ESTUDIOS ACÚSTICOS DE COORDINACIÓN SOCIAL, ECOLOGÍA TRÓFICA Y CARACTERIZACIÓN DEL HÁBITAT DE CETÁCEOS DE BUCEO PROFUNDO EN CANARIAS

ACOUSTIC STUDIES OF SOCIAL COORDINATION, TROPHIC ECOLOGY AND HABITAT CHARACTERIZATION OF DEEP-DIVING CETACEANS IN THE CANARY ISLANDS

Doctoral Thesis
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Universidad
de La Laguna

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CERTIFICA

Que la tesis doctoral titulada “Estudios acústicos de coordinación social, ecología trófica y caracterización del hábitat de cetáceos de buceo profundo en Canarias” presentada por D. Jesús Alcázar Treviño, ha sido realizada bajo su dirección en el Departamento de Biología Animal, Edafología y Geología de la Universidad de La Laguna.

Así mismo, la Dra. Dña. Patricia Arranz Alonso, Investigadora Agustín de Betancourt del Departamento de Biología Animal, Edafología y Geología de la Universidad de La Laguna

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Que es la codirectora de la citada tesis.

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ACOUSTIC STUDIES OF SOCIAL COORDINATION, TROPHIC ECOLOGY AND HABITAT CHARACTERIZATION OF DEEP-DIVING CETACEANS IN THE CANARY ISLANDS.

PhD Program in Biodiversity and Conservation of the Universidad de La Laguna, research line in Biodiversity and Conservation of the Marine Environment

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In the following report I support the International Mention for the Doctorate for the following research work: “Acoustic studies of social coordination, trophic ecology and habitat characterization of deep-diving cetaceans in the Canary Islands”, presented as a PhD by Jesús Alcázar-Treviño at La Laguna University, Canary Islands, Spain (ULL), and supervised by Natacha Aguilar de Soto and Patricia Arranz Alonso (ULL).

This work represents a substantial contribution to the body of scientific knowledge in a very active area of research that uses passive and active acoustics to study the behavior of marine organisms and thereby inform details of their functional ecology. Cutting-edge technology is used in novel ways to discern patterns that would otherwise be imposible to study. Jesús used multi-sensor acoustic recording tags to study the foraging behavior of two hard-to-study beaked whales species and found that these species are behaving more like social herbivores than like social predators in that their foraging is only loosely coordinated. That coordination is largely limited to the maintainance of acoustic synchrony in their diving. The purpose of this synchrony (and other details of their movement) appears to be a deliberate attempt to minimize the risk of predation by their primary threat … killer whales. Jesus also used data from these biologging tags to study the comparative foraging strategies of five deep-diving cetacean species at a variety of locations worldwide. He shows that all five species have unique and different foraging strategies and that some of these differences help explain the intra-species aggression that has been witnessed by others. Finally, Jesus studies the acoustic environment in the vicinity of the Canary Islands and finds an evening chorusing of biological origin, posibly mesopelagic fish. He combines both passive and active acoustic methods to study these organisms and their behavior.

This dissertation is distinguished in both the quality and the originality of the work. The beaked whale studies are directly relevent to my research, and I have already cited the publications from Chapters 2 & 3 in my recent publications. These species are particularly hard-to-study, and this work required originality and creativity to overcome these impediments.

Overall, this dissertation meets or excedes all international standards for a PhD. I heartily recommend that this thesis be awarded an International Mention.

Jay Barlow

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October 20, 2021

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In the following report I support the International Mention for the Doctorate for the following research work: *"Acoustic studies of social coordination, trophic ecology, and habitat characterization of deep-diving cetaceans in the Canary Islands"* presented by Jesús Alcázar Treviño at La Laguna University, Canary Islands, Spain (ULL) and supervised by Dr. Natacha Aguilar de Soto and Dr. Patricia Arranz Alonso (Universidad de La Laguna, Spain).

This thesis advances our understanding of the foraging ecology, sociality, and habitat use of one of the most enigmatic groups of whales, the beaked whales. Using cutting-edge tagging technology Jesus, sets first the stage in Chapter 1 by describing the high group synchronicity of beak whale's echolocation behavior during foraging dives, and their coordinated yet unpredictable and quite surfacing patterns. Together, these behaviors appear to minimize predation risk by killer whales in the study area. In Chapter 2, Jesus tests the potential trade-offs of such group synchronicity. Do group synchrony in echolocation generates signal interference that impacts foraging performance? Do animals eavesdrop on each other's signals? Jesus, test several predictions and findings show that group diving and echolocation synchronization do not reduce foraging performance. In Chapter 3, Jesus used whale's searching clicks and their echoes from the seafloor to describe the foraging niche of each species, and their overlap. The results show temporal and depth partitioning of the foraging space between species. The study also highlights the potential for foraging habitat lost due to bottom-trawling and other destructive fishing practices in the study areas. In the final Chapter, Jesus presents a soundscape analysis of the study area combining data from chorusing noise levels and the Deep Scattering Layer (DSL) and find a correlation between chorusing events and upward migration of the DSL at dusk.

This thesis is based on exhaustive field work, cutting edge technology (DTAG), thorough data processing and analysis, and well thought out statistical analysis. Jesus's dissertation provides a strong and exciting scientific contribution to the biology of beaked whales. The importance of his work to the general scientific community is reflected in that two chapters are already published. The first chapter made it to the public via various social media (IFLS, Phys.org, Science News, etc.) educating the public about the important of these mysterious mammals and inspiring many graduate students including those in my lab. I would like to congratulate Jesus and both of his advisors, Natasha, and Patricia for this important contribution. I recommend this thesis be awarded an International Mention for the Doctorate.

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A mis padres

y a mi tía Victoria

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Permítanme que dedique unas palabras en inglés a continuación para agradecer a colaboradores internacionales. There are two researchers that have acted as mentors for several part of this thesis, and I really appreciate their help, effort, and kindness: Mark Johnson and Peter Madsen, it has been an honour working with you. Thanks for sharing your knowledge and incredible data with me.

I had the great opportunity to visit the Institute of Marine Research (IMR) in Bergen, Norway, as part of my PhD studies. Thank you very much Rolf Korneliussen for supervising me there, and for enrolling me in the course on the LSSS software. Even during a pandemic, you allowed me to stay with your excellent group and to learn from your experience with scientific echosounders. I would also want to thank Egil Ona for your kindness during my stay, and for your help in the calibration of our echosounder.

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I would like to thank the organizers of the Acoustic Communication course from the University of Southern Denmark (SDU) and all the professors that taught us. It was an amazing opportunity for me to attend such a prestigious course, with great teachers and colleagues. A special thanks to Pernille and Chloe, it has been a pleasure to work with you again and to (virtually) attend to your respective thesis defence.

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Durante los años del máster y de tesis, tuve la inmensa suerte de participar en muchas campañas de zifios en El Hierro. Me gustaría dedicar un agradecimiento especial a las patronas y coordinadoras de esas campañas, Agus Schiavi y Crístel Reyes. Gracias por compartir conmigo tantas aventuras en el Mar de Las Calmas, por enseñarme tanto de los zifios herreños y por vuestra profesionalidad. Gracias Agus por todo el trabajo que hemos compartido después, y toda tu ayuda durante esta tesis, ¡pum para arriba!

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Data for this PhD was collected thanks to funds from several projects, from both national and international organizations, which are acknowledged in each manuscript forming the Chapters of this thesis.

INDEX / ÍNDICE

Notice that for this thesis each chapter has its own list of literature references, figures and tables are enumerated in order of appearance within each chapter and are independent between chapters. The published papers are literally reproduced in the text.

This thesis is the product of close collaboration with a number of colleagues, mostly the co-authors of each manuscript but also collaborators in the field for data-gathering. All of them deserve proper recognition, as shown in the co-author contributions and acknowledgements sections of each chapter.

EXTENDED SUMMARY

Sound is key for deep-diving cetaceans foraging at the twilight zone of great oceanic depths. Here, these predators use both their own active acoustic signals and passive monitoring to probe their surroundings and to mediate biological functions from courtship to predator/prey detection. Thus, studying the bioacoustics of these soniferous animals and their acoustic environment can reveal relevant aspects of their biology and behaviour that cannot be directly observed, from the individual to the group and to their relation with their habitat. This thesis contributes knowledge about the behavioural ecology of deep diving whales and the acoustic characteristics of their deep-water habitat. This information is essential to understand their life requirements and thus basic to design measures towards the conservation management of their populations. This, in turn, repercutes in the conservation of the deep-water ecosystem, as deep diving odontoceti act as top-down regulators in oceanic trophic webs. Most biologging studies of deep-diving whales have described the behaviour of individuals, this thesis moves from the one to the group and to the habitat, addressing four main hypotheses and objectives: *i*) Group-living beaked whales are obligated vocalisers to forage by echolocation at depth. These sounds can attract acoustic guided predators such as killer whales. Beaked whales are defenceless if found as their small social units are not fitted for group defence from predators. Then, beaked whales should aim to reduce their detectability by killer whales. This was tested analysing animal-borne biologging data rendering observations of highly synchronized diving and vocal behaviour of groups of beaked whales and we modelled how this synchronization unavoidably reduces predation risk from orcas; *ii)* Synchronized vocalizations can generate interferences with conspecifics vocalising at the same time, as well as render foraging benefits to individuals eavesdropping on the success of other group members. We used beaked whales as model organisms to study cost-benefit balance in acoustic social foragers, quantifying vocal rates of Blainville's and Cuvier's beaked whales while foraging, and the possible effects of group size on these rates. Results have inferences on evolutionary limitations to group size in beaked whales. Also, results are applicable to improve the reliability of estimations of density of beaked whales from passive acoustic monitoring (PAM); *iii)* Deep-diving whales relate with other species in addition to their own. Species may compete, collaborate or ignore each other, and this will be dictated

by their niche overlap and their behavioural characteristics. We studied foraging habitat overlap of five deep-diving odontoceti in the water column from epi- to meso-, bathy- and bentho- pelagic habitats; their foraging niche width (use of these layers) and its diel variation, and related the results with observations of agonistic encounters or spatial coexistence among studied species. In the last chapter the thesis moves from the whales to their habitat: *iv)* the mesopelagic realm and the migration of the Deep Scattering Layer (DSL) from meso- to epipelagic waters were found to be highly important for the five studied deep-diving species. Biomass estimations of mesopelagic fauna still differ within orders of magnitude and it would be timely to improve these estimations towards ecosystem-based management of emergent proposals of fishing the DSL considering non-human predators. The thesis used PAM to investigate a potential acoustic signature of the migrating DSL indicated by an evening chorus coincident with this migration. This was related with simultaneous active acoustic data in order to explore the possibility of estimating density of migrating DSL organisms from chorusing levels.

The main methodological contributions of this thesis are the following:

I. To gather and use biologging data from DTAGs (digital tags) deployments to quantify the coordination of dive profiles and acoustic behaviour of beaked whales living in social groups and how this would reduce the probability of being detected by acoustic-guided predators such as orcas.

II. To combine biologging data from DTAGs deployed singly and in pairs of whales within the same group and to analyse click and buzz rates, heading and depth data from acoustic recordings and orientation sensors (i.e., magnetometers and accelerometers) to investigate potential trade-offs of sociality for extreme deep-diving Blainville`s and Cuvier's beaked whales i.e., acoustic interference and eavesdropping, cooperative foraging or competition for prey.

III. To estimate the vertical foraging habitat overlap and segregation between five species of deep diving odontocetes by combining biologging data, i.e., the analysis of foraging depth and altitude above the seafloor, with stomach content data from the bibliography and adapting foraging niche index equations to study the foraging habitat, i.e., Levin's and Pianka's indexes of foraging niche width and overlap, respectively.

IV. The simultaneous use of active and passive acoustic instruments to sample the water column in the open ocean to characterize an evening chorus and relate it to the diel vertical migration of part of the DSL.

The main scientific contributions of this thesis are:

I. Analysing biologging data from Blainville's and Cuvier's beaked whales (14 and 12 tagged whales, respectively), we showed that these animals overlap foraging times by 98% with group members and perform a coordinated and silent ascent after foraging at great depths, in unpredictable direction and covering a mean of 1 km from their last vocal position. The highly synchronised and stereotypical diving and acoustic behaviour of groups of beaked whales can be explained by the evolution of behaviour in a soundscape of fear of predation. However, this successful predator-abatement strategy has turned partly maladaptive in the Anthropocene, when naval sonar induced extreme responses lead to mass strandings of beaked whales.

II. DTAG data from deployments on 16 Blainville's and 10 Cuvier's beaked whales off the Canary Islands and Ligurian Sea shows that group members could hear their companions for a median of at least 91% of the vocal foraging phase of their dives. This enables whales to coordinate their mean travel direction despite differing individual instantaneous headings as they pursue prey on a minute-by-minute basis. While beaked whales coordinate their echolocation-based foraging periods tightly, individual click and buzz rates are both independent of the number of whales in the group. Thus, their foraging performance is not affected by intra-group competition or interference from group members, and they do not seem to capitalize directly on eavesdropping on the echoes produced by the echolocation clicks of their companions. We conclude that the close diving and vocal synchronization of beaked whale groups that quantitatively reduces predation risk has little impact on foraging performance.

III. This thesis analysed 81 DTAG deployments in subtropical to warm temperate waters on adult whales of five deep-diving species: 16 Blainville's (Md) and 10 Cuvier's (Zc) beaked whales, 27 short-finned pilot whales (Gm), 12 Risso's dolphins (Gg) and 16 sperm (Pm) whales. Pianka's Index values of niche overlap varied for all pairs of species between day and night due to differences in the adaptations of each species to the nictemeral migration of the DSL. Values were high (>0.9) during the day among Md, Zc, Gm and Pm because they all foraged mainly within the mesopelagic realm (between 200-1000 m depth). Values were lower (0.5 to 0.8) during the night as Zc shifted to the bathypelagic. Gg had low overlap with all the others but overlapped with Gm only at night, when both exploited the upwards migration of the DSL to forage in the epipelagic (0-200 m). This did not occur for any of the other species. All the species preyed on benthopelagic resources (at < 100 m of the seafloor), but this was less important for Gm (6 & 0% for day and night, respectively) than for the others (5-31% overall). Niche overlap can contribute to explain observations of agonistic behaviours of Gm and Gg towards Pm. These species can be territorial thanks to their numerous groups. In contrast, Md and Zc can coexist in the same area in spite of high niche overlap, probably because their small groups do not support territorial confrontations with other species. Thus, bevioural ecology can help to understand the distribution of these deep-diving apex predators. The reliance of all species on meso- and benthopelagic resources indicates that bottom-trawling, deep-sea mining and DSL fisheries can pose threats to these protected apex predators of the deep ocean.

IV. The report for the first time in the Atlantic Ocean of an evening chorus similar to findings in the Pacific and Indian oceans. The chorus occurs concurrently with the upwards migration of the DSL at dusk. Moreover, the maximum received level of the chorus is positively correlated with the acoustic backscatter of DSL organisms that migrate from mesopelagic to epipelagic depths at dusk. We conclude that mesopelagic fish are most likely responsible for the chorusing event by degasification during the ascent. Measures of chorus levels could provide estimates of the abundance of mesopelagic organisms, some of them targeted by apex predators such as deep-diving cetaceans.

RESUMEN

El sonido es esencial para los cetáceos de buceo profundo que se alimentan en las grandes profundidades del océano, en la zona crepuscular. Aquí, estos depredadores usan tanto sus propias señales de acústica activa como el monitoreo pasivo para sondear el entorno y para mediar funciones biológicas desde el cortejo a la detección de presas y depredadores. Por tanto, estudiar la bioacústica de estos animales sonoros y su hábitat puede revelar importantes aspectos de su biología, así como comportamientos que no pueden observarse directamente, tanto a nivel individual como de grupo, y su relación con el hábitat. Esta tesis contribuye a la adquisición de conocimientos sobre la ecología del comportamiento de cetáceos de buceo profundo y las características acústicas de su hábitat de aguas profundas. Esta información es esencial para entender sus requerimientos vitales y, de esta manera, resulta básica para diseñar medidas encaminadas a conservar estas especies. Esto, a su vez, repercute en la conservación del ecosistema de aguas profundas, ya que los odontocetos de buceo profundo actúan como reguladores ‘top-down’ (de arriba abajo) en las redes tróficas oceánicas. Estudios de marcaje animal o ‘biologging’ han caracterizado el comportamiento a nivel de individuo. Esta tesis continúa esta caracterización pero a nivel de grupo y del hábitat, tratando cuatro objetivos e hipótesis principales: *i)* Los zifios viven generalmente en grupos, y son obligadamente vocales para alimentarse en las profundidades, empleando la ecolocalización. Estos sonidos que emplean pueden atraer a depredadores capaces de detectarlos acústicamente como las orcas. Los zifios se encuentran indefensos si son encontrados por orcas, ya que sus unidades sociales son pequeñas y no ofrecen defensa de grupo frente a los depredadores. De esta manera, los zifios deberían conseguir reducir su detectabilidad por parte de las orcas. Esto fue comprobado usando datos de marcaje animal que aportaron muestras del comportamiento vocal y de buceo altamente sincronizado en grupos de zifios. Además, se hicieron modelos de cómo esta sincronización reduce el riesgo de ser depredados por orcas; *ii)* Las vocalizaciones sincronizadas podrían generar interferencias con conspecíficos que estuvieran vocalizando al mismo tiempo, así como ofrecer beneficios durante la alimentación si los individuos pueden escuchar los sonidos de alimentación de otros miembros del grupo cuando consiguen cazar una presa. Utilizamos a los zifios como organismos modelo para estudiar el balance coste-beneficio en depredadores acústicos y

sociales, cuantificando las tasas de vocalización de zifios de Blainville y de Cuvier mientras se alimentan, y los posibles efectos del tamaño de grupo sobre estas tasas. Los resultados incluyen inferencias en las limitaciones evolutivas del tamaño de grupo en los zifios. Además, los resultados son aplicables para mejorar la fiabilidad de estimas de densidad de zifios usando monitoreo acústico pasivo (PAM por sus siglas en inglés); *iii*) Los cetáceos de buceo profundo se pueden relacionar con otras especies además de con conspecíficos. Las distintas especies de buceadores profundos podrían competir, colaborar o ignorarse mutuamente, lo cual estaría gobernado por sus características comportamentales y en caso de existir solapamiento en sus nichos tróficos. Hemos estudiado el solapamiento del hábitat de alimentación en cinco especies de odontocetos de buceo profundo en la columna de agua desde los hábitats epi-, meso-, bati- y bentopelágicos; su amplitud de nicho trófico (el uso de estas capas) y su variación circadiana (día-noche). También hemos relacionado los resultados con observaciones de encuentros agonísticos entre las especies estudiadas o con su coexistencia en un mismo área. En el último capítulo, la tesis continúa de los cetáceos a su hábitat: *iv*) Se vio que la zona mesopelágica y la migración de la capa de reflexión profunda (DSL por sus siglas en inglés) del meso- al epipelágico son de elevada importancia para las cinco especies de cetáceos de buceo profundo estudiadas. Las distintas estimas de biomasa de fauna mesopelágica todavía difieren órdenes de magnitud entre sí, por lo que sería conveniente mejorar dichas estimas con el fin de gestionar desde una perspectiva ecosistémica las propuestas emergentes de explotar como pesquería la DSL. En esta tesis se empleó PAM para investigar un posible sonido firma asociado a la migración de la DSL indicado por un coro detectado al atardecer, coincidiendo con la migración. Este coro estaba relacionado con datos de acústica activa tomados simultáneamente con el fin de explorar la posibilidad de estimar la densidad de organismos migrantes de la DSL a partir de los niveles sonoros del coro.

Las principales contribuciones metodológicas de esta tesis son las siguientes:

I. Recopilar y analizar datos de marcaje animal o ‘biologging’ obtenidos con DTAGs (marcas digitales) colocadas en zifios para cuantificar la coordinación de perfiles de buceo y comportamiento acústico de estos cetáceos viviendo en grupos sociales y cómo esto podría reducir la posibilidad de ser detectados por depredadores guiados por el sonido como las orcas.

II. Combinar datos de marcaje animal con DTAGs colocadas por separado o en parejas de animales del mismo grupo y analizar las tasas de emisión de chasquidos y zumbidos, datos de orientación y profundidad obtenidos de sensores como magnetómetros y acelerómetros para investigar el balance coste-beneficio de vivir en grupos sociales y realizar buceos extremadamente profundos en los zifios de Blainville y de Cuvier, por ejemplo si se da interferencia acústica o si los animales utilizan sonidos de congéneres, o si se da caza cooperativa o competencia por las presas.

III. Estimar el solapamiento y/o segregación en el hábitat vertical de alimentación en cinco especies de odontocetos de buceo profundo combinando datos de marcaje, por ejemplo mediante el análisis de la profundidad y altitud de alimentación sobre el fondo marino, con datos de contenidos estomacales de la bibliografía y adaptando ecuaciones de índices de nicho trófico para estudiar el hábitat de alimentación, con los índices de Levin y Pianka para la amplitud y solapamiento de nicho trófico, respectivamente.

IV. Emplear simultáneamente instrumentos de acústica activa y pasiva para estudiar la columna de agua en aguas abiertas de Canarias con el fin de caracterizar el coro al anochecer y relacionarlo con la migración vertical circadiana de parte de la DSL.

Las principales contribuciones científicas de esta tesis son las siguientes:

I. Analizando datos de marcaje en zifios de Blainville y de Cuvier (14 y 12 animales marcados, respectivamente), demostramos que estos animales solapan sus tiempos de alimentación con los miembros de su grupo en un 98% y realizan un ascenso a superficie coordinado y en silencio tras su alimentación a grandes profundidades, en dirección impredecible que cubre una media de 1 km desde su última posición vocal. Este comportamiento altamente sincronizado y estereotipado en el buceo y el comportamiento acústico en los grupos de zifios podría haber sido moldeado por el miedo a la depredación. Actualmente, esta estrategia anti depredadora podría ser adaptativamente desventajosa en el Antropoceno, ya que parece que sonares navales inducen una respuesta extrema en estos zifios, similar a la respuesta natural a la presencia de orcas, conllevando a varamientos masivos de estos animales.

