2014; 8: Antunes et al., 2014; 9: Curé et al., 2015; 10: Miller et al., 2015; 11: Sivle et al., 2015; 12: Wensveen et al., 2015a; 13: Curé et al., 2016; 14: Southall et al., 2016; 15: Visser et al., 2016; 16: Isojunno et al., 2016; 17: Bowers et al., 2018; 18: Curé et al., 2019; 19: Wensveen et al., 2019

6.5: Conclusion

Cetaceans are able to process the sounds produced by other species to infer information about their ecological relationship with the vocalising individuals, and respond in appropriate ways. The fineness of the information they obtain from heterospecific sounds vary across species, but fine discrimination abilities exist in both mysticete and odontocete cetaceans.

Among the many behavioural responses observed to anthropogenic sounds, some are reminiscent of anti-predator behaviours and draw the picture of anthropogenic sounds being perceived as a threat not as acute as predation risk. However, some aspects of behavioural responses are specific to natural or anthropogenic stimuli.

More information is necessary to get a more detailed insight of interspecific acoustic interactions in cetaceans and of the impacts of anthropogenic sounds on marine environments.

Additional playbacks of killer whale sounds from different ecotypes would be necessary to highlight which acoustic features underlie the discriminative abilities of humpback whales and other species. We hypothesised that tail slaps and echolocation clicks were key elements for the identification of herring-feeding killer whales by their sounds. How would humpback whales react to chimera stimuli, such as mammal-eating killer whale sounds associated with tail slaps and/or echolocation clicks, or herring-feeding killer whale calls alone? Playback of the sounds of other species than killer whales may be used to discover whether cetaceans respond to all unfamiliar whale sounds in the same way, or if they can make some sort of inference from the acoustic properties of the sounds, such as determining the size of the callers, or their number.

More behavioural response studies are needed to untangle the behavioural response of cetaceans to naval sonars. Varying the exposure conditions, such as the signal type (frequency range, frequency modulation pattern, source level, duty cycle, etc.), the size and movement pattern of the source vessel, and the ecological context of the exposure (behavioural state, topography, breeding vs. feeding grounds, etc.) could provide important insight into how cetaceans perceive and respond to naval sonar.

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Education/Employment

DGA, French Ministry of Defence/UMRAE, Ifsttar-Cerema **Rouen, France**
Post-doc *incoming: February-July 2020*
Analysis of the collective responses of sperm whale to naval sonar transmission

University of Strasbourg **Strasbourg, France**
Ph.D. in ecology-ethology *in progress: September 2016-January 2020*
Behavioural responses of cetaceans to natural and anthropogenic sounds
Supervised by Dr. Valérie Dufour (Univ. of Strasbourg, France)
Co-supervised by:

- Dr. Charlotte Curé (UMRAE, Ifsttar-Cerema, Rouen, France)
- Dr. Patrick Miller (Univ. of Saint-Andrews, United-Kingdom)

Ecole Normale Supérieure de Lyon (ENSL) **Lyon, France**
Master's Degree, major in Life Sciences - Earth and Universe Sciences *2015-2016*
Preparation for the highest level national certification for the ability to teach biology and earth sciences
Eligible

ENSL **Lyon, France**
Master's Degree, major in Biology, 13.80/20 *2013-2015*
Subects included: Evolution, Ecology, Complex systems modelling, Paleobiology

ENSL **Lyon, France**
Bachelor's Degree, major in Biology, 12.98/20 *2012-2013*
Subjects included: Statistics, Evolution, Informatics, Biological systems modelling, Population genetics, Development, Cellular and molecular biology

Bel Air High School **Saint-Suzanne, France**
High school diploma, highest distinctions *June 2010*

Experience

Research

Sea Mammals Sonar Safety consortium (3S) **Northern Norway**
Field campaigns during Ph.D. *2016-present*
Playback of killer whale sounds and controlled exposure to sonar transmission on free-ranging cetaceans.
Tasks:

- *Tag technician*: calibration and setting of the tags before deployment, data processing and checking after tag recovery, investigation of tag technical issues;
- *Playback operator*: installation of the playback material, testing of the material, execution of the broadcasts during experiments;
- *Marine mammal observer*: visual detection and tracking of cetaceans, telemetry to identify tagged whales and to retrieve tags after detachment:
- Photos for individual identification.

IPHC-DEPE **Strasbourg, France**
Vocal repertoire and individual vocal signature in the Rook *January-June 2015*
21-week-long internship under the supervision of Dr. Charlotte Curé and Dr. Valérie Dufour. Published article (first author).

- Bird feeding;
- Acoustic and behavioural data collection;
- Data analysis.

University Claude Bernard **Lyon, France**
Gene expression evolution during six convergent habitat shifts *September-December 2014*
14-week-long innternship under the supervision of Dr. Tristan Lefébure and Dr. Marie Sémon.

- Individual collection in the field;
- Transciptomic data analysis;
- Development of data treatment techniques.

University of York **York, United-Kingdom**
Influence of the zoo environment of the stress level of captive chimpanzees *February-June 2014*
14-week-long internship under the supervision of Dr. Katie Slocombe. Co-author in a published article.