II. 16 zifios de Blainville y 10 zifios de Cuvier fueron previamente marcados con DTAGs en Canarias y el Mar de Liguria (Mediterráneo occidental). El análisis de los datos muestra que los miembros del mismo grupo pueden oír a sus compañeros durante al menos el 91% de la fase vocal de alimentación de sus inmersiones. Esto permite a los zifios coordinar la dirección general de desplazamiento, aunque las direcciones individuales medidas minuto a minuto difieran, mientras cada animal persigue a sus propias presas. Aunque los zifios coordinan sus periodos de alimentación en los que emplean la ecolocalización, las tasas individuales de emisión de chasquidos y zumbidos son independientes del número de animales en el grupo. De esta manera, la actividad de alimentación no se ve afectada por competición intra grupal o por interferencia entre miembros del mismo grupo, y no parecen utilizar los ecos producidos por los chasquidos de ecolocalización de sus congéneres. Concluimos que la estrecha sincronización vocal y de buceo en los grupos de zifios, que reduce cuantitativamente los riesgos de depredación, tiene un impacto ínfimo en el rendimiento de sus inmersiones de alimentación.

III Se analizaron 81 marcas DTAG colocadas en cinco especies de cetáceos de buceo profundo: 16 eventos de marcaje en zifios de Blainville (Md), 10 en zifios de Cuvier (Zc), 27 en calderones tropicales (Gm), 12 en calderones grises (Gg) y 16 en cachalotes (Pm). Los valores del índice de Pianka de solapamiento de nicho variaban entre las especies comparadas por pares durante el día y la noche debido a las diferentes adaptaciones de cada especie a la migración nictemeral de la DSL. Los valores obtenidos fueron altos (>0.9) durante el día entre Md, Zc, Gm y Pm debido a que todas estas especies se alimentan principalmente en la zona mesopelágica (200-1000 m de profundidad). Los valores fueron menores (de 0.5 a 0.8) durante la alimentación nocturna, ya que Zc pasa a alimentarse principalmente en el batipelágico. Gg presentó un menor solapamiento con las demás especies, aunque sí solapaba con Gm durante la noche, cuando ambas especies aprovechan la migración de la DSL para alimentarse de ella en el epipelágico (0-200 m). Esto no ocurría en las otras especies. Todas las especies depredan en la región bentopelágica (a < 100 m del fondo marino), pero con menor importancia en Gm (6 y 0% durante el día y la noche) respecto a las otras especies (entre 5-31% tanto de día como de noche). El solapamiento de nicho podría explicar observaciones de comportamientos agonísticos de Gm y Gg hacia Pm. Estas especies pueden ser territoriales gracias a sus grupos numerosos. En cambio, Md y Zc pueden coexistir en un mismo área aunque solapen altamente sus nichos tróficos, probablemente debido a que sus poco numerosos grupos sociales no permiten confrontaciones territoriales con otras especies. De esta manera, la ecología del comportamiento puede ayudar a entender la distribución de estos depredadores apicales. La dependencia de todas las especies sobre recursos meso- y bentopelágicos conllevaría que la pesca de arrastre sobre el fondo marino, la minería de aguas profundas y la explotación pesquera de la DSL pueden constituirse como amenazas para la conservación de estos depredadores apicales del océano profundo.

IV. Se documenta por primera vez en el Océano Atlántico un coro al anochecer similar a los detectados en aguas profundas de los océanos Pacífico e Índico. El coro ocurre simultáneamente con la migración a superficie de parte de la DSL al anochecer. Además, el nivel sonoro máximo recibido está positivamente correlacionado con la dispersión acústica registrada para organismos de la DSL que migran desde profundidades mesopelágicas al epipelágico al anochecer. Concluimos que los responsables más probables de la producción de este coro son peces mesopelágicos, al expulsar gases durante el ascenso a aguas someras. Medir los niveles de este coro diario podría proporcionar estimas de abundancia de organismos mesopelágicos, algunos de los cuales son presa habitual de depredadores apicales como los cetáceos de buceo profundo.

Chapter I: General Introduction

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Deep diving cetaceans in the Canary Islands

The Canary Islands Archipelago consists of eight islands and five islets (Figure 1). It is located some 100 km from the North-West African coast. The islands act as a barrier for the Canary Current and the NE trade winds, which determines the presence of calm waters to the leeward of each island (Barton et al. 1998). The archipelago has a volcanic origin with islands rising mostly independently from the seafloor. This renders a steep bathymetry and the existence of deep canyons (Krastel et al. 2001), with depths of up to 3000 m between islands. This results in mixing of neritic and oceanic, shallow and deep-waters ecosystems near the coast of the islands. This heterogeneous ecotone effect favours that the Canary Islands are highly diverse for cephalopods (Escánez et al. 2021) and deep-diving cetaceans (Carrillo 2007), amongst other taxa. Research of these species is favoured by the existence of deep calmed waters in the leeward SW side of each island, facilitating access of scientists to study these species in cost-effective fieldwork compared to most open-ocean studies carried out from continental waters.

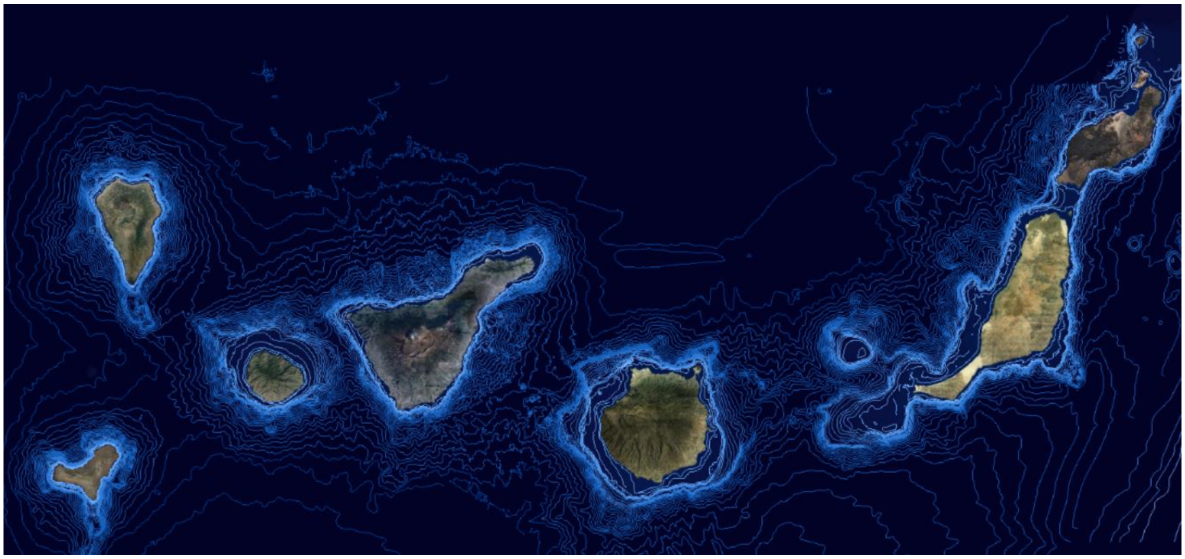

Figure 1. Bathymetry of the Canary Islands Archipelago. Scale 1:1825415. GRAFCAN, Gobierno de Canarias (visor.grafcan.es, Spain)

The Canary Islands hold the highest cetacean diversity within the European region, with 32 species cited in the archipelago (Table 1)(Vonk & Martin 1989). Seven species belong to the Superfamily Mysticeti and 25 to the Odontoceti. Within the odontocetes, 13 are deep-divers, i.e. they routinely forage at depths greater than 200 m (Table 1).

Regarding their site-fidelity, we find resident, transient and migrant/seasonal cetaceans in the Canary Islands. To confirm the resident status of cetacean populations in the archipelago, photo-identification studies have been carried out for some species. These studies revealed that, at least, four species have resident populations, Blainville's and Cuvier's beaked whales off El Hierro island (Aparicio 2008; Reyes Suárez 2018), short-finned pilot whales off SW Tenerife (Heimlich-Boran 1993; Marrero Pérez et al. 2016; Servidio et al. 2019) and Risso's dolphins off Fuerteventura (V. Martín pers. com.; Sarabia-Hierro & Rodríguez-González 2019).

Although information is scarce or lacking regarding other islands and/or species, other deep-divers are regularly sighted in the archipelago, and are probably resident too, like sperm whales (André 1998; Fais et al. 2016), and Blainville's, Cuvier's and Gervais' beaked whales in Lanzarote and Fuerteventura (Tejedor et al. 2011). Therefore, the Canary Islands hold a high diversity of deep diving odontocetes, with a clearly non-uniform distribution along the waters off the archipelago. These differences in spatial occurrence of deep divers could be reflecting habitat preferences and niche partitioning, behavioural differences, and/or unequal tolerance to anthropogenic disturbances, among other factors.

Table 1. Cetaceans (Infraorder Cetacea Brisson, 1762) cited for the Canary Islands. Banco de Datos de Biodiversidad de Canarias (https://www.biodiversidadcanarias.es/biota/) based on studies of Vonk & Martin (1989) and others (see 'Resident' column). Total cetacean species in the Canary Islands: 32 (7 Mysticeti & 25 Odontoceti), of which 13 are considered deep-divers. Although some species can be sighted through the year, they appear marked as 'possible' resident if there is no publication demonstrating so.

Superfamily Mysticeti Flower, 1864				
Family	**Genus**	**Species**	Deep-diver	Resident
Balaenidae Gray, 1825	*Eubalaena* Gray, 1864	*Eubalaena glacialis* (Müller, 1776)		
Balaenopteridae Gray, 1864	*Balaenoptera* Lacépède, 1804	*Balaenoptera acutorostrata* Lacépède, 1804		
		Balaenoptera borealis Lesson, 1828		
		Balaenoptera edeni Anderson, 1878		Possible
		Balaenoptera musculus (Linnaeus, 1758)		
		Balaenoptera physalus (Linnaeus, 1758)		
	Megaptera Gray, 1846	*Megaptera novaeangliae* (Borowski, 1781)		
Superfamily Odontoceti Flower, 1867				
Family	**Genus**	**Species**	Deep-diver	Resident
Delphinidae Gray, 1821	*Cephalorhynchus*	*Cephalorhynchus heavisidii* (Gray, 1828)		
	Delphinus	*Delphinus delphis* Linnaeus, 1758		
	Feresa	*Feresa attenuata* Gray, 1874		
	Globicephala	*Globicephala macrorhynchus* Gray, 1846	Yes (Aguilar de Soto et al. 2008)	Yes (Vonk & Martin 1989; Marrero Pérez et al. 2016; Servidio et al. 2019)
		Globicephala melas (Traill, 1809)	Yes (Baird et al. 2002)	

	Grampus	*Grampus griseus* (G. Cuvier, 1812)	Yes (Arranz et al. 2019)	Yes (Sarabia-Hierro & Rodríguez-González 2019)
	Lagenodelphis	*Lagenodelphis hosei* Fraser, 1956		
	Orcinus	*Orcinus orca* (Linnaeus, 1758)		
	Pseudorca	*Pseudorca crassidens* (Owen, 1846)	Yes (Minamikawa et al. 2013)	
	Stenella	*Stenella attenuata* (Gray, 1846)		
		Stenella coeruleoalba (Meyen, 1833)		
		Stenella frontalis (G. Cuvier, 1829)		
		Stenella longirostris (Gray, 1828)		
	Steno	*Steno bredanensis* (G. Cuvier en Lesson, 1828)		
	Tursiops	*Tursiops truncatus* (Montagu, 1821)		
Kogiidae Gill, 1871	*Kogia*	*Kogia breviceps* (de Blainville, 1838)	Yes (McAlpine 2009)	
		Kogia sima (Owen, 1866)	Yes (McAlpine 2009)	
Phocoenidae	*Phocoena*	*Phocoena phocoena* Linnaeus, 1758		
Physeteridae	*Physeter*	*Physeter macrocephalus* Linnaeus, 1758	Yes (Watwood et al. 2006)	Possible
Ziphiidae Gray, 1850	*Hyperoodon*	*Hyperoodon ampullatus* (Forster, 1770)	Yes (Hooker & Baird 1999)	
	Mesoplodon	*Mesoplodon bidens* (Sowerby, 1804)	Yes (Mead 2002)	
		Mesoplodon densirostris (de Blainville, 1817)	Yes (Tyack et al. 2006)	Yes (Aparicio 2008; Reyes Suárez 2018)
		Mesoplodon europaeus (Gervais, 1855)	Yes (Mead 2002)	Possible
		Mesoplodon mirus True, 1913	Yes (Mead 2002)	
	Ziphius	*Ziphius cavirostris* G. Cuvier, 1823	Yes (Tyack et al. 2006)	Yes (Aparicio 2008; Reyes Suárez 2018)

This thesis focuses mainly on Blainville´s and Cuvier´s beaked whales, and then performs a comparative study of vertical habitat use by these species and three other deep-diving odontoceti.

Blainville’s beaked whale

Blainville’s beaked whales, *Mesoplodon densirostris* (de Blainville, 1817), are medium-sized odontocetes of the Family Ziphiidae, presenting average lengths of 4.5 m and a maximum estimated weight of a tonne (Allen et al. 1984). These whales present a long beak and sexual dimorphism, with the adult males possessing two teeth that erupt from the middle of their strongly curved lower jaw (Besharse 1971; Allen et al. 1984). In females and young males these teeth do not erupt and the curvature of the jaw is not so pronounced (Figure 2). These animals can be found solitary or in small groups, presenting a fission-fusion social strategy (Claridge 2006; Reyes Suárez 2018).

There is scarce information on the diet of this species, although it is well known that they forage in mesopelagic waters, i.e. between 200 and 1000 m depth (Tyack et al. 2006). Analysis of stomach contents from stranded animals provided proxies of the diet of these whales, showing they prey mostly on fish and cephalopods (Santos et al. 2007). Preferable prey appears to be fish from the Family Gadidae and Myctophidae, and cephalopods from the Family Cranchiidae, Histioteuthidae and Octopoteuthidae (Santos et al. 2007), some of these have been found floating at the surface near of sightings of Blainville’s beaked whales (Figure 3).

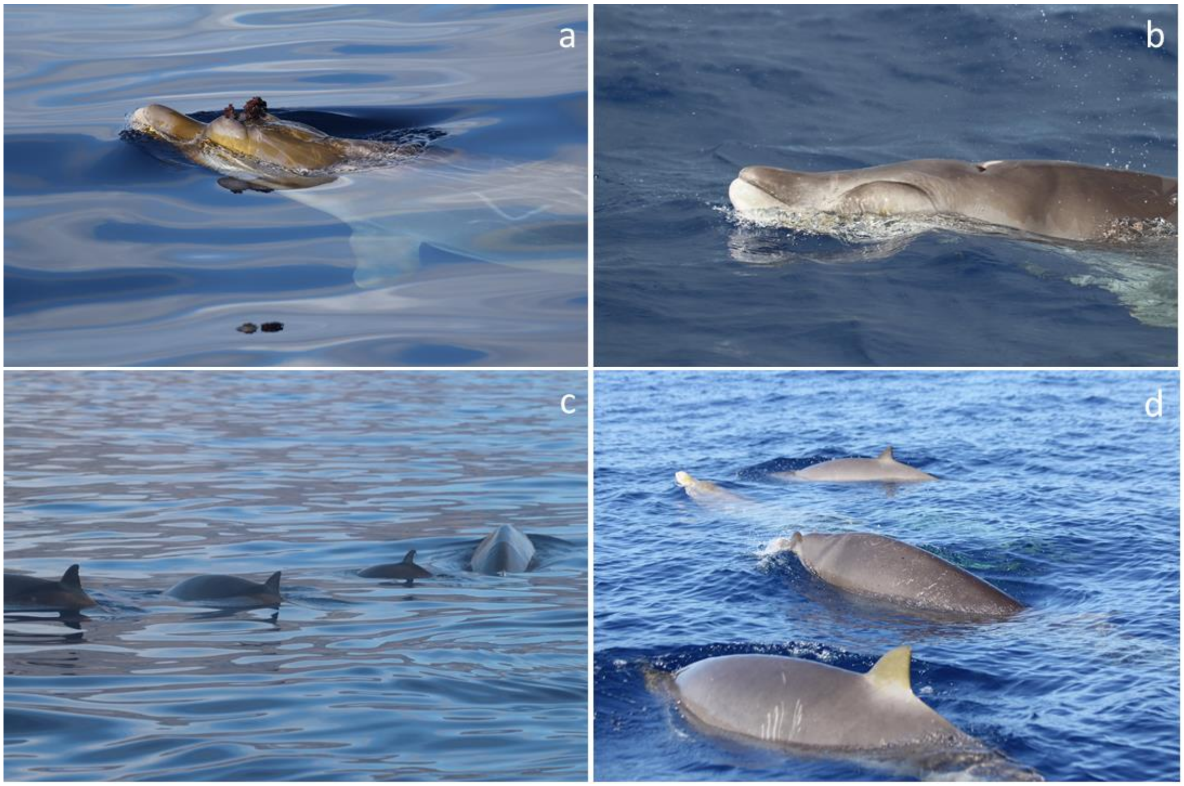

Figure 2. Blainville’s beaked whales photographed off El Hierro (Canary Islands). The different curvature of the lower jaw can be seen in pics a-b, with the first animal presenting erupting teeth (adult male). Cohesive behaviour of groups at the surface is usually seen, as in pics c-d. All pictures were taken with all the permits during research cruises of University of La Laguna, and taken by Talía Morales (a), Agustina Schiavi (b, c) and Jesús Alcázar (d).

Figure 3. Cranchiidae squid (left) and Myctophidae fish (right) found floating near surfacing Blainville’s beaked whales off El Hierro island. Pictures taken by Jesús Alcázar (left) and Chloe Yzoard (right).

Both the diving and acoustic behaviour of Blainville's beaked whales have been thoroughly described from biologging studies off El Hierro island and the Bahamas using DTAGs (Madsen et al. 2005; Aguilar de Soto 2006; Johnson et al. 2006; Tyack et al. 2006; Arranz et al. 2011; Dunn et al. 2013). These tag deployments showed that Blainville's beaked whales present a stereotyped diving behaviour that consists of a deep foraging dive (average 835 m depth) during which they echolocate to search for prey, followed by a median number of six silent shallower dives (average depth and duration of 71 m and 9.3 min, respectively) with an average dive cycle duration of 92 min (Tyack et al. 2006). Shallow dives are believed to serve a recovery purpose (Tyack et al. 2006; Zimmer & Tyack 2007; Fahlman et al. 2014). These animals remain silent during these recovery dives probably to reduce detection by acoustic-guided predators, like orcas (Aguilar de Soto et al. 2012).

During the foraging phase of their deep dives, these whales emit echolocation clicks to search for prey, as other odontocetes do. The search clicks in Blainville's beaked whales are frequency-modulated (FM), presenting an upsweep from 20 to 48 kHz (Johnson et al. 2004). The clicks have average durations of 250 µs and are emitted in click trains with inter-click-intervals (ICI) between 0.2-0.4 s during the searching and approach phase to prey (Johnson et al. 2006). Once the detected prey is at a body distance of the echolocating animal, the whale will start emitting a buzz to perform a prey capture attempt (Johnson et al. 2006). Buzzes produced by Blainville's beaked whales are click trains with clicks more similar to those produced by delphinids, with a shorter duration (some 105 µs) and without frequency modulation. The ICI of buzzes typically starts at 0.1 s and rapidly drops to 0.012 s, reaching even 0.003 s (Johnson et al. 2006).

The acute hearing of these animals at mid-high frequencies (Pacini et al. 2011) makes them especially sensitive to mid-frequency naval sonar (McCarthy et al. 2011; Tyack et al. 2011). The most accepted explanation to mortalities related to sonar is a startle response leading to fat and gas emboli consistent with decompression sickness (Fernández et al. 2005).

The global conservation status of this species is considered of Least Concern in the IUCN Red List, although it is stated that some subpopulations could be assigned to threatened categories (Pitman & Brownell 2020). The species is considered cosmopolitan albeit absent in cold waters, with distribution mainly in tropical and warm-temperate waters (Figure 4). New techniques are being developed to estimate Blainville's beaked whales density using Passive Acoustic Monitoring (PAM) (Marques et al. 2009, 2019; Moretti et al. 2010). PAM is also applied to gather finer-scale knowledge of the distribution and abundance of these whales, which is still largely unknown excepting in some concentration areas such as Bahamas (Claridge 2006), Hawaii (McSweeny et al. 2007) and the Canary Islands (Aguilar de Soto 2006).

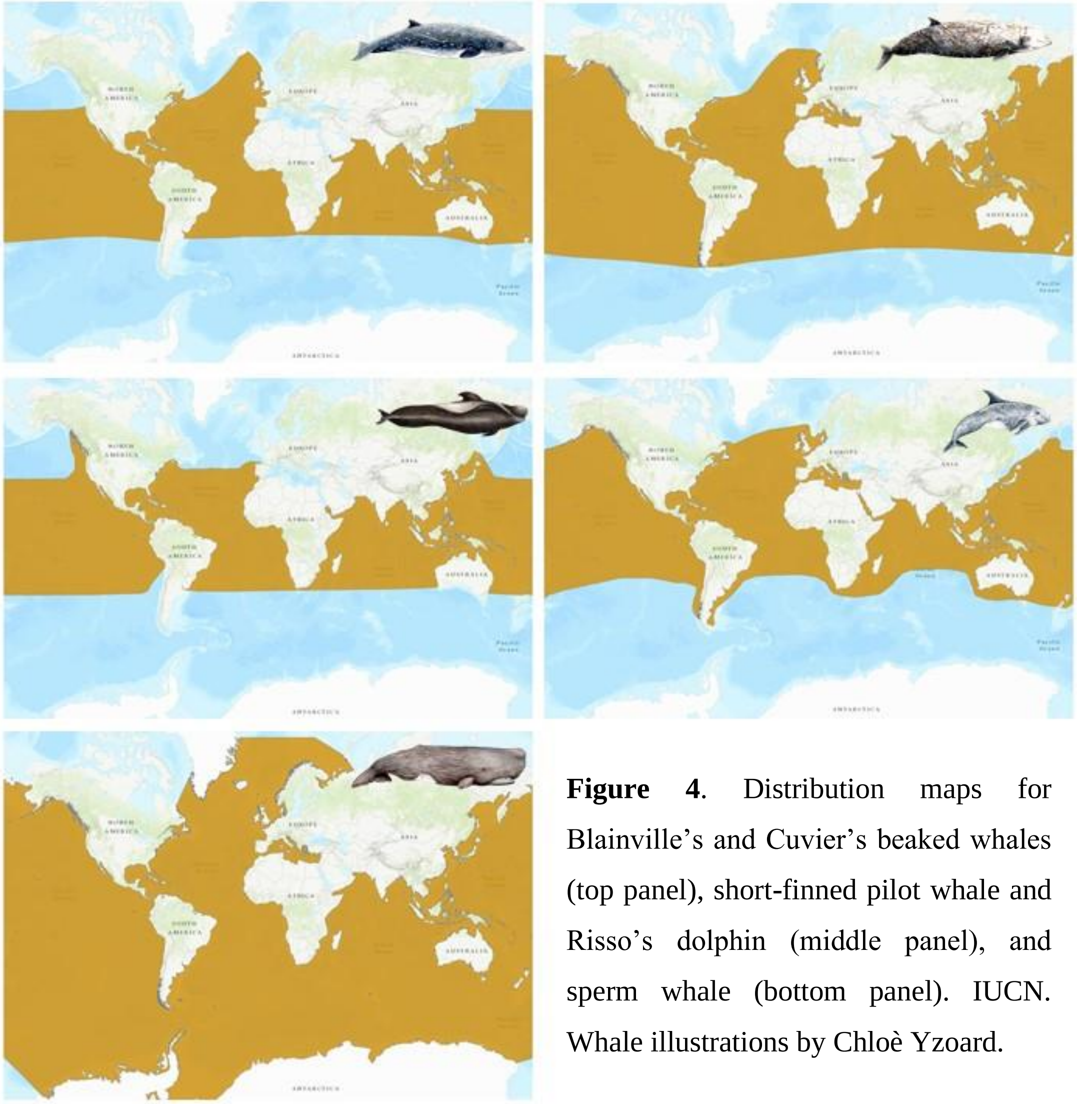

Figure 4. Distribution maps for Blainville's and Cuvier's beaked whales (top panel), short-finned pilot whale and Risso's dolphin (middle panel), and sperm whale (bottom panel). IUCN. Whale illustrations by Chloè Yzoard.

Cuvier's beaked whale

Cuvier's beaked whales (*Ziphius cavirostris* G. Cuvier, 1823, Figure 5) belong to the Family Ziphiidae, and can reach up to 3 tonnes in weight and 6.3 m in length. They have a short beak with a slightly curved mouth and sexual dimorphism (Mead 2002). Adult males present at the tip of their beaks a pair of teeth, which are absent in females and juvenile adults (Heyning & Mead 2009). They occur singly or in small groups of two to six whales, and they have a fission-fusion social strategy with male-male alliances (Cioffi et al. 2021).

Figure 5. Cuvier's beaked whales photographed off El Hierro island. Teeth erupt from the tip of the beak in males of this species (a-b). In El Hierro this species can be found in groups near the coast with cohesive behaviour at the surface (c-d). All pictures were taken with all the permits during research cruises of University of La Laguna, and taken by Adrián Martín (a), Agustina Schiavi (b), Crístel Reyes (c) and Jesús Alcázar (d).

These animals forage via suction feeding (Heyning & Mead 1996) at on average 1070 m depth (Tyack et al. 2006). This species holds the dive duration and depth record of all mammals, with a maximum registered dive duration of three hours and 42 minutes and maximum reached depth of 2992 m (Schorr et al. 2014; Quick et al. 2020). Stomach content analyses on stranded whales indicate that this species prey mostly on oceanic squid from the families Cranchiidae, Histioteuthidae, Mastigoteuthidae and Octopoteuthidae (Santos et al. 2007), but there is evidence suggesting a more opportunistic foraging behaviour that includes deep-water fish (Heyning & Mead 2009).

Cuvier’s beaked whales present a stereotyped diving behaviour: they routinely perform a deep foraging dive (average 1070 m depth) that is followed by a median number of two silent shallower dives (221 m depth and 15.2 min duration) with an average dive cycle duration of 63 min (Tyack et al. 2006). These animals remain silent during the recovery dives (Warren et al. 2017). During their foraging dives, these whales emit FM clicks deeper than 200 m to search for prey (Zimmer et al. 2005). These clicks are emitted with an ICI of 0.6-0.68 s (Warren et al. 2017) and have durations of some 200 µs, showing a frequency upsweep from 35 to 45 kHz (Zimmer et al. 2005), although recent studies suggest a combination of both upsweep and downsweep chirps forming each click (Guilment et al. 2020). Once near a prey item, Cuvier’s beaked whales emit a buzz, a rapid series of frequency-unmodulated and short-duration clicks that indicate a prey capture attempt (Johnson et al. 2004; Zimmer et al. 2005). The hearing sensitivity and the deep-diving behaviour of this species result in a high vulnerability to anthropogenic noise, like mid-frequency naval sonar. These sounds can disrupt the stereotyped dive behaviour of this species through a startle response that disrupts the recovery dive cycle and result in the death of the whale (Aguilar Soto et al. 2006; DeRuiter et al. 2013; Fahlman et al. 2014).

Cuvier’s beaked whales are considered as Least Concern in the IUCN Red List (Taylor et al. 2008), although this categorisation is marked as ’needs updating’. They present the most extensive distribution range within the Family Ziphiidae (Figure 4), but similarly to the Blainville’s beaked whales, studies at a finer scale are needed to estimate abundance and population trends (Barlow et al. 2013; Hildebrand et al. 2015; Barlow et al. 2021).

Short-finned pilot whale

Short-finned pilot whales (*Globicephala macrorhynchus* Gray, 1846), hereon pilot whales, are medium-sized delphinids (Family Delphinidae) that have recently been proposed as two subspecies: the Naisa and Shiho short-finned pilot whales (Van Cise et al. 2019). Until a more profound genetic study is performed, all the Atlantic short-finned pilot whales are taxonomically placed within the Naisa type. This type of pilot whale presents a square-shaped melon and a dark saddle patch in the dorsum (Figure 6). The females can reach some 4 m in length, while the males are visibly more muscular and larger, reaching up to 5.25 m (Chivers et al. 2018).

In the Canary Islands, there is a resident population of short-finned pilot whales off SW Tenerife (Heimlich-Boran 1993; Servidio et al. 2019). Pilot whales in this area are distributed in groups that average 12 individuals (Heimlich-Boran 1993), with associations known as constant companions. These groups are hierarchically organized in clans that together constitute a Canary Islands population (Servidio 2014).

Analyses of stomach contents from stranded animals in the Canary Islands reveal a preference by these animals for hunting oceanic squid within the families Cranchiidae, Cycoteuthidae and Ommastrephidae (Hernández-García & Martín 1994). Stomach contents from strandings occurring in the western North Atlantic showed that they also prey on mesopelagic fish of the Family Melamphaidae (Mintzer et al. 2008). Currently, studies using isotopes and fatty acids are being carried to adequately characterize the diet of these whales in the Canary Islands (Marrero Pérez et al. 2016; Íñiguez Santamaría 2020).

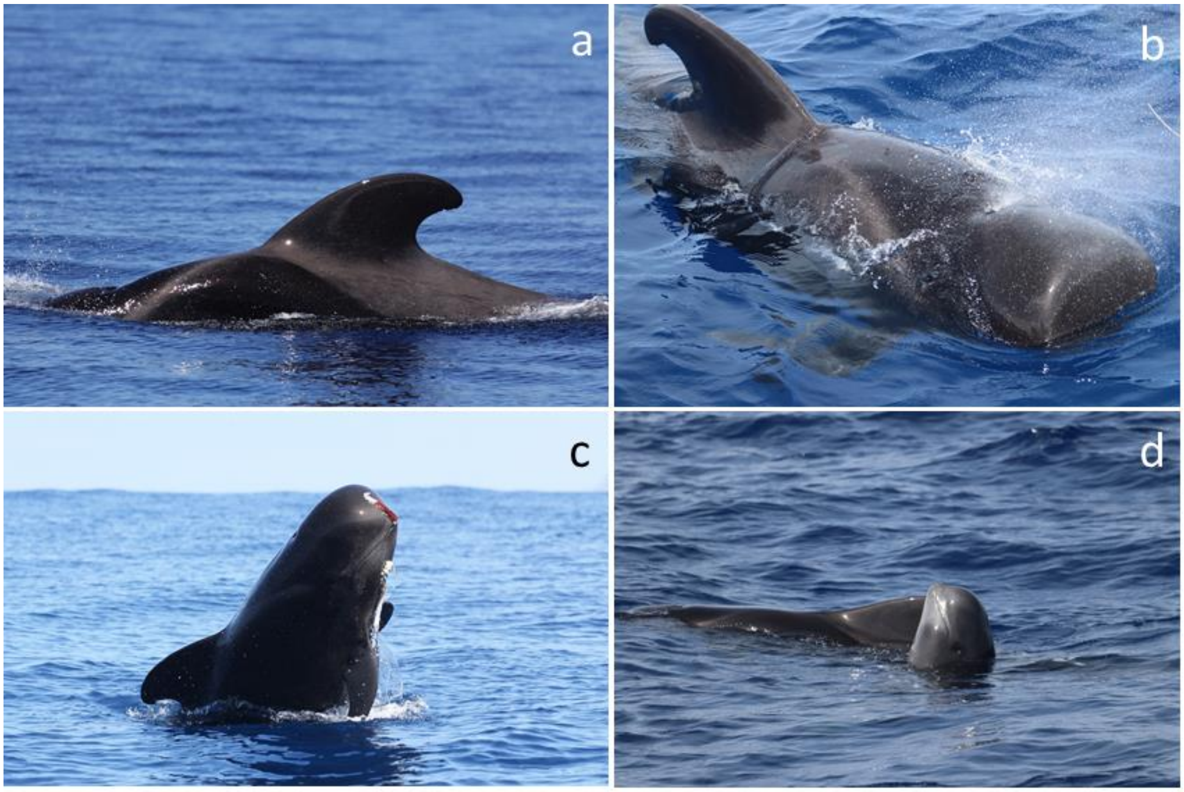

Figure 6. Short-finned pilot whales photographed off El Hierro (a) and Tenerife islands (b-d). These animals present square-shaped melons and a dark saddle patch in the dorsum (a-b), occasionally seen with tentacles of the squids they prey on emerging from the mouth (c). A pilot whale calf spyhopping in the company of its mother or carer (d). All pictures were taken with permits during research cruises of University of La Laguna (a, b, d) and Asociación Tonina (c).

Pilot whales routinely perform deep dives for a maximum duration and depth of 21 min and 1018 m (Aguilar Soto et al. 2008). During the day, these dives are deeper (at a median depth of 762 m), present a median of one buzz per dive and a prey chase with whale swimming speeds up to 9 m/s prior to emitting the buzz or prey capture attempt. Due to this hunting tactic pilot whales of Tenerife were coined “cheetahs of the deep”. At night pilot whales off Tenerife forage shallower (at a median of 96 and 672 m depth for the shallow and deep night-dives, respectively) (Aguilar de Soto 2006) and perform more prey capture attempts per dive (median 5 buzzes) without chasing (Aguilar Soto et al. 2008).

Pilot whales are vocal animals, and as most studied odontocetes they use echolocation clicks to search for prey and buzzes during capture attempts (Aguilar Soto et al. 2008). These clicks are short (duration 57 µs) with a centroid frequency of 40 kHz (Pedersen et al. 2021). Pilot whales are also socially vocal (Jensen et al. 2011), with at least four main types of acoustic communication signals: rasps (click trains with average ICI of 21 ms), low- and mid-frequency calls and two-component calls (Pérez et al. 2017).

Pilot whales react to anthropogenic noise like pulses from scientific echosounders (Quick et al. 2016) and airgun ramp-up procedures (Weir 2008) by increasing their alertness and swimming in the opposite direction from the sound source. However, long-finned pilot whales react to killer whale playbacks by confrontation, travelling towards the noise source (Curé et al. 2012). Pilot whales do not perform shallow recovery dives as those in beaked whales (Tyack et al. 2006; Aguilar de Soto et al. 2008). Their diving behaviour, performing dives at similar depths than beaked whales in one third-one quarter of the time on average, as well as their different response to predator-like playbacks, could explain that pilot whales are not involved in mass strandings related to naval sonar as beaked whales, i.e. pilot whales may have higher buffer capabilities to disruptions of their normal diving behaviour, and they may not react so strongly to predator sounds (Curé et al. 2012)

This species has a pantropical distribution excluding the Mediterranean Sea (Figure 4) and is listed as Least Concern in the IUCN Red List (Minton et al. 2018).

Risso’s dolphin

Risso’s dolphins (*Grampus griseus* Cuvier, 1812, Family Delphinidae) are robust cetaceans with a bulbous head and a tall dorsal fin (Figure 7). They can reach up to 4 m in length and they get covered in white scars as they age (Baird 2009). These dolphins are gregarious and are usually seen in groups of 10-50 animals (Baird 2009).

Figure 7. Risso’s dolphins tagged off Santa Catalina Island (California, USA) with digital tags. Pictures taken by Ari Friedlaender under permit NMFS 14534.

Analyses of stomach contents from stranded Risso’s dolphins in the Western Mediterranean showed a diet mainly based on oceanic cephalopods, with presence of species belonging to the families Ommastrephidae, Histioteuthidae and Onychoteuthidae and being the *Argonauta argo* from the Family Argonautidae the most abundant prey item (Würtz et al. 1992; Blanco et al. 2006).

Risso's dolphins forage both in shallow waters near the shore (20 m depth) and in the open ocean, reaching mesopelagic depths (500 m depth) (Arranz et al. 2019). Like other odontocetes, these dolphins emit echolocation clicks to search for prey, with centroid frequencies of 56.5 kHz and duration of 40-70 µs (Philips et al. 2003). Once they encounter a target, they produce a fast series of echolocation clicks in a buzz to attempt to capture their prey (Arranz et al. 2016). Risso's dolphins use knowledge regarding prey distribution in the water column and foraging success in the previous dive to plan for the next dive (Arranz et al. 2018). Risso's dolphins present a wide repertoire of communicative sounds, including whistles, burst-pulses and a combination of whistle and burst-pulsed sound (Corkeron & Van Parijs 2001; Arranz et al. 2016).

Risso's dolphin is a Least Concern species in the IUCN Red List (Kiszka & Braulik 2018) and presents a pantropical distribution (Figure 4).

Sperm whale

The sperm whale (*Physeter macrocephalus* Linnaeus, 1758, Family Physeteridae) is the largest odontocete (Whitehead 2018). This species presents a hypertrophied nose that represents more than ¼ of its body length (Maeda 1965) (Figure 8). Sperm whales present the most pronounced sexual dimorphism both in body length and weight among all cetaceans, with females reaching lengths of 11 m and weighing 15 tons, while males are physically mature at some 16 m length and 45 tons (Whitehead 2018). The social structure is matrilineal family units of 12 whales on average: females and their young, while subadult males form only-male associations and large males are solitary (Whitehead 2003; Sarano et al. 2021).

Figure 8. Sperm whales photographed off El Hierro island, near the coast (a). Detail of the hypertrophied nose (b), the triangular dorsal fin (c) and the fluke used in photo-ID (d). These animals are found in groups of females with their young in tropical and subtropical waters (e). All pictures were taken by Jesús Alcázar, with all the permits during research cruises of University of La Laguna.

Stomach contents from stranded sperm whales in the Western Mediterranean and the Canary Islands reveal species within the families Cranchiidae, Chiroteuthidae, Architeuthidae (i.e. the giant squid) and Octopoteuthidae with a preference for cephalopods of the family Histioteuthidae (Fernández et al. 2009; Foskolos et al. 2019).

The average dive cycle in sperm whales usually consists in a deep-foraging dive of 45 min duration reaching mesopelagic depths (averaging between 644-985 m depth for animals tagged in the Atlantic Ocean, the Gulf of Mexico and the Ligurian Sea), followed by a 9 min surface interval (Watwood et al. 2006). Their behaviour is more varied in high latitudes inhabited only by adult males that feed from the epi- to the bathypelagic (Teloni et al. 2008; Fais et al. 2016). Thanks to their hypertrophied nose, the echolocation clicks emitted by these whales constitute one of the most powerful sounds in the animal kingdom (Møhl et al. 2003). These clicks have durations of 100 µs, centroid frequencies of 15 kHz and source levels reaching 236 dB re 1 µPa (RMS), enabling long-range detection of prey (Møhl et al. 2003; Tønnesen et al. 2020). Similar to other odontocetes, once the whale is close to the detected prey and attempts to catch it, the whale will emit a buzz, called creak in this species (Gordon 1987; Miller et al. 2004). These whales are highly social and communicative vocalizations include ‘trumpets’ sounds reported in the Mediterranean (Teloni et al. 2005) and clicks sequences known as codas, with geographic differences classified as dialects (Schevill 1977; Rendell & Whitehead 2005).

Sound-exposure experiments using naval sonar on sperm whales resulted in changes in behaviour such as avoidance from the source and ceasing on foraging or resting behaviour, so these whales are likely affected by naval exercises using sonar (Sivle et al. 2012; Curé et al. 2016).

The sperm whale is listed as Vulnerable with a ’needs updating’ warning in the IUCN Red List (Taylor et al. 2019) and can be found in all oceans (Figure 4). They have a different distribution depending on sex and age class (Whitehead 2018): females and their young remain at waters with surface temperature higher than 15 ºC (less than 40º latitude in both hemispheres). As they grow, young males leave their mothers and move to higher latitudes, with large adult males reaching the edge of pack ice in both poles, and only returning to their breeding grounds in tropical and subtropical waters to mate.

Conservation of deep-diving odontocetes and their habitat

Most deep-diving odontocetes are sensitive to a broad number of anthropic disturbances, some of which are summarised below.

Acoustic disturbances

As other cetaceans, deep-diving odontocetes have an acute hearing that can be negatively affected by constant and/or transient powerful noise, like boat traffic, pile driving and echosounders (Yang et al. 2021). The best hearing frequencies of these animals, i.e. 4-80 kHz in Risso’s dolphins, 20-80 kHz in Gervais beaked whale (*Mesoplodon europaeus*) and 4-100 kHz in long-finned pilot whales (*Globicephala melas*) (Mooney et al. 2012), fall within the most used sonar frequencies both in commercial fish-finders (some 50 kHz) and scientific echosounders (12, 38 & 70 kHz) causing them to react to some of these artificial sounds (Cholewiak et al. 2017; Quick et al. 2017). Moreover, several studies have proven that these whales are negatively affected by Medium-Frequency Active Sonar (MFAS) (Tyack et al. 2011; DeRuiter et al. 2013; Southall et al. 2016; Simonis et al. 2020). MFAS are thought to be responsible of drastic behavioural changes in deep-diving beaked whales, altering their highly stereotyped dive patterns and leading to fat and gas emboly consistent with decompression sickness, which can result in mass strandings and death of the animals even without stranding (Fernández et al. 2005; Fernández 2012; Arbelo et al. 2013). Anthropogenic noise can also reduce communication space for these vocal animals, like the noise produced by passing ships in shallow and deep waters masking delphinid whistles and calls in Australia and Tenerife (Jensen et al. 2012).

Chemical pollution

As most odontocetes are top predators of their respective ecosystems, bioaccumulation and biomagnification of chemical pollutants is especially harmful for them. Some of the most deleterious effects of this pollution are caused by the PCBs (polychlorinated biphenyls), affecting entire populations of orcas and Indo-Pacific dolphins (Andvik et al. 2021; Guo et al. 2021). Other harmful substances that these apex predators can accumulate are heavy metals (Storelli et al. 1999, 2002; Carvalho et al. 2002; Lozano-Bilbao et al. 2021), that can negatively affect physiological processes of these animals.

Plastic pollution

Plastic debris in the ocean can be found along the water column, firstly floating at the surface (Cózar et al. 2014) where it starts to decompose in microplastics particles and sink within epipelagic and mesopelagic waters. At any of these depths, microplastic can be incidentally incorporated to the food web. Surprisingly, there seems to be higher microplastic densities in mesopelagic fish than in epipelagic species, with the highest concentrations between 200-

600 m depth (Choy & Drazen 2013; Wieczorek et al. 2018; Choy et al. 2019). These depths fall within the typical foraging depths of most deep-divers (Tyack et al. 2006; Aguilar Soto et al. 2008; Fais et al. 2015; Arranz et al. 2018) and explain why some stranded deep diving whales have been found with macro and microplastic in their digestive system (Secchi & Zarzur 1999; Shoham-Frider et al. 2002; Gomerčić et al. 2006; Jacobsen et al. 2010; de Stephanis et al. 2013).

If plastic is not biologically incorporated, it reaches the seafloor. Recent studies show an alarming abundance in litter on the deep seabed in the Pacific Ocean (Amon et al. 2020), Western Mediterranean (Galgani et al. 2000; Cau et al. 2018) and North and Central Atlantic & Indian Oceans (Quattrini et al. 2015; Woodall et al. 2015). Blainville's and Cuvier's beaked whales along with sperm whales are known to forage near the seafloor (Arranz et al. 2011; Tønnesen et al. 2020; Visser et al. 2021), which could make them ingest these seabed-associated litter.