- Behavioural data collection;
- Data analysis.

IPHC-DEPE **Strasbourg, France**
Vocal communication in the Rook *July-August 2013*
7-week-long internship under the supervision of Dr. Valérie Dufour.

- Bird feeding;
- Acoustical and behavioural data collection;
- Data analysis.

Teaching

University of Strasbourg **Strasbourg, France**
Animal biodiversity undergraduate student monitoring mission *September-December 2016*
Monitoring of practicals and tutorials, and participation in the elaboration and correction of written and practical tests.
Teaching in French, with support documents in English.

Languages

French: Native speaker

English: C1-C2 *CLES2 (french certification)*

German: A2

Italian: A2

Computer skills

Office: MicrosoftOffice, OpenOffice, LaTeX **Biliography**: Zotero, Mendeley

Statistics: R, python **Programming**: Matlab, python, perl

Other

Volleyball: Opposite hitter **Driving licence and own car**: yes

Membership: SFECA (french society for the study of animal behaviour

Publications

- Benti B, Miller PJO, Biuw M, and Curé C (submitted to Animal Behaviour) *Behavioural responses to the sounds of heterospecifics are influenced by trophic relationships and ecological contexts*
- Benti B, Curé C, and Dufour V (2019) *Individual signature in the most common and context-independent call of the Rook (Corvus frugilegus)* The Wilson Journal of Ornithology 131(2):373-381. DOI: 10.1676/18-41
- Lam FP, Fvadsheim PH, Isojunno S, van IJsselmuide S, Wensveen PJ, Hansen RR, Siemensma M, Sivle LD, Kleivane L, López LMM, Benti B, Dekeling R., and Miller PJO (2018) *Behavioural response study on the effects of continuous sonar and the effects of source proximity on sperm whales in Norwegian waters: the 3S-2017-CAS cruise report* TNO Report 2018 R10958. URL: https://repository.tudelft.nl/view/tno/uuid:5d9fdf72-ac5e-4cb1-81d5-659d62ff5d1a
- Wallace EK, Altschul D, Körfer K, Benti B, Kaeser A, Lambeth S., Waller BM, and Slocombe K (2017) *Is music enriching for group-housed captive chimpanzees (Pan troglodytes)?* PLoS ONE 12(3):e0172672. DOI: 10.1371/journal.pone.0172672

Communications

Animal Linguistics **Paris, France**
Poster *June 2019*
Exploring an innovative classification method for characterizing the vocal repertoire of cetacean species, the long-finned pilot whale

SFECA colloquium **Lille, France**
Poster *June 2019*
Fuzzy clustering for the classification of marine mammal calls - performance comparison with a catalogue-based approach

ESOMM **The Hague, Netherlands**
Poster (presented by Miller PJO) *September 2018*
Humpback whales can discriminate between the sounds of different killer whale ecotypes

Biologging symposium **Constance, Germany**
Poster *September 2017*
Can humpback whales discriminate between the sounds of different killer whale ecotypes?

SFECA colloquium **Gif-sur-Yvette, France**
Talk, Best student talk award (Prix Castor) *May 2017*
Discrimination of the sounds of different killer whale ecotypes by humpback whales

Benjamin BENTI

Responses of two cetacean species to natural and anthropogenic sounds

Résumé

Il est crucial pour les animaux de se servir des stimuli environnementaux pour localiser et évaluer la qualité des ressources et menaces présentes dans les environs. Dans l'océan, les stimuli acoustiques sont privilégiés. Les cétacés sont susceptibles de détecter les sons produits par une multitude de sources, dont les autres espèces et les sources anthropiques. J'ai étudié les réponses comportementales de deux espèces de cétacé, la baleine à bosse et le globicéphale noir, à des stimuli acoustiques d'origine naturelle (sons d'orques) et anthropique (sonars militaires). J'ai montré que les baleines à bosse sont capables de différencier les sons de différents écotypes d'orques. J'ai développé un algorithme de classification des vocalisations animales qui prend en compte la nature graduelle de certains répertoires vocaux et ai utilisé cet algorithme pour décrire les réponses vocales des globicéphales noirs aux sons d'orques et aux sonars militaires.

Mots-clés : cétacés, acoustique, sons anthropogénique, interactions interspécifiques

Résumé en anglais

It is crucial for animals to use environmental stimuli to locate and evaluate the quality of resources and threats present in their surroundings. In the ocean, acoustic stimuli are privileged. Cetaceans are susceptible to detect acoustic stimuli produced by a multitude of sources, including other cetacean species and anthropogenic sources. I studied the behavioural responses of two cetacean species, the humpback whale and the long-finned pilot whale, to natural and anthropogenic acoustic stimuli (respectively killer whale sounds and naval sonars). I found that humpback whales were able to discriminate between the sounds of different killer whale ecotypes. I developed an unsupervised classification algorithm which takes into account the graded nature of animal vocalisations, and used this algorithm to describe the vocal responses of long-finned pilot whales to killer whale sounds and naval sonars.

Keywords: cetaceans, acoustics, anthropogenic sounds, interspecific interactions