Interactions with boats: whale watching and collisions

There is a growing concern with cetacean mortality due to ship-strikes in the Canary Islands, where strike mortality increased since fast-ferries started to operate within the archipelago (Aguilar de Soto 2006; de Stephanis & Urquiola 2010). In some species that rest at or near the surface to recover from highly energy-demanding deep dives like sperm whales (Miller et al. 2008), the speeds of the ferries from 35 to 40 knots prevent these animals to avoid the collision with the upcoming vessel, as well as the skipper to manoeuvre to avoid the collision (Carrillo & Ritter 2010). Moreover, the life history traits of these long-lived animals such as the low reproductive rates make every whale death a significant one for the population of the

Canary Islands (Fais et al. 2016). Collisions with smaller boats may occur with smaller cetaceans, i.e. pilot whale juveniles (van den Berg 2019).

Deep waters fisheries and mining

Since some deep-diving odontocetes forage on organisms from the Deep Scattering Layer (DSL) and the Benthic Boundary Layer (BBL, at < 100 m of the seafloor) (Arranz et al. 2011; Fais et al. 2015; Copeland et al. 2019), human activities exploiting these large concentrations of biomass could negatively affect foraging in these cetaceans. Deep waters fisheries, including bottom-trawling, operate globally and have relevant impacts on the deep waters ecosystems that have long recovery times (Clark et al. 2016). Deep-sea mining is an emerging industrial activity that is thought to radically affect the whole deep-water ecosystem (Halfar & Fujita 2007; Van Dover et al. 2017; Niner et al. 2018), which would include effects on top predators such as deep-diving cetaceans that rely on deep waters resources to survive.

There are other human activities currently affecting deep-diving odontocetes, i.e. inducing high levels of stress-hormones (Dunstan et al. 2012), with animals getting injured in some interactions with fisheries or even dead as they are caught as bycatch (Bearzi et al. 2011).

The importance of protecting cetaceans extends further than their conservation. They are considered ‘umbrella species’ meaning that protecting them means protecting their habitat, as they are top predators of the ecosystems they are integrated in (Roberge & Angelstam 2004; Sergio et al. 2008). Being so, most of the actions promoted to preserve these animals would allow to also protect their ecosystems, as they cover extensive spatial ranges.

Moreover, cetaceans can act as indicators of the environmental status of the ecosystem (Azzellino et al. 2014). A healthy ecosystem can support a bigger cetacean population than an impacted ecosystem so, at the same time, cetaceans act as indicators of human disturbances like noise, plastic, chemical pollution, and stress responses (Van Bressem et al. 2003; André 2010; Bonanno & Orlando-Bonaca 2018).

Before taking conservation actions, knowledge of the basic biology of the species to protect must be held. This knowledge may not only be at the individual level, but also the group, population, species and ecosystem level. Here, I aim to contribute to gather some of this knowledge needed to inform conservation measures by addressing the following topics, which constitute the main chapters of this thesis:

- Synchronous vocal and diving behaviour in deep-diving beaked whales: applications for Passive Acoustic Monitoring
- Ecological niche and inter-specific competition in deep-diving odontocetes
- Deep-water habitat: combining passive and active acoustic monitoring to characterize deep-diving odontocetes soundscape and to study the Deep Scattering Layer

Synchronous vocal and diving behaviour in deep-diving beaked whales: applications for Passive Acoustic Monitoring

Passive Acoustic Monitoring (PAM) is a very extended methodology used to detect vocal animals with little environmental impact, as it just requires placing acoustic recorders in a specific location of interest. These techniques are becoming more efficient and new tools are being developed to use PAM to estimate animal density in an area. PAM is being applied to studies from insects to primates on land (Mankin et al. 2011; Kalan et al. 2015) and from fish to cetaceans at sea (Zimmer 2011; Wall et al. 2013). PAM-density estimations could be of particular value for inconspicuous species such as beaked whales (Cetacea: Family Ziphiidae) that remain only some 2 min at the surface but vocalize to search for prey (Arranz et al. 2011). Except for some higher density areas from which they can be sighted from land observatories (Arranz et al. 2014), beaked whales are extremely difficult to study using visual surveys, thus the importance of developing specific PAM techniques for these odontocetes. However, acoustic detections need to be calibrated to produce reliable animal counts. Density estimate models based on PAM need specific multipliers, as vocalization rates are not uniform throughout time nor space, as shown for bottlenose dolphins and Blainville's and Cuvier's beaked whales (Jones & Sayigh 2002; Warren et al. 2017). For beaked whales, it is unknown if group size affects individual click rates, as it seems to occur in shallow foragers like orcas and bottlenose dolphins (Barrett-Lennard et al. 1996; Jones & Sayigh 2002). Other factors that can influence emission rates are acoustic interference, cooperative foraging and/or eavesdropping.

In Chapter II, I participated in a broad collaborative study where digital archival tags (DTAGs, Johnson & Tyack, 2003) were deployed on Blainville's and Cuvier's beaked whales to study their synchronous acoustic and diving behaviour. Then, in Chapter III I used the same DTAG dataset to elucidate if group size affects individual click rates on these species, and I also tested if beaked whales living in groups suffer from interference and/or benefit from eavesdropping on conspecific echolocation clicks.

Ecological niche and inter-specific competition in deep-diving odontocetes

Deep waters of the open ocean harbour fish and squid that constitute a relevant trophic resource that is accessible to some predators when part of this biomass migrates towards the surface at dusk (Ramirez-Llodra et al. 2010; Irigoien et al. 2014; Ariza et al. 2016). However, deep-diving odontocetes have adaptations that allow these species to access deep resources 24 hours a day (Johnson & Tyack 2003; Miller et al. 2004; Tyack et al. 2006; Fahlman 2012). The diel behaviour of their prey could imply that these odontocetes change their foraging tactics in a diel pattern, and so present a different vertical niche width. The extreme diving capabilities of deep-diving odontocetes could also lead to interspecific competition between deep-divers foraging in the water-column of the open ocean. Moreover, stomach contents found in stranded animals have shown some deep divers forage on similar or identical prey (Clarke & Pascoe 1985; Hernández-García & Martín 1994; Santos et al. 2007; Fernández et al. 2009). Studying possible niche overlap between apex predators through their foraging habitat is relevant to understand geographic distribution of deep-divers and interspecific interactions.

In Chapter IV, I used DTAGs deployments on Blainville's and Cuvier's beaked whales, short-finned pilot and sperm whales and Risso's dolphins at similar latitudes to study their foraging habitat regarding at which depth and distance to the seafloor they attempt to catch prey. With these data, we can estimate the foraging habitat width of each species and its diel evolution, and elucidate how much of the foraging habitat of some deep-divers overlaps. The overlap in foraging habitat could explain interspecific agonistic behaviours observed in the wild, and so the geographic distribution of these deep-divers.

Deep-waters habitat: combining passive and active acoustic monitoring to characterize deep-diving odontocetes soundscape and to study the Deep Scattering Layer

For soniferous species like echolocating toothed whales, it is relevant to characterize the soundscape where they inhabit and monitor this acoustic space to detect possible variations in biological activities and/or disruptions caused by anthropogenic noises that sometimes overlap in frequency components with biological sounds (Weiss et al. 2021). The mesopelagic waters where deep-diving odontocetes forage are inhabited by one of the largest biomass concentrations on the planet, the Deep Scattering Layer, DSL, mainly consistent on Myctophidae and Gonostomatidae fishes (Sutton 2013) and zooplankton. Part of this biomass participates in the largest scale diel migration, swimming vertically from mesopelagic depths to the epipelagic realm at dusk and going back to the deep at sunrise (Sutton 2013; Ariza et al. 2016). There is some evidence suggesting that a chorusing event detected in deep waters of the Pacific and Indian Oceans is related to this diel migration (McCauley & Cato 2016; Lin & Tsao 2018), and it may be produced by migrating Myctophidae fish. However, the precise source of this chorus is still unknown, and the chorus has not been reported in the Atlantic Ocean yet. If there is a consistent chorusing event related to the diel DSL migration that could be detected and related to the migrating organismal density, this could be a highly useful and non-invasive PAM tool. The chorus levels could be used to assess the state and abundance of the migrating DSL in a given area and plan conservation measures i.e. temporally banning certain fishing techniques in the region or reducing boat traffic during the night, when the DSL approaches the surface and is more vulnerable to anthropogenic disruption.

In Chapter V, I analysed deployments of two hydrophones simultaneously sampling shallow and deep waters to characterize the soundscape of oceanic waters off El Hierro and Tenerife islands. A concurrent sampling with a scientific echosounder was conducted in order to elucidate if there is an evening chorusing event off these waters, and if it can be related to the organismal density estimated with the echosounder.

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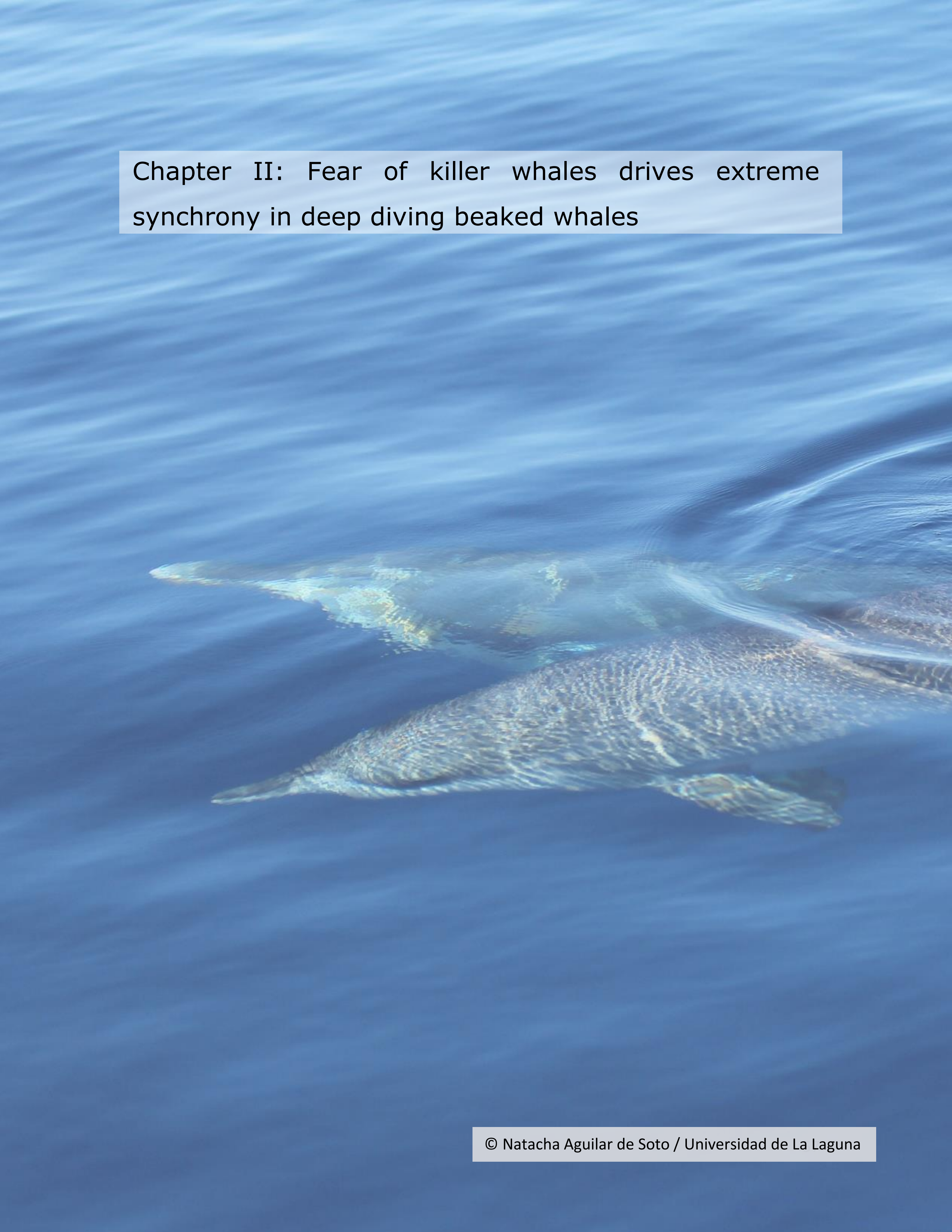

Chapter II: Fear of killer whales drives extreme synchrony in deep diving beaked whales

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Contribution statement. The publication of this Chapter II is literally reproduced in the next pages as it was accepted for publication, as it is of extreme relevance for the Chapter III. In order to clarify my involvement on the paper, these are the analyses for which I actively participated in: detecting the start and end of the vocal phase of each tagged whale in all their foraging dives, click train detection for tagged Blainville's beaked whales off El Hierro and Cuvier's off Azores, and distance estimates between paired tagged whales within the same group.

Abstract

Fear of predation can induce profound changes in the behaviour and physiology of prey species even if predator encounters are infrequent. For echolocating toothed whales, the use of sound to forage exposes them to detection by eavesdropping predators, but while some species exploit social defences or produce cryptic acoustic signals, deep-diving beaked whales, well known for mass-strandings induced by navy sonar, seem enigmatically defenceless against their main predator, killer whales. Here we test the hypothesis that the stereotyped group diving and vocal behaviour of beaked whales has benefits for abatement of predation risk and thus could have been driven by fear of predation over evolutionary time. Biologging data from 14 Blainville's and 12 Cuvier's beaked whales show that group members have an extreme synchronicity, overlapping vocal foraging time by 98% despite hunting individually, thereby reducing group temporal availability for acoustic detection by killer whales to <25%. Groups also perform a coordinated silent ascent in an unpredictable direction, covering a mean of 1 km horizontal distance from their last vocal position. This tactic sacrifices 35% of foraging time but reduces by an order of magnitude the risk of interception by killer whales. These predator abatement behaviours have likely served beaked whales over millions of years, but may become maladaptive by playing a role in mass strandings induced by man-made predator-like sonar sounds.

Introduction

Deep-diving marine mammals are expected to maximise time spent foraging in deep prey layers to offset the energetic and physiological costs of diving (Fedak & Thompson, 1993). But Cuvier's and Blainville's beaked whales (*Ziphius cavirostris* and *Mesoplodon densirostris*, respectively) employ a diving behaviour unlike that of other deep-diving toothed whales: they restrict echolocation to the deepest part of long and deep foraging dives that are typically followed by extended series of shallower and silent non-foraging dives that result in less than 20% of time devoted to biosonar-mediated foraging (Tyack et al. 2006; Arranz et al. 2011; Aguilar de Soto et al. 2012; Madsen et al. 2014). Further, these species ascend slowly and silently from deep dives at a low pitch angle (Tyack et al. 2006). This unusual and costly diving style has been interpreted as serving to mitigate decompression sickness or to accommodate lactate build up from foraging dives that may exceed the aerobic dive limit (Hooker et al. 2012), but see Velten et al. (2013). However, satisfactory physiological mechanisms to support these interpretations have yet to be found. When other toothed whales dive to similar depths, they do not display such a diving behaviour: both pilot whales that are similar in size to these beaked whales and the larger sperm whales ascend nearly vertically from their deep foraging dives (Miller et al. 2004; Aguilar de Soto et al. 2008) and often emit calls during the ascent to mediate reunion with non-diving group members (Jensen et al. 2011; Marrero et al. 2017; Visser et al. 2017). Because the highly stereotyped group diving and vocal behaviour of beaked whales is difficult to explain by foraging niche or physiology (Tyack et al. 2006) an alternate proposition is that it serves to abate predation risk (Tyack et al. 2006; Baird et al. 2008; Aguilar de Soto et al. 2012). Fear of predation can induce profound changes in the behaviour and physiology of prey species even if predator encounters are infrequent (Creel & Christianson 2008; Zanette et al. 2011). This is especially so for long-lived, slow-reproducing species such as whales for which even costly behaviours to abate predators have net fitness benefits (Ford et al. 2008).

While beaked whales can be attacked by sharks (McSweeney et al. 2007) and can be disturbed by delphinids (Cañadas, comm. pers.), their pre-eminent predators are killer whales (Jefferson et al. 1991; Wellard et al. 2016; Gualtieri et al. 2019). The problem of avoiding predators with acute hearing such as killer whales is compounded for echolocating toothed whales that must make sound to find food (Johnson et al. 2004), making them detectable at long ranges by listening predators. In contrast, killer whales are often silent when hunting mammals, giving little advance notice of their presence (Barrett-Lennard et al. 1996), and their power and speed (Williams & Noren 2009) limit the opportunities for last-minute escapes. Predation pressure from killer whales is thought to have driven some toothed whale species to vocalize beyond the hearing range of killer whales (Andersen & Amundin 1976; Morisaka & Connor 2007), while large aggregations of other species, from dolphins to cohesive groups of sperm and pilot whales, provide social defence (Curé et al. 2013; De Stephanis et al. 2014). However, smaller species of beaked whales have adopted neither strategy: they produce medium frequency clicks (Johnson et al. 2004) that are detectable at considerable ranges (Marques et al. 2009) and live in small groups that offer scant social defence (Baird et al. 2019). This apparent lack of a predator abatement strategy is at odds with their intense reactions to playbacks of killer whale and mid-frequency sonar sounds: even sound exposure levels close to the ambient noise can cause intense behavioural responses in beaked whales (Tyack et al. 2011; DeRuiter et al. 2013; Allen et al. 2014; Miller et al. 2015) suggesting that sonar-related mortalities (Frantzis 1998; Jepson et al. 2003) are rooted in an extreme anti-predator response (Bernaldo de Quirós et al. 2019). This leads us to posit that fear of predation is a major driver of the overall social and movement behaviour of beaked whales.

Here we test whether the distinctive features of beaked whale diving behaviour and group cohesiveness have quantitative benefits to reduce risk of predator encounters. We do so by analysing biologging data from Blainville's and Cuvier's beaked whales, that are among the best-known beaked whale species and also those most commonly found in mass strandings related to naval sonar (D'Amico et al. 2009). We propose that fear of predation shapes the minute-by-minute behaviour of these long lived, elephant-sized marine mammals which pay this heavy cost to access a privileged foraging niche and mitigate interception by a stealthy large-brained cosmopolitan predator.

Results and Discussion

We used biologging data from sound and movement recording tags (Johnson & Tyack 2003) on beaked whales, together with data reported in the literature, to quantify the predator abatement benefit of two aspects of their behaviour: (i) diving and vocal coordination, and (ii) ascent swimming.

Coordination

Killer whales are large brained and muscular predators with a limited diving capacity (Williams & Noren 2009; Miller et al. 2010). Although they can take fish from fishing lines up to 1000 m depth (Towers et al. 2019), biologging data suggest that they spend most of their time at <20 m depth (Miller et al. 2010). Further, the protracted and intense pack hunting effort required for killer whales to subdue cetaceans (Wellard et al. 2016), and their restricted

~10 min dive duration (Miller et al. 2010) strongly suggest that they can only hunt mammals at or near the sea-surface. We therefore propose that deep waters are a refuge where beaked whales are safe from killer whale attacks, and we predict that groups of beaked whales will coordinate their sound production and movements so as to minimise acoustic and visual detection when abandoning the deep refuge to return to the surface. We used two sources of data to test this notion: pairs of whales in the same social group were tagged simultaneously in three instances (two Cuvier's pairs and one pair of Blainville's) giving a complete quantification of their spatial relationship and coordination. Tagged whales were adults or subadults of both sexes swimming in larger social groups and we assume that their behaviour is a random sample of the behaviour of other group members. These data were supplemented with an analysis of movement patterns and inferred group vocal behaviour for a larger set of whales tagged individually, as well as an extensive dataset of sightings of both species.

Using the data from paired tags, we analysed coordination in deep dives while the whale pairs remained in the same group. For each whale pair we identified the deep dives (i.e., >500 m) performed by the first tagged whale. For each such dive we then found the deep dive with closest start time performed by the second whale. This resulted in 10 deep-dive pairs for analysis (Figure 1) with each deep dive of both whales associated with just one dive-pair. For these pairs of dives, the dive overlap, i.e., the proportion of the longest dive in each pair during which the other whale is also diving, averages 99% (SD 0.3%), while the overlap in the vocal phase, i.e., the part of the dive in which regular echolocation sounds are made, is 98% (SD 4%) (Table 1). One of the tagged pairs was in a group of Cuvier's in the Azores which was observed to split after 9 hours, separating the tagged whales. The dive cycle recorded after this whale pair split had a dive overlap of only 29% while vocal overlap disappeared completely (Figure 1). Table 1 reports the results of dive coordination for all whale pairs. For the Azores whale pair, the results are reported separately for the time before and after the whale pair split because from this point on the two whales were not in the same social group.

To test if the tight synchronization observed in whales swimming in social groups could simply be a consequence of the highly stereotyped dive cycles of these species, we analysed the overlap between the real dive profile of one whale of each pair and a simulated profile obtained from the other whale by permuting its dive cycles (i.e., each deep dive plus the following series of shallow dives before the next deep dive). This analysis excluded the Blainville's pair that only completed one dive cycle. All permutations of the two Cuvier's whale pairs had lower dive and vocal overlap than the actual profiles, with permuted averages of 64% and 54% overlap, respectively. Close dive and vocal timing in whale pairs is therefore the result of active coordination among group members. This interpretation is supported by the immediate loss of coordination when the Azores whale pair split. It is also corroborated with a larger dataset by examining the vocal overlap of group members audible in tag sound recordings from 12 Blainville's (46 deep dives) tagged separately in the Canary Islands (Table 2). The low ambient noise in this field-site means that presence/absence of echolocation clicks of group members can be reliably inferred. On average, group members began and ended clicking in deep dives within 1.8 (SD 1.5) and 0.9 (SD 1.0) min, respectively, of the tagged whales, giving an average vocal overlap of 99% of the mean 26 min long vocal phase of these dives. Thus, groups of beaked whales closely coordinate their deep dives resulting in almost complete overlap of the approximately five hours per day in which they produce sound to forage. This high vocal coordination means that groups of beaked whales are available for passive acoustic detection by eavesdropping killer whales less than 25% of the time, practically independent of group size.

Table 1. Diving and vocal coordination of three pairs of whales tagged in the same social group for overlapping time periods. For each pair of whales we located the deep dives performed by one whale and identified the deep dive of whale two with the closest start time. This resulted in 10 dive pairs including all deep dives of both whales. For these dives we quantified the time overlap and the vocal phase overlap (i.e., the minimum percent of time that one whale is diving/vocal when the other whale also is). Time overlap is computed separately for deep dives where whales forage using echolocation, and for silent shallow dives. Results are expressed as mean (range). Max depth: maximum depth of the paired dives; Depth diff: difference in maximum depth of the paired dives. Dur: dive duration. ♂ Male; ♀ Female; Ind: indeterminate sex.

Whale pair	**# dive pairs**	**Max. depth (m)**	**Depth diff. (m)**	**Dur. (min)**	**Dur. diff. (min)**	**Total time overlap (%)**	**Vocal time overlap (%)**
Blainville's Canary Islands ♂♀	Deep n = 1	639	16	46	2	99	98
	Shallow n = 6	56 (37–108)	8 (2–13)	11 (9–14)	0.7 (0.5–1.2)	93 (91–96)	—
Cuvier's Liguria Ind-Ind	Deep n = 4	954 (724–1600)	49 (6–135)	55 (48–64)	0.2 (0.2)	100 (99–100)	95 (90–100)
	Shallow n = 11	173 (114–275)	21 (6–42)	17 (15–20)	0.3 (0.1–1)	98 (94–100)	—
Cuvier's Azores (pre-group split) Ind-Ind	Deep n = 5	1544 (1296–1669)	287 (89–769)	61 (60–62)	0.3 (0.1–0.6)	100 (100–100)	100 (100–100)
	Shallow n = 12	166 (142–189)	39 (22–61)	19 (16–22)	0.6 (0.2–0.8)	97 (95–98)	—
Cuvier's Azores (post-group split) Ind-Ind	Deep n = 1	1574	134	61	0.1	29	0
	Shallow n = 3	270 (149–382)	65 (50–82)	19 (6–25)	7 (2–16)	42 (0–65)	—

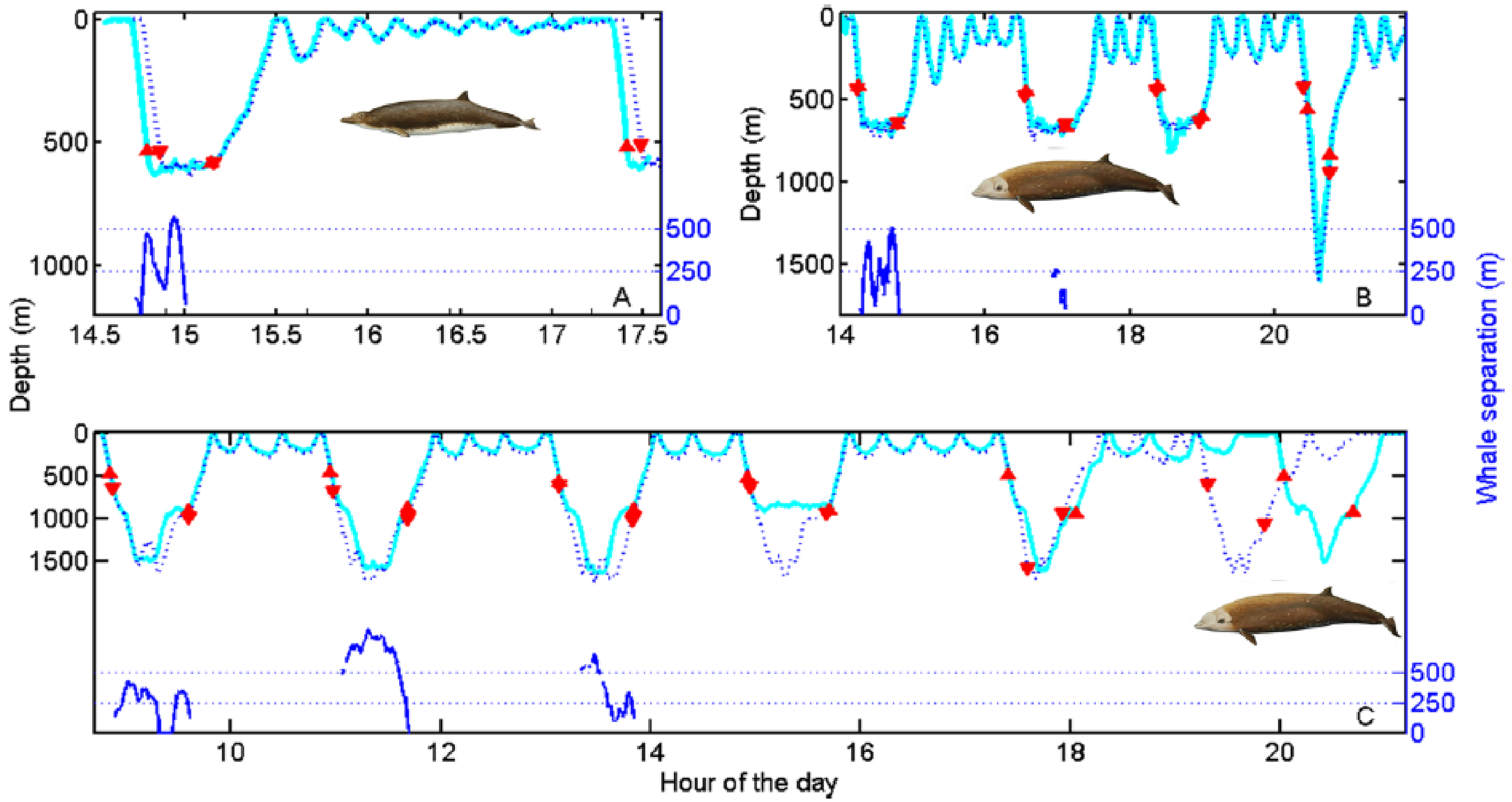


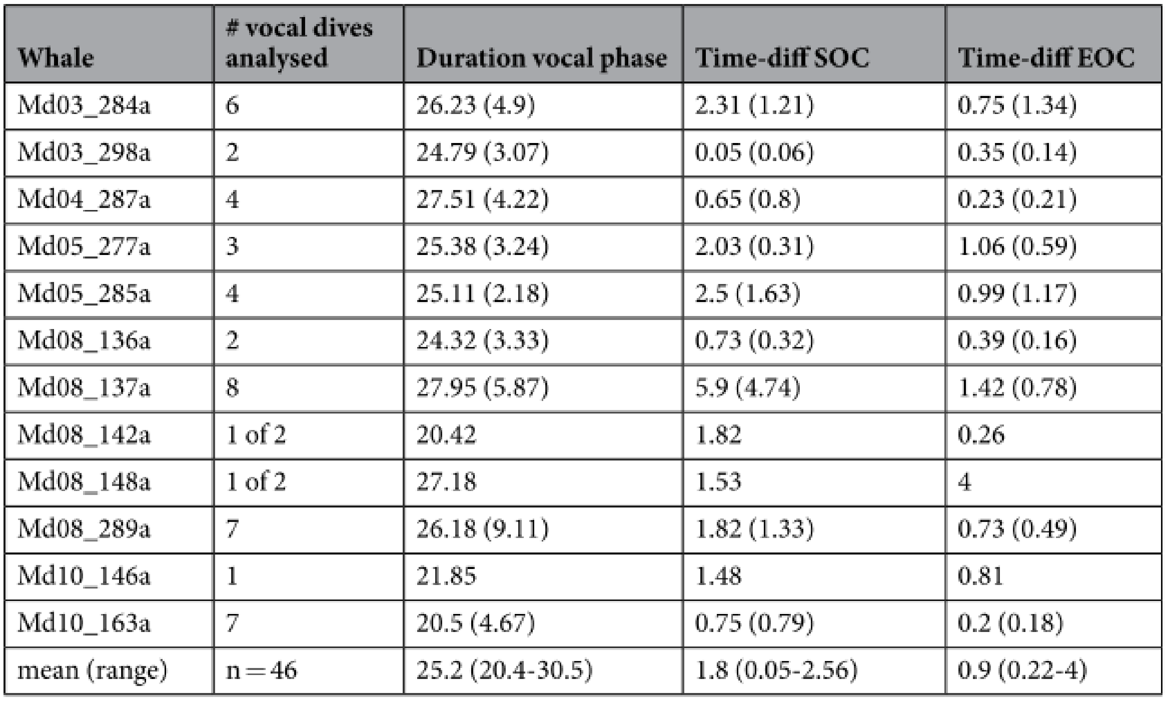
Figure 1. Dive profiles of three pairs of beaked whales tagged simultaneously in the same social group: (A) Blainville's, Canary Islands; (B) Cuvier's, Ligurian Sea and (C) Cuvier's, Azores. For each pair, dive profiles are represented by cyan solid and blue dashed lines. Up and down red triangles mark when the first and second whale of the pair starts and finishes vocalising. The remarkable synchronization of dive and vocal activity of the whales while in a group (the Azorean group were observed to split at about 19:00), results in the whales being silent, and therefore largely undetectable by predators that rely on passive acoustics, some 80% of the time. Blue lines at the base of some dives indicate whale separation where this could be calculated from the travel time of the clicks emitted by one whale to the tag carried by its companion. Whales separate horizontally, and in one case vertically, by several hundreds of metres at the base of dives indicating individual foraging despite tight alignment of dive duration, ascent rate and vocal interval. Whale drawings by Brett Jarrett.

Beaked whales live in fission-fusion societies and form groups of individuals of different age groups and sizes which nonetheless coordinate their diving and surfacing times. Even young beaked whales are observed to dive along with adults: in 18 years of field observations in the field-site of El Hierro, Canary Islands, comprising some three thousand sightings of Blainville's and Cuvier's groups, young have consistently been observed to dive and re-surface in close coordination with adults. This is in contrast with other deep diving species that leave young at the surface under alloparental care of group members (Whitehead 1996; Augusto et al. 2016) or whose calves perform shorter shallower dives, or both (Tønnesen et al. 2018).

The impact of coordinated diving on foraging efficiency might be less severe if beaked whales hunted as a pack, e.g., actively aggregating patches of deep prey. To test this possibility, we examined the separation distance during foraging dives between the three pairs of whales tagged in the same group, using the acoustic travel time of clicks between each pair to precisely track the animals. Whales were as close as 11 m (mean 154 m, SD 15 m, range 11–305) when they began echolocating at a mean depth of 450 m. They then separated by a mean of 287 m (SD 57 m, range 11–468 m) while hunting but closed in at the end of the vocal phase to a mean distance of 127 m (SD 15 m, range 28–297) (Figure 1). These results are consistent with the diving behaviour of beaked whale groups inferred from acoustic tracking with hydrophone arrays (Gassmann et al. 2015). Beaked whales therefore appear to separate to forage individually within dives but are constrained by the need to approach group members before they ascend to the surface in silence. Thus, beaked whale groups are in effect joined by an acoustic leash during deep dives limiting the total foraging footprint of the group to the distance over which group members can maintain acoustic contact and reunite during a carefully timed ascent. This coordination may benefit beaked whales if they monitor acoustically successful group members to guide prey search, but coordinating may also have foraging disadvantages. Beaked whales attempt to hunt some 20–30 prey per dive (Johnson et al. 2004; Tyack et al. 2006; Arranz et al. 2011; Aguilar de Soto et al. 2012; Madsen et al. 2014). This means that a group of e.g. five whales diving in synchronicity need to find some 100-150 prey in 20-30 min of echolocation within an area defined by the detection distance of their clicks.

The consistently high diving and vocal coordination demonstrated by both tagged whale pairs and individually tagged whales within groups, covering two species and different geographical areas, strongly suggest that collective behaviour is critical for social beaked whale groups: although the obligate deep vocal foraging intervals put beaked whales at risk of detection and stalking by killer whales performing passive acoustic tracking, beaked whales are safe to vocalize while in their deep refuge and their collective diving behaviour frees them from the need to vocalize during ascents to re-join non-diving members at the surface. This is in contrast to pilot whales or sperm whales that often vocalize during ascents to mediate group reunion acoustically (Jensen et al. 2011; Oliverira et al. 2016; Marrero et al. 2017; Visser et al. 2017). That beaked whales of different genera (*Mesoplodon*, *Ziphius*) show the same coordinated behaviour suggests that the coordination of diving and vocal activity in social groups may have evolved millions of years ago or has had sufficient evolutionary value as to drive convergence towards a strikingly similar strategy.

Table 2. Difference in the timing of start and end of clicking (SOC and EOC, respectively) between individually tagged Blainville's beaked whales and any untagged whale within acoustic range of the tags. Results are given in minutes and expressed as the mean (SD) for each tag deployment. The name of the tag deployment is formed by the two last digits of the year, the Julian day of the deployment and a letter indicating the consecutive tag order of the day. All vocal dives were analysed except for the two indicated in which clicks from other animals could not be assessed due to elevated background noise (primarily flow noise on tags located posteriorly on the whale), or in which EOC could not be assessed because the tag released before the end of the dive.



Whale	# vocal dives analysed	Duration vocal phase	Time-diff SOC	Time-diff EOC
Md03_284a	6	26.23 (4.9)	2.31 (1.21)	0.75 (1.34)
Md03_298a	2	24.79 (3.07)	0.05 (0.06)	0.35 (0.14)
Md04_287a	4	27.51 (4.22)	0.65 (0.8)	0.23 (0.21)
Md05_277a	3	25.38 (3.24)	2.03 (0.31)	1.06 (0.59)
Md05_285a	4	25.11 (2.18)	2.5 (1.63)	0.99 (1.17)
Md08_136a	2	24.32 (3.33)	0.73 (0.32)	0.39 (0.16)
Md08_137a	8	27.95 (5.87)	5.9 (4.74)	1.42 (0.78)
Md08_142a	1 of 2	20.42	1.82	0.26
Md08_148a	1 of 2	27.18	1.53	4
Md08_289a	7	26.18 (9.11)	1.82 (1.33)	0.73 (0.49)
Md10_146a	1	21.85	1.48	0.81
Md10_163a	7	20.5 (4.67)	0.75 (0.79)	0.2 (0.18)
mean (range)	n = 46	25.2 (20.4-30.5)	1.8 (0.05-2.56)	0.9 (0.22-4)

Silent ascent swimming

Although tight vocal overlap reduces the acoustic detectability of beaked whales, they nonetheless face the risk that eavesdropping predators are waiting for them when they return to the surface. Compared to terrestrial mammals that must choose between refuges and foraging, beaked whales live in a through-the-looking glass world: they are safe while making sound to forage at depths beyond the reach of killer whales but are at maximum risk when they come to the surface to breathe. Unlike most prey species (Clinchy et al. 2013), for beaked whales foraging is not risky but breathing is.

The low-angled powered ascents that are a distinctive feature of the foraging dives of Cuvier's and Blainville's (Tyack et al. 2006) have been proposed to serve in managing decompression sickness (Hooker et al. 2012) but the wide variability in overall ascent vertical speed from dive-to-dive (0.3-1.1 m/s Md, 0.4-0.9 m/s Zc, Martín López et al. 2015) is difficult to reconcile with a physiological need for a particular decompression rate. However, low pitch angle ascent swimming confers the direct advantage that beaked whales can cover a substantial horizontal distance during their silent ascents, potentially moving them away from waiting predators. We therefore hypothesise that beaked whales will move horizontally during ascents in such a way as to make it difficult for shallow diving killer whales tracking echolocation clicks produced at depth by beaked whales to predict where will they surface. Such a strategy is only possible for beaked whales because they do not need to re-join non-diving members at the surface. For other deep diving species such as pilot whales and sperm whales, non-diving group members, including calves left alone or under alloparental care at or near the surface (Whitehead 1996; Augusto et al. 2016; Tønnesen et al. 2018), form a surface anchor to which diving animals must return. In contrast, the collective behaviour of beaked whales frees them to choose their surfacing location.

To test the predictability of beaked whale travel during ascents we estimated dead-reckoned tracks (Johnson & Tyack 2003), constructed from the pitch, roll, heading and depth data recorded by the DTAG, for 64 and 37 silent ascents of 14 Blainville's and 10 Cuvier's, respectively. These tracks were plotted with respect to the mean heading during the last five minutes of vocal activity before initiating the silent ascent. The resulting tracks show that beaked whales frequently adopt headings that translate them away from the surfacing position that would be predicted by an eavesdropping predator (Figure 2C, D). On average, whales covered one kilometre horizontal distance from the point where they stopped clicking until they reached the surface (SD 430 and 710 m for Blainville's and Cuvier's respectively). This behaviour creates a large circular locus of potential surfacing positions that must be searched by killer whales and which they must search visually rather than using echolocation to avoid alerting their prey (Barrett-Lennard et al. 1996).

The average 1 km horizontal distance covered by beaked whales in silence during the ascent renders a surfacing uncertainty circle with an area of 3.1 km^2 (Figure 2B) which waiting killer whales must search within the 2.5 min that Cuvier's and Blainville's spend on average at the surface after a deep vocal dive. Assuming a swimming speed of 2 m/s for killer whales (Williams & Noren 2009) and a maximum visual detection range in most oceans of some 50 m underwater (Berman et al. 1985), an individual killer whale can cover visually only some 1.2% of the potential surfacing area of beaked whales during a surfacing. Encounter probability increases with killer whale group size: groups of up to 12 whales have been observed attacking beaked whales (Wellard et al. 2016) (Figure 2a) which could still only cover some 15% of the potential surfacing area of beaked whales with a perfectly coordinated search pattern. Thus, even if killer whales detect beaked whale echolocation clicks acoustically, the unpredictable low-angle silent ascents decrease predator encounter rate by one to two orders of magnitude compared to the vertical ascents made by other deep diving whales (Miller et al. 2004; Aguilar de Soto et al. 2008). But for this strategy to work, and even just to maintain group cohesion, beaked whale group members must ascend with similar speed and direction without additional vocal cues. This adds to the critical importance of tight coordination at the end of the vocal foraging interval.

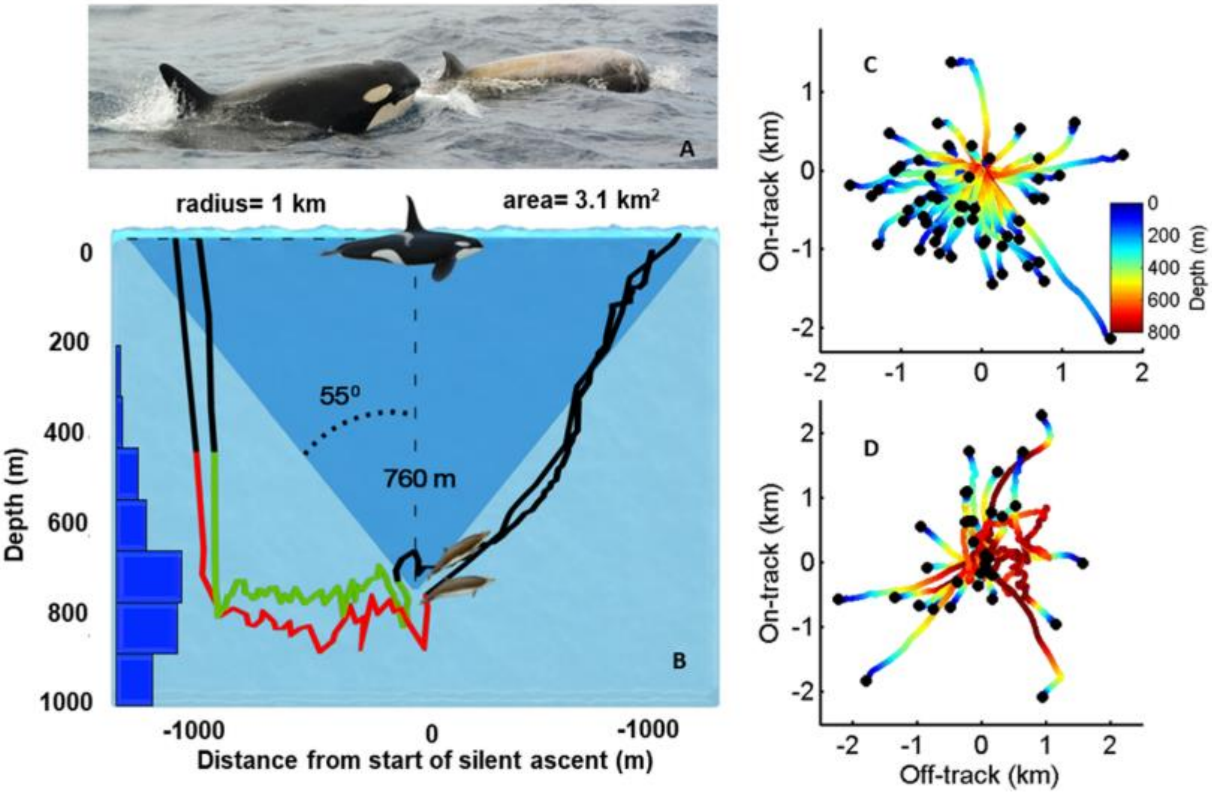


Figure 2. (A) Killer whales hunting a Cuvier's beaked whale (photo by Machi Yoshida, Naturaliste Charters Australia). (B) Foraging dive tracks of two Blainville's beaked whales tagged in the same group showing their activity synchronization. Coloured segments indicate hunting by echolocation whereas black segments indicate silent travel. Blue bars on the left show the depth distribution of all clicks from 14 tagged Blainville's beaked whales, confirming that they are silent at depths shallower than 200 m where killer whales restrict most of their dives. Cuvier's and Blainville's beaked whales begin a silent ascent at a mean of 760 m depth and ascend with a shallow angle (mean 35° from the horizontal) (Tyack et al. 2006; Martín López et al. 2015) in an unpredictable but coordinated direction. Dead-reckoned tracks show that ascending whales cover on average of 1 km horizontal distance from where they stopped clicking until they reach the surface, as represented schematically by the blue cone in panel B. (C, D) Horizontal dead-reckoned travel paths (coloured lines) of ascending Blainville's and Cuvier's beaked whales, respectively, with respect to their swimming direction before silencing. Travel in the same direction as the animal was moving prior to silencing is represented by the positive on-track axis in these plots while movements orthogonal to this are represented by the off-track axis. Surfacing positions (black dots) that are further from the centre of the plot are less predictable for an eavesdropping predator at the surface.

In the intervals between deep foraging dives, beaked whales maintain almost complete silence and so likely need occasional visual contact with other members of their social group to maintain cohesion. Between deep dives these whales typically perform a sequence of shallow non-foraging dives (Baird et al. 2006; Tyack et al. 2006; Baird et al. 2008), which can nonetheless reach 400 m depth and 25 min duration, and in which animals can move hundreds of metres horizontally (Tyack et al. 2006). We predicted that group cohesion should be evident as strong synchrony in the dive profiles of group members in the extended intervals between deep dives. To test this, we used again a permutation method on paired dive profiles. Shallow silent dives performed by the three whale pairs overlapped in duration by an average of 97% (SD 2.4, n = 29 paired dives). In contrast, the overlap of 3000 simulated shallow dive profiles (1000 per whale pair) constructed using dives randomly selected from the same whale pair, averaged just 30% (SD 4). This is consistent with field observations of Blainville's and Cuvier's (El Hierro), and from the tagged Cuvier pair in the Azores (Figure 1), where beaked whale groups tend to maintain close temporal and spatial cohesion in surfacing and diving, while coordination is lost when groups split.

The costs of hiding

The collective vocal and diving behaviour of beaked whales greatly reduces both the time intervals over which groups can be detected by acoustic predators, and the post-detection interception risk, in effect enabling beaked whales to hide from eavesdropping predators. Although there may be additional benefits of close vocal and movement coordination, e.g., in sharing foraging information via mutual acoustic monitoring, as has been observed in echolocating bats (Barclay 1982), this synchronization comes at a significant cost. The long silent ascents reduce the time available for foraging by some 35% as compared to vertical ascents, the common strategy of other deep-diving cetaceans (Miller et al. 2004; Aguilar de Soto et al. 2008), for the same dive duration. Moreover, the closely synchronized diving behaviour must accommodate group members across a range of diving capacities, further constraining the foraging time of larger individuals. This perhaps explains the unusually large size of newborn beaked whales (approx. 50% length of the mother, Mead 2002) in comparison to other toothed whales which are born at about one third of the adult size. A large birth length, and therefore weight, likely confers an advanced start for the ontogenetic development of diving capabilities and favours juveniles rapidly attaining the diving performance needed to dive with adults. Such large birth size may also explain why female beaked whales are similar in size or larger than males (Mead, 2002) despite inter-male fights that would be expected to drive sexual dimorphism towards larger males. Similar body size may have the further benefit of harmonising diving capacity among group members reducing the cost of accommodating diverse diving endurance within a group.

Conclusions and conservation implications

The unique diving and vocal behaviour of beaked whales could only evolve if the severe costs it imposes are outweighed by survival benefits. While the natural social and diving behaviour of beaked whales may be influenced by a whole suite of physiological, life history and ecological factors, we show here that the features that make beaked whale diving and vocal behaviour distinctive compared to other toothed whales confer major quantifiable advantages in abating predation risk from killer whales and even from visual predators at the surface such as sharks. These results provide the first quantitative support for previous hypotheses that the behaviour of beaked whales is influenced by predation risk (Tyack et al. 2006; Baird et al. 2008; Aguilar de Soto et al. 2012). Thus, while sperm whales and pilot whales, aided by either size or numbers, can choose to stay and fight off killer whale attacks (Pitman et al. 2001; Curé et al. 2013; De Stephanis et al. 2014), beaked whales with little social defence have adopted the strategy of hiding. Unlike many terrestrial prey species navigating landscapes of fear (Laundré et al. 2010) for which risk assessment is modulated temporally by perception of the state of predators and indirect predation cues (Creel & Christianson 2008; Zanette et al. 2011), beaked whales have little opportunity to assess risk, as mammal eating killer whales tend to hunt silently (Barrett-Lennard et al. 1996) and can only be seen at short range underwater (Berman et al. 1985). As a consequence, for beaked whales, tonal sounds above ambient noise that might signal killer whale presence or other threats could well provoke an anti-predator response (Tyack et al. 2011; DeRuiter et al. 2013; Allen et al. 2014; Miller et al. 2015). The beaked whale strategy of hiding is borne out in their responses to sonar and killer whale playbacks: silencing and avoidance (Tyack et al. 2011; DeRuiter et al. 2013; Allen et al. 2014; Miller et al. 2015). Evolution in a soundscape of fear therefore offers a mechanistic explanation for why beaked whales respond so strongly to playbacks of sonar and killer whale sounds at barely audible levels. Akin to ungulate escape responses from pursuing predators that can lead to death by physiological stress (Blumstein et al. 2015), naval sonar that inadvertently signals a strong risk-factor, such as the sounds of apex predators, may push beaked whales beyond their physiological limits and in some cases lead to sonar induced mortalities. As such, a successful predator abatement strategy shaped by natural selection has become maladaptive in the face of novel human activities. Given the vast zones over which mid-frequency navy sonars are audible and so may impact the behaviour of beaked whales (Tyack et al. 2011; DeRuiter et al. 2013; Allen et al. 2014; Miller et al. 2015), large-scale spatial avoidance of beaked whale habitats when mid-frequency sonar is used should provide the most effective mitigation measure for these cryptic species (Fernández et al. 2012).

Methods

Data collection

Beaked whales were studied using suction-cup attached DTAGs (Johnson & Tyack 2003) containing depth and orientation sensors (3-axis accelerometers and magnetometers) sampled at 50 or 200 Hz and two hydrophones sampled with 16-bit resolution at 96, 192, or 240 kHz. Blainville's beaked whales (n = 14), were tagged off El Hierro (Canary Islands, Spain) (Arranz et al. 2011; Aguilar de Soto et al. 2012); Cuvier's beaked whales were tagged in the Gulf of Genoa (Ligurian Sea, Italy) (Tyack et al. 2006), n = 10, and off Terceira (Azores, Portugal), n = 2. Whales were approached slowly from a small boat and the tag was deployed on the back of the whales with the aid of a handheld pole. Tags remained attached for up to 20 hours and were located for recovery using VHF tracking after their release from the whales.

Analysis of tag data

Tag data were analysed in Matlab (www.mathworks.com). Depth and movement data were calibrated with standard procedures (Johnson & Tyack 2003). Sound recordings were examined as in previous analysis of beaked whale DTAG data (Johnson et al. 2004; Tyack et al. 2006; Arranz et al. 2011; Aguilar de Soto et al. 2012) with custom tools from the DTAG toolbox (www.soundtags.org) to identify vocalizations of the whales. Vocalizations comprised echolocation clicks and buzzes (Johnson et al. 2004), as well as rasps and more-rarely whistles with an apparent communication function (Aguilar de Soto et al. 2012). Echolocation clicks were located individually with the aid of a supervised click detector (Johnson et al. 2004).

Cuvier's and Blainville's beaked whales perform deep and long foraging dives (deeper than 500 m) interspersed with series of shallow dives defined as dives between 20 and 500 m depth (Tyack et al. 2006). Surfacing intervals separating consecutive dives (i.e. deeper than 20 m) lasted on average 2.5 min (SD 0.6) and 2.6 min (SD 1.3) for Cuvier's and Blainville's beaked whales, respectively (mean of the median duration of the surface intervals performed by each whale, grouped by species).

When echolocating in deep foraging dives, beaked whales produce 2-3 clicks per second with occasional buzzes and short pauses. The vocal phase was defined as the interval in which this regular clicking and buzzing takes place in a deep dive (Johnson et al. 2004; Tyack et al. 2006).

Coordination of diving and vocal behaviour

Diving behaviour was analysed as in previous analysis of beaked whale DTAG data (Tyack et al. 2006; Arranz et al. 2011; Aguilar de Soto et al. 2012; Madsen et al. 2014). Groups of beaked whales were defined as clusters of whales observed together at the surface. No inferences were made about short or long-term group stability. Whales in these clusters were most often observed to surface together for the duration of the visual follow, albeit groups can also split. On three occasions (one per field site) we succeeded in tagging two whales in the same social group. Tag deployments on the two members of these whale-pairs overlapped in time during 3, 9 and 12 hours; the 6 whales forming these whale-pairs performed in total 22 deep and 64 shallow dives.

The *separation* *distance* between whales in each tagged whale pair was estimated during the vocal phases. This was achieved by measuring the time delay between the emission of a click by one tagged whale and the reception of the same click on the tag carried by the other whale in the pair. Comparison of time delays for clicks produced by each of the two whales allowed for estimation of the clock offset between the two tags. Clock offset was subtracted from the measured time delays to give the acoustic time of flight which was then converted to distance by multiplying by the path-integrated sound speed. Depth profiles of sound speed for each location were used together with the known depths of each animal to derive the path-integrated sound speed for each click. Sound speed profiles were gathered from CTD (RBR Ltd. and Sea-bird Scientific Inc.) deployments performed in El Hierro and the Ligurian Sea at the time of tagging, and from the AZODC database for Azores (http://oceano.horta.uac.pt/azodc/oceatlas.php) in a relatively close area and season of the year with respect to the tagging event.

Ascents from deep dives

Blainville's and Cuvier's beaked whales only forage during the deeper part of deep dives. In these dives they end echolocation at a mean depth of 738 m (Blainville's) and 856 m (Cuvier's). Descents in deep dives are performed with a pitch angle close to 90° and a vertical speed of 1.5 m/s (Blainville's) and 1.6 m/s (Cuvier's). However, both species ascend with a low pitch angle (approx. 35°) and a vertical rate of about 0.7 m/s (0.7 ± 0.1 Blainville's and 0.8 ± 0.15 Cuvier's) (Martín López et al. 2015). This means that whales take on average 9 min (Blainville's) and 11.5 min (Cuvier's) longer in ascending than if they were to ascend with the same speed and vertical posture that they use in descents. Given the average vocal phase duration of 26 min (Blainville's) and 33 min (Cuvier's) (Tyack et al. 2006), the extended duration of the ascent represents about 35% of the duration of the foraging time for both species.

Surfacing uncertainty area due to slow ascents

To assess the predictability of horizontal movements during ascents, dead-reckoned tracks (Johnson & Tyack 2003) were computed for the ascent (i.e., from the end of vocal activity until the whale reached the surface) of each deep dive of tagged whales for which the orientation of the tag on the animal could be estimated reliably, resulting in 52 and 33 ascent tracks from 14 Blainville's and 10 Cuvier's. As the DTAG lacks a speed sensor, the average orientation-corrected depth rate (OCDR) (Miller et al. 2004) over each ascent was used as a speed proxy in dead-reckoning. The OCDR is sensitive to noise at low pitch angles and so speed values were omitted from the average when the absolute pitch angle was less than 20 degrees. The ascents tracks were rotated by the negative of the average heading during the final five min of vocal activity in each dive so that an ascent track that continued in the same direction as the whale was moving while vocalizing would have a heading of 0°. We considered that horizontal movements taking the ascending whale away from the point of last vocalization would be increasingly unpredictable for an eavesdropping predator at the surface. The average surfacing location predicted from the dead-reckoned tracks was horizontally offset by 999 m (S.D. 434 m) and 1019 m (S.D. 709 m) from the last vocal position in Blainville's and Cuvier's, respectively (Figure 2C, D), with the tracks largely moving away from the direction of travel that the animals held in the last 5 min of vocal activity. This horizontal movement of a mean of 1 km in any direction gives a potential surfacing circle with area 3.1 km^2 (Figure 2B) that would need to be searched visually by a predator to locate beaked whales that had been tracked acoustically while diving.

Ethics and permissions

All experiments were performed in accordance with relevant guidelines and regulations for studying wild animals. Data were gathered with ethics authorization of Woods Hole Oceanographic Institution Animal Care and use Committee, the University of La Laguna Animal Use Ethics Committees and the KMR Institutional Animal Care and Use Committee. Research permits were granted by the US NMFS permits 981-1578-02 and 981-1707-00 (for data gathered at Italy) and the Governments of Spain and the Canary Islands, and by the Secretaria Regional do Mar, Ciência e Technologia, Direção Regional dos Assuntos do Mar (permit number 10/2015/DRA, for Azores).

Author contributions

P.T.M., M.J. and N.A.S. are equally contributing and corresponding authors, they gathered data in the field, analysed them and wrote the paper. F.V., P.A. and **J.A.** gathered data and contributed to data analysis. All authors (P.T.M., M.J., F.V., P.A., **J.A.**, P.T., G.R. and N.A.S.) revised and improved the manuscript.

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Chapter III: Deep-diving beaked whales dive together but forage apart

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Abstract

Echolocating animals that forage in social groups can potentially benefit from eavesdropping on other group members, cooperative foraging or social defence, but may also face problems of acoustic interference and intra-group competition for prey. Here, we investigate these potential trade-offs of sociality for extreme deep-diving Blainville's and Cuvier's beaked whales. These species perform highly synchronous group dives as a presumed predator-avoidance behaviour, but the benefits and costs of this on foraging have not been investigated. We show that group members could hear their companions for a median of at least 91% of the vocal foraging phase of their dives. This enables whales to coordinate their mean travel direction despite differing individual headings as they pursue prey on a minute-by-minute basis. While beaked whales coordinate their echolocation-based foraging periods tightly, individual click and buzz rates are both independent of the number of whales in the group. Thus, their foraging performance is not affected by intra-group competition or interference from group members, and they do not seem to capitalize directly on eavesdropping on the echoes produced by the echolocation clicks of their companions. We conclude that the close diving and vocal synchronization of beaked whale groups that quantitatively reduces predation risk has little impact on foraging performance.

Keywords: beaked whales, collective behaviour, acoustic interference, eavesdropping, cooperative foraging

Introduction

For social animals, the benefits from group living may include lower predation risks or increased foraging efficiency (Turner & Pitcher 1986; Townsend et al. 2011; McInnes et al. 2017). However, aggregating may also have costs involving physical interference such as intra-group competition for resources, or sensory interference of the visual, chemical or acoustic cues used to find food or to mediate group coordination (Strandburg-Peshkin et al. 2013). Acoustic signals used for communication often have long durations and low directionality, making them vulnerable to interference from other vocal group members (Grafe 1996; Kok et al. 2020). For example, when the acoustic signals of nearby animals overlap in time and frequency, it can result in signal interference either for communication, hunting or habitat exploration (Egnor et al. 2007). By contrast, the powerful foraging echolocation clicks of many social-living toothed whales, used to identify prey, are short (10–250 μs) and directional (Jensen et al. 2018) and are thus inherently less susceptible to direct acoustic interference, also known as jamming. However, clicks from other animals could reduce the detection of weak echoes returning from prey via direct interference as well as forward and backwards masking, i.e. due to a transiently increased detection threshold for weak echoes that immediately precede or follow a conspecific click (Elliott 1971). It has been postulated that some bats and dolphins mitigate interference by changing the frequency, amplitude and/or timing of their echolocation signals, or increase their silent periods when animals forage close to each other, known as a jamming avoidance response (Chiu et al., 2008; Jones et al., 2018; Kloepper & Branstetter 2019). These strategies differ between species and can be absent or remain undiscovered for others. For example, some bats shift the frequency of their signals when foraging close to conspecifics, while other species of echolocating bats lack any apparent jamming avoidance response (Ulanovsky et al. 2004).

Despite the potential for interference, echolocating within a group can have benefits if the group is herding prey in a cooperative manner (Benoit-Bird et al. 2009) or if foraging individuals can eavesdrop and interpret the acoustic cues produced by conspecifics (Barclay 1982). Of particular value for eavesdropping may be rapid click sequences, called buzzes, which appear to be produced by all echolocating animals when approaching prey (Madsen & Surlykke 2013; Wisniewska et al. 2014). Some echolocating bats are attracted by conspecific buzzes in laboratory experiments suggesting eavesdropping (Dechmann et al. 2009). Eavesdropping has also been suggested for wild foraging orcas (*Orcinus orca*) and bottlenose dolphins (*Tursiops truncatus*) (Barrett-Lennard et al. 1996; Jones & Sayigh 2002).

The foraging trade-offs imposed by group living may be especially acute for social deep-diving toothed whales such as beaked whales that must capture enough food in physiologically limited dives to compensate the energy expended in reaching their deep prey resources (Tyack et al. 2006; Madsen et al. 2014). Blainville's and Cuvier's beaked whales (*Mesoplodon densirostris* and *Ziphius cavirostris*, abbreviated hereon as Blainville's and Cuvier's, respectively) are echolocators that forage in light-limited deep waters and perform highly coordinated foraging dives when associated in small social groups (Aguilar de Soto et al. 2020), exacerbating the potential impact of acoustic interference and/or competition. Group members of both species show close temporal coordination of their foraging dives and of periods of hunting by echolocation within dives; this coordination has been proposed to increase survival by reducing predation risk from orcas. This is because diving in coordination enables beaked whales to ascend from deep vocal dives in silence and with a random direction, thus surfacing at unpredictable locations some 1 km from their last vocal position and presumably avoiding being detected by orcas (Aguilar de Soto et al. 2020). This fitness benefit could be augmented if they additionally gain hunting benefits by foraging in groups, e.g. by cooperative hunting or eavesdropping. Acoustic and/or physical interference resulting from vocal aggregation and competition could be the price to pay for these potential benefits. We expect that for a given prey density, intra-group competition and acoustic interference would reduce the availability of prey for each individual, resulting in a decrease in hunting rates. The decrease should be roughly proportional to the number of members of the social group mainly when beaked whales target prey in patches (Johnson et al. 2008; Madsen et al. 2013). This expectation assumes that the probability of success of each prey capture attempt is independent of the number of animals.

Here, we analyse the acoustic activity of Blainville's and Cuvier's beaked whales echolocating in groups to understand how these animals may experience and manage the above trade-offs of group foraging. For both species, we used suction cup attached multi-sensor tags to record their individual sound production and movements throughout foraging dives to test the null hypothesis that beaked whale foraging performance is unaffected by group size. We specifically tested the following predictions: (i) if beaked whales experience intra-group foraging competition, individual buzz rates will tend to decrease in larger groups; (ii) if acoustic interference from vocalizations of other group members causes jamming or masking, individual click rates would change with increasing group size to compensate (Chiu et al. 2008); (iii) if beaked whales benefit from eavesdropping on the vocalizations of other group members, individual click rates would reduce with increasing group size as animals take advantage of shared information, while individual buzz rates would increase due to the expanded detectability of prey items through eavesdropping.

Methods

Multi-sensor archival DTAGs (Johnson & Tyack 2003) were attached to Blainville's (16 deployments on 11 whales) off El Hierro (Canary Islands, Spain) and to Cuvier's (10 whales) in the Ligurian Sea (Italy) during field experiments performed between 2003 and 2018 (Table 1). Animals were approached from a small boat and the tags were attached to the dorsum of the whales with suction cups using a long pole for deployment. Pairs of whales were tagged in the same social group on one occasion each in El Hierro and Liguria (Aguilar de Soto et al. 2020). DTAGs recorded depth, three-dimensional magnetic field and acceleration (sampling rate of 50 Hz or higher) as well as acoustic data with one or two hydrophones sampling at 96 kHz in 2003 and 192 kHz thereafter (Johnson & Tyack 2003). The size and social composition of the groups of tagged whales were visually assessed. Tags detached from the whales after 3–30 h (median 8.6 h) of recording and floated to the surface where they were retrieved with the aid of VHF tracking.

Tag data were analysed using custom software (Johnson 2015) for MATLAB v7 (MathWorks). A supervised click detector (Johnson et al. 2006) was used to locate echolocation clicks and thereby identify foraging dives. Clicks produced by tagged whales were typically identifiable in the sound recordings by the presence of low frequencies that were absent in clicks from untagged whales (Johnson et al. 2009). Foraging dives were divided into phases of silent descent and ascent, and vocal foraging based on the presence of clicks. Click trains from untagged whales were identified regularly in the recordings when ambient noise was low. To quantify clicking activity from conspecifics the vocal phase of the tagged animal was divided into minutes, and for each minute, the maximum number of concurrently detected click trains was noted representing the minimum number of animals vocalizing at the same time. To verify the identification of clicks from tagged whales, we used the inter-click-interval (ICI) and angle of arrival (AoA) of the clicks at the stereo tags (Johnson et al. 2006; Johnson et al. 2009; Pérez et al. 2017). The AoA and ICI of clicks produced by the tagged whale showed little and smooth variations. Conversely, click trains from untagged whales show wider variations in the AoA within a short time period (Johnson et al. 2009), as well as highly variable, and generally lower, received levels, due to the varying direction and aspect of untagged whales relative to the tag (Johnson et al. 2006; Johnson et al. 2009; Pérez et al. 2017).

Trains of frequency-modulated usual echolocation clicks emitted by tagged whales were interspersed by fast series of unmodulated clicks (buzzes) associated with prey capture attempts (Johnson et al. 2004; Madsen et al. 2005; Johnson et al. 2006). Buzzes were defined as non-frequency modulated click trains with an ICI < 100 ms (Johnson et al. 2006). Foraging buzzes can be readily distinguished from social sounds like whistles (which are tonal sounds produced rarely by Blainville's and not yet found in Cuvier's) and rasps, which consist of frequency-modulated click trains with median ICI of 5 ms (Aguilar de Soto et al. 2012).

We constructed predictive models to assess the influence of group size on click and buzz rates of the tagged whales, i.e. the total number of clicks or buzzes in the vocal phase of each dive divided by the duration of the vocal phase. These models also allow us to determine if periods of silence are increased as an anti-jamming response, via a reduction in click rates per dive. Since our data contained multiple observations per individual, generalized estimation equations (GEEs) were fitted in R (Allaire 2012; Bailey et al. 2013; R Core Team 2013; Warren et al. 2017) with package geepack (Højsgaard et al. 2006) using foraging dive as the sampling unit and tag deployment as the clustering factor. Click and buzz rates per foraging dive were the response variables in separate models with group size as the predictor variable. Although the dependent variables were rates, which are usually Poisson-distributed, the counts of clicks and buzzes were large and thus were fitted with an identity link function (Gaussian family). We used an auto-regressive correlation structure (AR1) in which the expected correlation between observations (values per dive) within each cluster (tag ID) decreased as observations become further apart in time (Thomas et al. 2013). Although the group size of Cuvier's ranged 1–5, the dataset was dominated by groups of 4–5 individuals (Table 1). Because of this, foraging dives performed by the less frequent groups of 1–3 animals were pooled. A non-parametric Kolmogorov–Smirnov test (Massey 1951) was then used to check whether click and buzz rates in the dives performed by the smaller groups fit the same distribution as in dives performed by larger groups.

Vocalizing animals in a group of foraging beaked whales at a given time might be less than the actual group size, and individuals might potentially respond to jamming from a nearby animal by either silencing or increasing their acoustic output (Chiu et al. 2008; Foskolos et al. 2020). To test for these tactics, a Pearson correlation test was performed to evaluate the relationship between group size and the mean rate of clicks (i.e. clicks/sec) from untagged animals recorded by the tag for each minute of the vocal phase of the tagged whale. The rate was quantified by dividing the number of clicks from untagged whales received at the tag during the vocal phase by the duration of this phase. This analysis was limited to a subset of recordings with the lowest ambient noise, i.e. without sounds from other marine mammal species or boat traffic noise, and low noise from water flow over the tag due to the tag being located forward on the body of the whale. Also, we computed (i) the amount of time-tagged whales were silent (i.e. the sum of pauses in clicking greater than 1 s long), and (ii) the apparent source levels (ASLs) of tagged whale clicks, and if these were influenced by the number of other vocalizing animals during each minute of the vocal phase of all dives with low ambient noise. The tag position behind the head precludes measurement of the spectral characteristics or intensity of the forward-directed clicks (Johnson et al. 2009). However, the intensity of clicks from the tagged animal as recorded by the tag (the ASL) provides a relative measure of on-axis level (Madsen et al. 2005). We measured ASL by the first highpass filtering the sound data to remove noise at low frequencies (5 kHz, 4-pole Butterworth filter) and then calculating the root mean squared (RMS) level of each filtered click over a 1.4 ms window aligned to the start of the click waveform (Johnson et al. 2006). To test the relationships between minute-averaged animal counts and pauses and ASL, we used GEEs as described above, using the dive as the clustering factor and the tagged whale and minutes within foraging dive as the sampling unit. Although spectral adjustments are another potential response to jamming, these cannot be reliably measured in data from either the tagged animal or other nearby whales except in rare cases when conspecifics are echolocating directly towards the tag (Johnson et al. 2006).

In the two instances when pairs of whales were tagged in the same social group, the independence of the click rates of the pair was investigated. These data, previously analysed by Aguilar de Soto et al. (Aguilar de Soto et al. 2020) consisted of highly synchronized dive profiles and vocal periods. The independence of the click rates of the pairs was tested by comparing the time-paired minute average ICI sequences of the two whales with a Pearson correlation test. This involved calculating the average ICI per coincident minute of clicking, i.e. starting from the first second when both animals were simultaneously echolocating until the earliest end of clicking of the two tagged whales (n = 17 and 31 coincident minutes in Blainville's and Cuvier's, respectively). The minute averaging interval was chosen to reduce potential serial correlation in the ICI. Buzzes and pauses in clicking were removed from this analysis by selecting ICIs between 0.1 and 1 s.

To examine if the whales tagged in the same social group travelled in the same average direction during their synchronized dives, we plotted the heading of the two tagged whales, computed from the magnetometer in the tag, while producing each click using the CircStat toolbox (Berens 2009) for MATLAB. We also calculated the average headings of each whale in the pair for the full duration of their vocal foraging phase. To test if whales coordinated their heading on a finer timescale, we compared the average travel directions of the two tagged whales of the pair within each coincident minute of the vocal phase using a Pearson correlation test.

Table 1. Number of foraging dives analysed for each tag deployment along with visually observed group size. Deployments are codified by two letters indicating the species followed by the tagging year and Julian day and a letter indicating the tagging order of the day. Tagged whales are classified as: adult male (♂), adult female (♀) or indeterminate (I) which are adults or sub-adults of unknown sex. Most Blainville's are identified by their photo-ID catalogue code (http://www.cetabase.info). Some individuals were tagged more than once throughout the study.

species	individual (sex)	tag deployment	group size	no. of foraging dives
Blainvillés beaked whale	MdH1 (♂)	Md03_284a	5	5
		Md05_294b	3	4
		Md08_137a	4	5
	MdH6 (♂)	Md05_277a	5	3
		Md08_136a	4	2
	MdH15 (I)	Md03_298a	2	2
	MdH22 (♀)	Md04_287a	5	4
		Md05_294a	3	1
		Md08_289a	6	7
	MdH43 (♀)	Md05_285a	3	4
	MdH74 (♂)	Md08_142a	4	1
	MdHC1 (♂)	Md08_148a	2	2
	Md10_146a (I)		3	1
	Md10_163a (♂)		3	6
	Md17_168a (♂)		6	2
	MdH23 (♀)	Md18_297b	6	1
total	11	16		50
Cuvier's beaked whale	Zc03_263a (I)		4	7
	Zc04_160a (♂)		3	2
	Zc04_161a (I)		5	3
	Zc04_161b (I)		5	8
	Zc04_175a (I)		1	3
	Zc04_179a (I)		4	2
	Zc05_167a (♂)		5	3
	Zc05_170a (I)		4	5
	Zc06_204a (I)		4	2
	Zc06_205a (I)		4	4
total	10			39

Results

Tagged whales occurred in groups ranging 2–6 animals (Blainville's) and 1–5 (Cuvier's) (Table 1). Blainville's performed foraging dives that lasted on average 49.4 ± 6.5 min with vocal periods lasting a mean 24.2 ± 5 min, while Cuvier's dives lasted 59.3 ± 10.5 min during which they were vocal 33.9 ± 7 min.

The two pairs of whales tagged simultaneously in the same social group demonstrated highly coordinated dives (Figure 1, electronic supplementary material, Figure S1, Aguilar de Soto et al. 2020). Tags carried by each whale received clicks produced by the other tagged animal of the pair in 100% of the coincident vocal minutes when both tagged whales were clicking (Figure 1). The stereo tags recorded click trains of at least one other beaked whale (most probably a group member) during a median 91% of the vocal time of the tagged whales, within the subsampled low-noise dives (electronic supplementary material, Figure S2). As the detection probability of clicks from untagged whales is likely well less than 1 (Zimmer et al. 2008), the minimum number of whales counted for each group acoustically was similar to, but generally underestimated the group size estimated visually in the field (Figures 2 and electronic supplementary material, Figure S2). A similar assessment could not be performed for Cuvier's beaked whales tagged in Liguria due to the higher ambient noise level in this area of the Mediterranean Sea.

The average headings of the two whales of each pair during the vocal phase of their synchronized dives were very similar (129° and 128° for the two Blainville's and 161° and 126° for the two Cuvier's, Figure 3). However, despite the similarity of overall dive swimming direction, there was no evidence of the correlation between the average per minute headings of the tagged whales (Pearson correlation, R^2=0.04 and 0.08 and p-values=0.47 and 0.11 for Blainville's and Cuvier's, respectively).

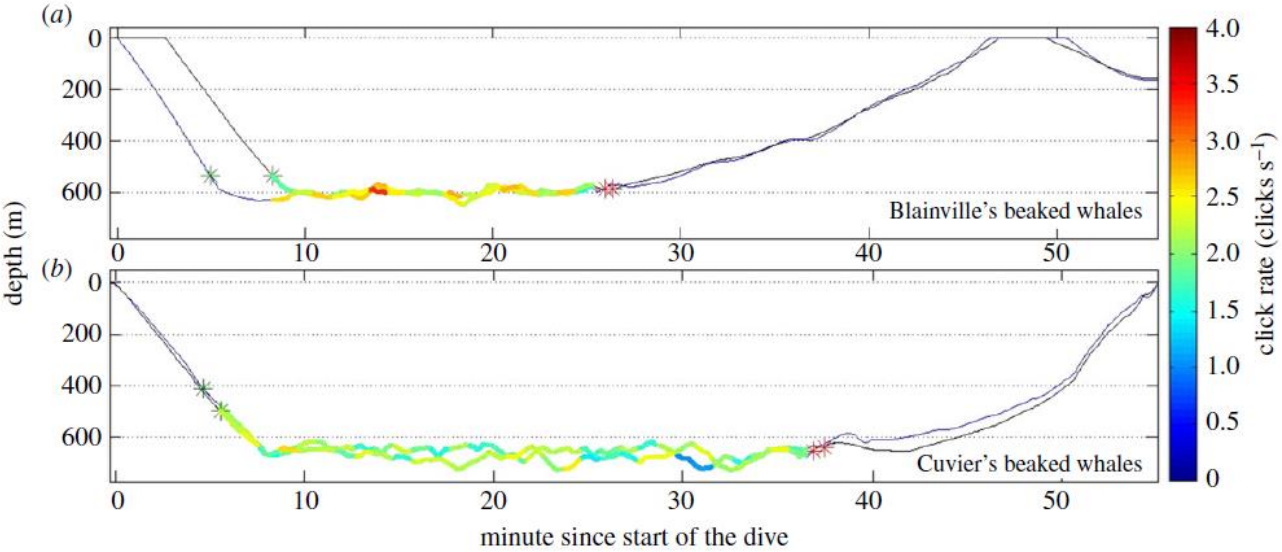

Figure 1. Coordinated dives of two pairs of tagged whales (Blainville's (a) and Cuvier's (b)) coloured by individual click rate. The start and end of the vocal phase of each animal are marked with asterisks (*), and the coincident vocal phase for each whale is shown as a thick line coloured by its click rate.

Despite the large potential for eavesdropping or interference, we found no evidence that individual acoustic activity was influenced by group size or by the acoustic behaviour of other group members (electronic supplementary material, table S1). Click rates averaged 2.41 ± 0.41 clicks/s for Blainville's and 1.54 ± 0.44 clicks/s for Cuvier's. Individual buzz rates averaged 1.1 ± 0.34 buzzes/min for Blainville's and 0.52 ± 0.37 buzzes/min for Cuvier's. No evidence of differences in the distribution of click and buzz rates of Cuvier's between small and larger groups was found (p-values for the K-S tests greater than 0.5). Also, the rate of clicks from untagged whales recorded at the tags showed no significant relationship with group size for the analysed Blainville's dives (Pearson correlation test: $R^2 = 0.12$, p-value = 0.08).

In addition to the dive-averaged click and buzz rates of individuals being uninfluenced by group size, whales within a group clicked at independent rates throughout the dive. Data from the two pairs of whales tagged simultaneously in the same social group showed no correlation in the minute-averaged ICI of the paired animals for either species ($R^2 = 0.002$ and p-value = 0.17 for Blainville's and $R^2 = 0.04$ and p-value = 0.57 for Cuvier's), albeit within the limitations of the small sample size. The number of nearby conspecifics detected by each tag did not influence the apparent source level of the clicks of tagged whales nor the amount of time-tagged whales were silent during the vocal phase of the dives (electronic supplementary material, table S2).

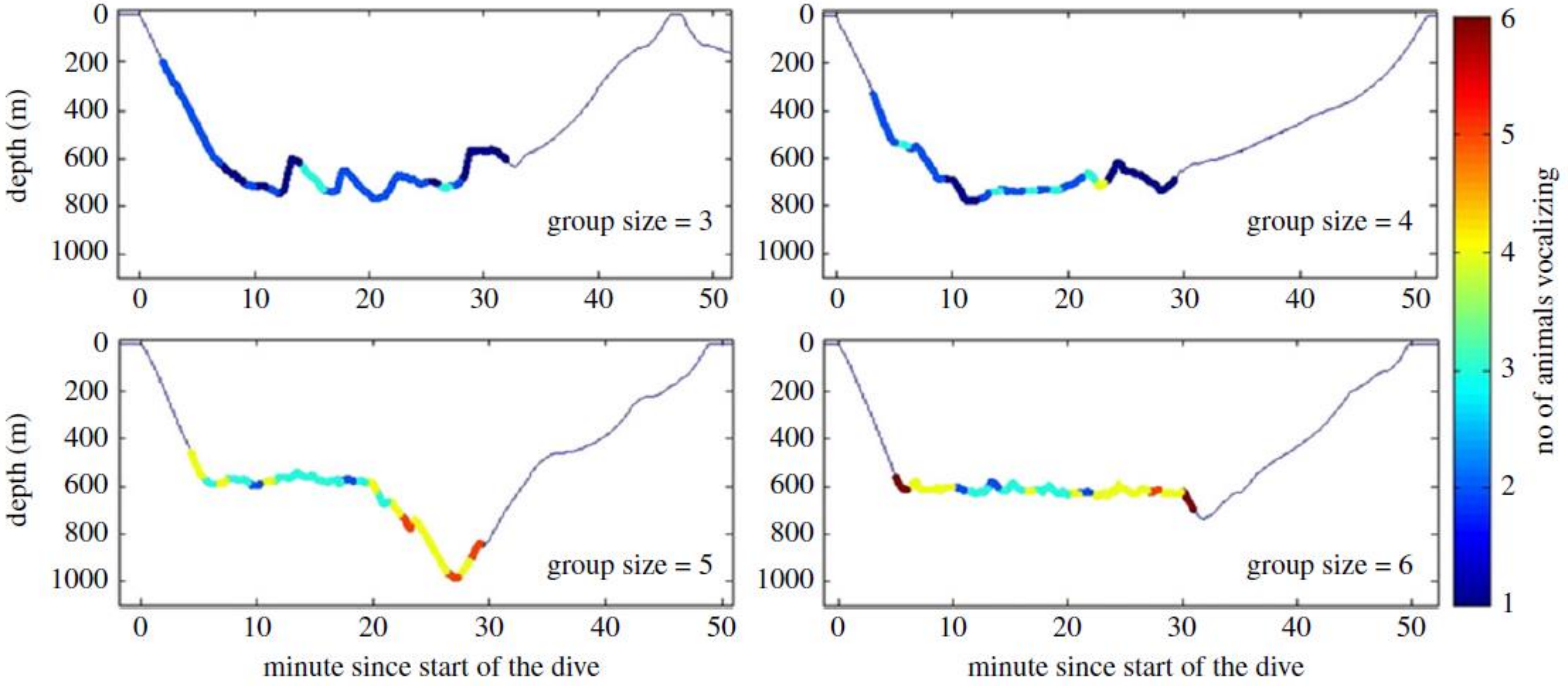

Figure 2. Examples of foraging dive profiles of tagged Blainville's beaked whales within social groups of 3–6 animals. The vocal phase of each dive is shown as a thick line coloured by the estimated number of animals vocalizing at the same time (including the tagged whale) measured as the maximum number of simultaneous click trains per minute received at the tag. Group size estimated visually in the field is indicated for each dive.

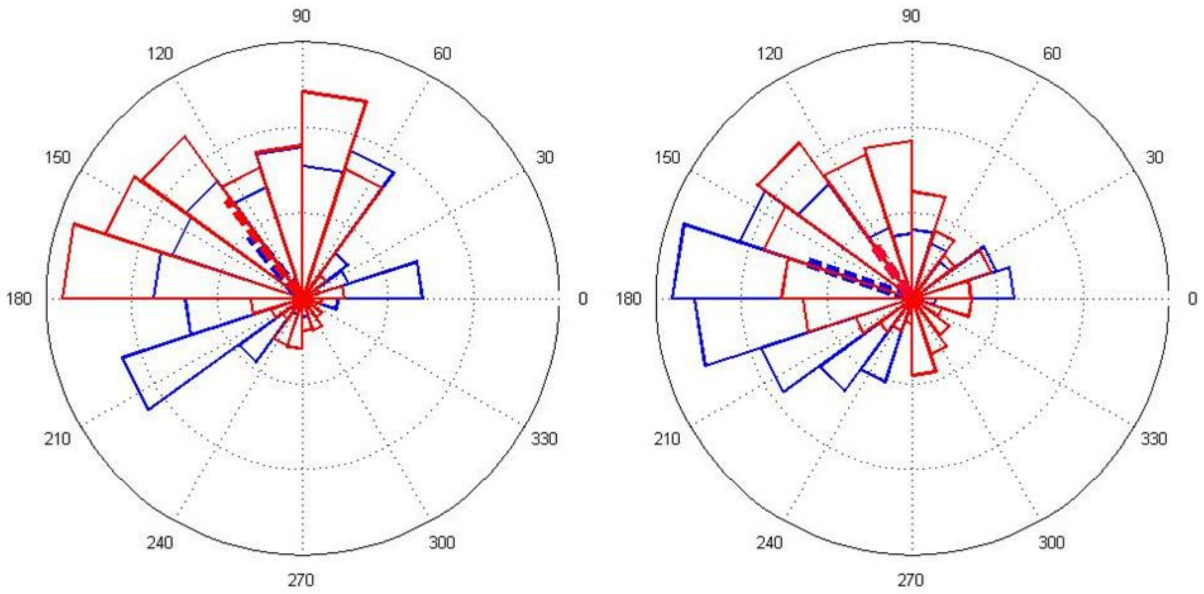

Figure 3. Circular histograms of the headings of pairs of tagged whales in a dive while emitting searching clicks (whale with tag A in red, and whale with tag B in blue) of two Blainville's (a) and two Cuvier's (b) beaked whales tagged in the same group. The dashed lines represent the average heading for each animal during the foraging dive and the line length is inversely proportional to the angular spread of each distribution.

Discussion

Deep-diving animals that live in groups face an apparent trade-off: if they stay close during dives to maintain social contact, competition and interference in hunting seem inevitable. Conversely, if they separate to hunt efficiently, they risk losing the group and the benefits of sociality, such as reduced predation risk (Aguilar de Soto et al. 2020). Allaying predation risk may be an especially strong evolutionary driver of the behaviour of Cuvier's (and most probably also Blainville's) beaked whales, given their strong responses to orca sounds and naval sonar (Aguilar de Soto et al. 2006; Tyack et al. 2011; Varghese et al. 2020). Here, we tested the hypotheses that echolocating beaked whales foraging with echolocation in highly coordinated groups may incur costs of aggregation due to intra-group competition for prey or interference of their echolocation signals, or may benefit from the proximity of group members through eavesdropping on their echolocation clicks and buzzes. Interference and eavesdropping seem particularly likely given the potential aggregation of their prey: in the mesopelagic realm, small fauna found in scattering layers can form patches some 20 to 150 m wide and beaked whales may target these small organisms in addition to larger predatory fauna also preying on these aggregations (Johnson et al. 2008; Madsen et al. 2013; Benoit-Bird et al. 2017).

We found no evidence that individual prey encounter rates (indicated by buzz rates) within dives were affected by group size, suggesting that on average there is little intra-group competition for foraging resources in social groups of beaked whales. Gregarious animals display a number of behaviour strategies to mitigate intra-group competition for food, e.g. sheep in large aggregations form subgroups to exploit different sub-patches of vegetation (Kurvers et al. 2010), and individual bees specialize in extracting pollen from different types of flowers around their colony (Heinrich 2004). Social mammals targeting a deep-water niche similar to beaked whales employ different strategies. Long- (*Globicephala melas*) and short-finned (*G. macrorhynchus*) pilot whales (Ottensmeyer & Whitehead 2003; Pérez et al. 2017) might reduce intra-group competition for prey by diving asynchronously and emitting calls to maintain acoustic contact between diving and surface group members (Pérez et al. 2017; Kok et al. 2020). Although these calls can provide cues to acoustic-guided predators, the strong cohesion of their large social groups enables pilot whales to perform mobbing responses against predators (Visser et al. 2016). Our data suggest that the behavioural tactic employed by beaked whales to reduce intra-group competition for prey is that group members diving in tight coordination spread out when foraging at depth. However, they then reunite to ascend together, avoiding the need to vocalize near the surface where they are more vulnerable to predator attacks (Aguilar de Soto et al. 2020). This behaviour might have co-evolved with small group sizes so that individuals can swim close enough to each other to coordinate their movements during dives, but sufficiently apart to find unexploited prey patches.

As expected for efficient independent foraging, we revealed that group members swim in directions which are uncorrelated on a short timescale while diving together. Nonetheless, they maintain a similar average heading over the full dive presumably to facilitate reunion during the ascent (Aguilar de Soto et al. 2020). While relative heading could only be measured directly in the two instances when animals were tagged in the same group, the usually continuous changing angles-of-arrival of clicks from group members recorded by all stereo tags supports this interpretation of independent movement (Johnson et al. 2009). Moreover, visual observations of groups of beaked whales regularly surfacing together after long dives affirms that overall swimming direction of group members is tightly coordinated during dives. Such coordination must be mediated by the near-continuous reception of the echolocation clicks of other group members, implying that foraging clicks have a secondary communicative function, acting as acoustic beacons of the relative position of animals while foraging.

The near-continuous inter-audibility of vocal group members is a consequence of beaked whales diving together and coordinating the vocal phase of their dives (Aguilar de Soto et al. 2020). However, the regular detection of one or more close group member throughout the foraging periods of the tagged whales raises the possibility that their echolocation signals might negatively interfere or alternatively that whales might beneficially eavesdrop on the echo returns of clicks from conspecifics. We found no evidence of jamming compensating behaviours: click rates of tagged whales were not affected by group size either for Blainville's or Cuvier's. This was also supported by the two pairs of whales tagged in the same social group. The individual click rates of these whales averaged over intervals of 1 min showed no correlation between pair members. Moreover, whales tagged singly in groups did not extend their silent periods (pauses in clicking) nor adjust the source level of their clicks when more conspecifics were audible as would be expected to enhance eavesdropping or combat jamming. Thus, we posit that acoustic interference does not constrain biosonar-mediated foraging in these species, and echolocation production is not detectably influenced by information-sharing, even if we cannot dismiss that whales might use the information provided by the acoustic activity of other group members. Instead, individual click rates in beaked whales have been observed to correlate with the movement patterns of the whales and may be influenced by prey distribution (Madsen et al. 2005, 2013).

The absence of compensatory behaviours in beaked whales contrasts with the 'anti-jamming' response proposed for bats where silent periods of individuals are increased when conspecifics are very close (Chiu et al. 2008). However, these taxa are subject to highly divergent ecological and physiological constraints. Echolocating animals that pause click production lose information on prey location and thus risk reducing their foraging efficiency (Foskolos et al. 2019). While bats can hunt continuously for an entire night, the rate and duration of breath-hold foraging dives of beaked whales are physiologically limited. This results in a stereotyped behaviour that affords them only 20–30 min of foraging time every hour or 1.5 h on average (Tyack et al. 2006; Arranz et al. 2011). It seems reasonable to hypothesize that these whales cannot afford to use silence as a strategy against jamming.

The lack of influence of group size on click production rate for beaked whales contrasts with observations of the acoustic behaviour of two species of delphinids: orcas and bottlenose dolphins (Barrett-Lennard et al. 1996; Jones & Sayigh 2002). These studies estimated individual click production rate by dividing the number of clicks from the group, detected by nearby drifting hydrophones, by a visual estimate of group size. Click rates in both species were observed to decrease on a per capita basis with increasing group size suggesting that individuals were reducing their click production rates and eavesdropping on echo information returning from clicks produced by group members (Barrett-Lennard et al. 1996; Jones & Sayigh 2002). The contrasting results for the beaked whales studied here might be explained by differences in behaviour and trophic niche. Fish-eating orcas and bottlenose dolphins forage most often in shallow waters (Baird et al. 2005; Miller et al. 2010) and sometimes coordinate their hunting (Elis et al. 2005), while Blainville's and Cuvier's beaked whales dive to mean depths of 800 m (Tyack et al. 2006) and hunt individually. The cacophony of clicks and their surface echoes from echolocating conspecifics in large groups of delphinids might clutter the acoustic scene of these shallow foragers, potentially making it beneficial to reduce individual clicking rates in preference for a scrounging or eavesdropping tactic. By contrast, a high resilience to jamming in echolocating dolphins (Kloepper & Branstetter 2019) has recently been revealed via low duty cycling of clicking and high directionality in sound transmission and hearing. Alternatively, contrasting observations from delphinids and beaked whales may result from methodological differences in these studies. Animal-borne acoustic tags used here on beaked whales offer a higher confidence when measuring individual click emission rates than do the drifting hydrophones used in the delphinid studies. This is because highly directional clicks may not be detected if they are not orientated towards drifting hydrophones, even when animals are at relatively short distances (Ladegaard et al. 2019), whereas they are more likely to be recorded on a tag carried by an animal. A further bias may be introduced if animals spread further apart when in larger groups, given that the detectability of animals at larger distances from the hydrophone would be reduced on average. Such an occurrence was found in Blainville's at El Hierro, with a reduction in per capita click rate observed with group size. Given that tag data show that the clicking rates are independent of group size, this means that progressively more clicks from untagged whales are missed at a point receiver as group size increases. This is consistent with an acoustic estimation of a group size of whales generally underestimating the visual count of whales as observed here and is likely associated with beaked whales separating and moving independently at depth to hunt (Aguilar de Soto et al. 2020). By contrast, the correlation between the detection rate of clicks from Blainville's and group size has been observed using an extensive array of deep moored hydrophones. In such a situation clicks have a high probability of being detected in any direction (Marques et al. 2019) and the probability of missing clicks is low. Such variability in observations when using differing methods highlights the importance of considering study design when interpreting results and also is particularly relevant when using passive acoustic monitoring (PAM) for density estimation of echolocating whales (Marques et al. 2009). This highlights that an improved understanding of group behaviour and detectability is crucial for appropriate application of acoustic methods for estimating population abundance, particularly when used for the effective management of these iconic megafauna.

Conclusion

Blainville’s and Cuvier’s beaked whales foraging in groups do not modify individual rates of echolocation and prey capture attempts in relation to group size. This indicates that sensory interference or competition from group members is unlikely to occur while hunting. Individuals are also unlikely to benefit from local enhancement directly by sharing information of echo arrivals from conspecific clicks. Tagged whales however, were in acoustic contact with other group members via eavesdropping almost all of their vocal (foraging) time. This presumably aids coordination of the timing and mean direction of their synchronized dives while they separate to hunt independently. Blainville’s and Cuvier’s beaked whales do not behave as cooperative hunting predators, but more like social foraging herbivores and frugivores such as ungulates and primates that coordinate group movements but forage independently (Doran & McNeilage 1998; Michelena et al. 2009). These collective behavioural tactics reduce intra-group competition allowing individuals to maintain foraging efficiency while gaining the social and predation risk abatement benefits of group living (Aguilar de Soto et al. 2020). Small group sizes in these species of beaked whales might thus be related to the foraging footprint of the group, as whales keep tightly coordinated during dives but still need to perform prey capture attempts per dive while hunting independently. This in turn suggests dependence upon a reliable foraging niche and sets an upper limit to the number of whales that can efficiently forage simultaneously.

Ethics

Tagging was approved by the University of La Laguna Animal Ethics Committee and authorized by the Canary Islands and Spanish Governments for El Hierro, and by the Woods Hole Animal Ethics Committee (previous affiliation of M.J.) for Liguria.

Data accessibility

Datasets basing the analyses of this paper are available in the electronic supplementary material, tables S3–S5 of the electronic supplementary material and per-minute datasets can be accessed from the Dryad Digital Repository: https://doi.org/10.5061/dryad.gqnk98sm0 (Alcázar-Treviño et al. 2021).

Author contributions

N.A.S., M.J., P.A., P.T.M. and **J.A.T.** collected the data. All authors analysed the data. **J.A.T.** wrote the paper with large contributions from N.A.S., M.J. and P.T.M. and all authors contributed to improve it.

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Electronic Supplementary Material can be consulted in the Appendix II.

Chapter IV: Comparative trophic ecology in deep-diving cetaceans derived from biologging

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Oases in the deep blue ocean: the importance of the DSL and the BBL for deep-diving whales.

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Abstract

Deep waters are compared to deserts, but they hold the largest biomass on Earth. This is exploited by air-breathing marine predators such as deep diving cetaceans. The behavioural ecology of these species might include interspecific competition leading to spatial segregation or coexistence. Here we used multisensor suction-cup attached DTAGs to investigate the vertical foraging niche of Cuvier´s (Zc) and Blainville's (Md) beaked whales, Risso's dolphins (Gg), and short-finned pilot (Gm) and sperm (Pm) whales. Depth and altitude above the seafloor of the whales while emitting echolocation clicks and buzzes indicated that: i) Md, Zc, Gm and Pm target mainly the mesopelagic realm; ii) Zc is the only species routinely targeting the bathypelagic; iii) Gm and Gg exploit the migration of the DSL to epipelagic waters to feed at night; iv) all prey on benthopelagic resources although Gm does so rarely. Levin's and Pianka's indexes show that Md, Zc, Gm and Pm are the species with higher niche overlap, and this is higher during the day than at night. Niche overlap and social structure might explain observations of interspecific agonistic behaviours in species with large group sizes that allow them to defend territories (Gm, Gg, Pm), in contrast with the spatial coexistence of species with small group sizes (Md and Zc) in spite of high niche overlap. The reliance of deep diving apex predators on resources of the DSL and BBL means that they would be negatively affected by emergent human activities such as fishing of the DSL or deep-sea mining.

Introduction

The largest megafauna species inhabiting planet Earth roam in the largest ecosystem: the blue ocean deserts (Thompson 1978). Open oceans harbour high levels of biodiversity and biomass in spite of their general oligotrophy (Ramirez-Llodra et al. 2010; Irigoien et al. 2014), but productivity concentrations are dynamic and vertically stratified. Oceanic top predators are thus generally nomadic and rely on exploiting oases of enhanced production (Thompson 1978). Oceanic waters present vertical zonation induced by depth-dependent environmental parameters: progressive pressure increment is accompanied by loss of light and decrease of temperature (Sutton 2013). Marine mammals in open waters can feed in the epipelagic realm (from the surface to 200 m water depth), mesopelagic (200-1000 m depth), and bathypelagic waters deeper than 1000 m (Ramirez-Llodra et al. 2010; Sutton 2013; Joyce et al. 2017). Also, where open waters encounter the seafloor, it is called the benthopelagic realm or Benthic Boundary Layer (BBL). The BBL has biological relevance due to the accumulation of organic matter. The altitude of the BBL is not constant but has been defined as some 100 m above the seafloor (Sutton 2013). The BBL acts as an ecotone where there is confluence of pelagic and demersal species by vertical and horizontal impingement (Mauchline & Gordon 1991; Sutton 2013). There is also vertical connectivity among pelagic layers due to the diel vertical migration of organisms that most often travel to shallower waters during the night to feed and return to depth before sunrise to avoid visual epipelagic predators (Sutton 2013; Ariza et al. 2016; Hernández-León et al. 2020). The Deep Scattering Layer (DSL), an amazing concentration of fauna that has been proposed as the largest biomass on the planet, forms the majority of this migration (Irigoien et al. 2014). The DSL includes migrant fauna and also non-migrant organisms forming a permanent DSL at some

600-800 m water depth (Ariza et al. 2016). Also, many deep-waters species undergo an ontogenetic migration where specimens shift their depth range to deeper waters as they grow (Arkhipkin & Bjørke 1999; Sutton 2013; Visser et al. 2021).

Deep-water resources are exploited by numerous predators, from seabirds that access deep prey only in shallow waters during the night, such as Cory's shearwaters (Dias et al. 2012), to mesopelagic sharks adapted to live at depth and hunt using bioluminescence as a cue (Claes et al. 2014). Some species of deep-diving odontocetes can forage day and night within a wide range of depths, e.g., short-finned pilot whales, beaked whales or sperm whales (Tyack et al. 2006; Aguilar Soto et al. 2008; Fais et al. 2015; Joyce et al. 2017). Biologging studies have revealed that these species use echolocation clicks to search for food and rapid sequences of high-rate clicks, named buzzes, when attempting to catch a prey (Johnson et al. 2004, 2006; Miller et al. 2004; Zimmer et al. 2005; Aguilar Soto et al. 2008; Arranz et al. 2016). Some of these studies have used the clicks of the whales as a bio-echosounder to estimate their altitude above the seafloor while foraging, revealing behaviours like Blainville's beaked whales following the steep bathymetry while foraging in the benthopelagic (Arranz et al. 2011).

Stomach content analyses of stranded Blainville's and Cuvier's beaked whales, short-finned pilot whales, Risso's dolphins, and sperm whales in the North Hemisphere have revealed some of the composition of their diet (Hernández-García & Martín 1994; Blanco et al. 2006; Santos et al. 2007; Fernández et al. 2009; Luna et al. 2021). Abundant beaks from the cephalopod family Cranchiidae have been found in stomachs of beaked, pilot and sperm whales, as well as beaks of the families Histioteuthidae and Octopoteuthidae in stomachs of beaked and sperm whales (Santos et al. 2007; Fernández et al. 2009; Foskolos et al. 2019) and more caloric Ommastrephidae cephalopods in stranded pilot whales and Risso's dolphins (Würtz et al. 1992; Hernández-García & Martín 1994; Blanco et al. 2006; Luna et al. 2021).

The overlap of prey species in the diet of deep-divers might result in interspecific trophic competition. Sperm whales have been sighted acting defensively in presence of short-finned pilot whales, and there is a report of a group of Risso's dolphins performing agonistic behaviours towards a group of sperm whales (Weller et al. 2006; Pérez et al. 2011). However, other deep-divers are regularly seen within the same area without apparent agonistic behaviour, e.g. Blainville's and Cuvier's beaked whales that are sighted year-round within the same bay off El Hierro (Canary Islands, Arranz et al. 2014). Learning more about the foraging interrelations of deep-divers is key to better understand their distribution. Further, the emergence of new potential anthropogenic activities in the deep sea, such as deep-sea mining and fishing of the DSL (Clark et al. 2016; Niner et al. 2018) underline the need to acquire data about the dependency of deep diving cetaceans of resources in the BBL and DSL to inform environmental impact assessment of these activities.

Here we analyse digital tags (DTAG, Johnson and Tyack, 2003) data to compare the foraging ecology of adult individuals of five deep diving species: Blainville's and Cuvier's beaked whales, short-finned pilot whales, Risso's dolphins and sperm whales feeding in subtropical to warm temperate waters. The depth of echolocation clicks and buzzes indicative of prey search and capture attempts, as well as the altitude above the seafloor at which these sounds were emitted, are used as a proxy to describe the foraging niche of each species and its diel variation. With these data, we can also investigate how much of the foraging niche of these deep-divers overlaps to inform hypothesis about potential intraspecific competition leading to habitat segregation or coexistence between species.

Material & Methods

Suction-cup attached tags (DTAGs, Johnson & Tyack 2003) recording acoustic, depth and triaxial movement data were deployed on five deep diving odontocete species in subtropical and warm temperate waters of the North Hemisphere (see tagging methods in Tyack et al. 2006; Aguilar de Soto et al., 2008; Arranz et al., 2019; and Supplementary Material). Two beaked whale species: Blainville's and Cuvier's beaked whales (*Mesoplodon densirostris* and *Ziphius cavirostris*, respectively); two deep-diving delphinids: short-finned pilot whales and Risso's dolphins (*Globicephala macrorhynchus* and *Grampus griseus*, respectively) and sperm whales (*Physeter macrocephalus*) (Figure 1, Supplementary Table S1).

First, foraging dives were identified as dives reaching > 20 m depth and containing vocal activity indicative of foraging (i.e., clicks and buzzes) as in Aguilar de Soto et al. (2008). For each foraging dive, buzzes were annotated as proxies of prey-capture attempts and all the echolocation clicks of the tagged animals were detected with the aid of a supervised click detector (Johnson et al. 2006; Marrero Pérez et al. 2017). These clicks were distinguished from non-tagged animal vocalizations using cues such as the angle of arrival of the clicks to the tag, their spectral characteristics and inter-click-intervals (Johnson et al. 2009; Alcázar-Treviño et al. 2021). Once the time cues for the searching clicks were extracted, echoes from the seafloor generated by these clicks were manually identified in echograms (Madsen et al. 2005; Arranz et al. 2011). The altitude of the echolocating whale above the seafloor was calculated by multiplying the two-way-travel-time (TWTT) by one half of the speed of sound in seawater, following Arranz et al. (2011). To estimate the foraging altitude, search clicks emitted up to 30 s before and/or after the buzz were used, since the lower source level of clicks emitted during a buzz often impedes the detection of seafloor echoes (Madsen et al.

2005; Arranz et al. 2011; Fais et al. 2015). Then, the estimated altitude of the whale within 1 min of the buzz was the result of averaging altitudes from all the detected seafloor echoes in that period. Depth and altitude of clicks and buzzes were used to allocate them to foraging layers (epi-, meso- and bathypelagic or benthopelagic). We followed definitions by Sutton (2013) to define these layers.

Clicking and buzzing data per tag for each species were pooled and allocated within 50 m depth bins from the surface to the rounded greatest depth recorded (2000 m). Then, relative click and buzz rates per 50 m depth bin per species were visually compared in plots for day and night observations. An additional comparative plot was made displaying the cases in which seafloor echoes were detected within 1 min of a buzz, showing the depth of the buzz and the altitude above seafloor of the foraging whale, for the five species, day and night. Lastly, a stacked bar plot was made showing the proportion of buzzes emitted in each pelagic layer during day and night, for each species. For this last plot, all buzzes with and without seafloor echoes detections were used from the pooled dataset of each species. Buzzes without seafloor echoes were assumed to be pelagic. To look for inter-individual variation in buzz depths, we calculated the proportion of buzzes emitted in each layer per tag deployment, and then made comparative boxplots with the data per tag for each species.

The distribution of emitted buzzes per species in different foraging layers was used to explore and compare the foraging habitat of the five deep-diving species by applying indices of trophic niche width and overlap. Analyses on trophic niche were performed using software R implemented through RStudio (R Development Core Team 2008; RStudio Team 2015). To estimate the foraging habitat amplitude of each species, we calculated diel trophic niche width for each species with the Levins standardized Index (Levins 1968; Sá-Oliveira et al. 2014), using the ‘MicroNiche’ package (Finn 2020) and the formula:

$$B_i = \frac{1}{(n-1)}\left(\frac{1}{(\sum_j p_{ij}^2)} - 1\right)$$

Where, in our case of studio, B_i = Levin's index of niche width, p_{ij} = proportion of buzzes of deep-diving species i within the water layer j, and n = total number of layers (in our case four layers). B_i values range from a species exploiting a single layer ($B_i = 0$) to a species exploiting the four layers in equal proportion ($B_i = 1$). We changed the proportion of diet for proportion of buzzes from the original definition of Levin's Index, and prey species for water layers, so that the index estimates foraging habitat width rather than prey-based diet width.

For the trophic niche overlap between species, we adapted definitions from Pianka's Index (Pianka 1973; Sá-Oliveira et al. 2014), using the package 'pgirmess' (Giraudoux 2021), with the formula:

$$O_{jk} = \frac{\sum_i^n p_{ij} p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}}$$

where O_{jk} = Pianka's index of niche overlap between species j and k; p_{ij} = the proportion of the ith resource in the diet of species j, in our case this was the proportion of buzzes within the layer i for the species j; p_{ik} = the proportion of the ith resource in the diet of species k, and n = the total number of water layers (instead of prey items).

For both indexes, the proportion of resources in the diet was adapted to the proportion of buzzes within each of the four defined layers, per species. Both indexes were calculated overall and separately for day and night data.

Results

This work analyses data of 81 DTAG deployments on adult or subadult whales of the five study species (Figure 1). The dataset of tagged whales is summarised in Table 1 per species (per whale data in Supplementary Table S1) and includes 484 foraging dives (254 during the day and 230 at night) and 6036 buzzes (3386 at day and 2650 at night).

Table 1. DTAG data deployments summary per species.

Species	**# tags**	**# dives** day | **night**	**# buzzes** day | **night** **# total (# with seafloor echoes)**
Mesoplodon densirostris	16	41 | **28**	1178 (485) | **658 (212)**
Ziphius cavirostris	10	19 | **13**	321 (39) | **270 (48)**
Globicephala macrorhynchus	27	75 | **49**	137 (12) | **259 (2)**
Grampus griseus	12	44 | **121**	432 (229) | **905 (207)**
Physeter macrocephalus	16	75 | **19**	1318 (533) | **558 (196)**
Total	81	254 | 230	3386 (1298) | **2650 (665)**

Vertical distribution of prey-search & prey capture attempts

The hunting behaviour of all studied species but Risso´s dolphins showed strong similarities in the main water depth ranges of daytime prey search effort and hunting. In contrast, the species diverged greatly in the nocturnal use of epipelagic resources, which were exploited only by pilot whales and Risso´s dolphins (Figures 2-3).

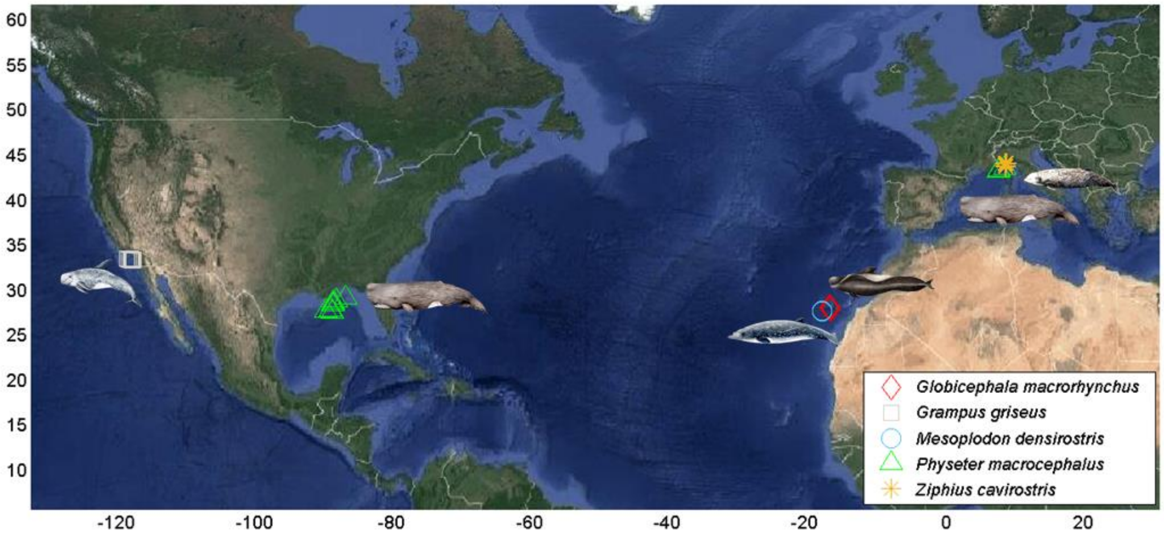

Figure 1. Tagging locations of Blainville’s and Cuvier´s beaked whales, short-finned pilot whales, sperm whales and Risso’s dolphins. Animal illustrations by Chloe Yzoard.

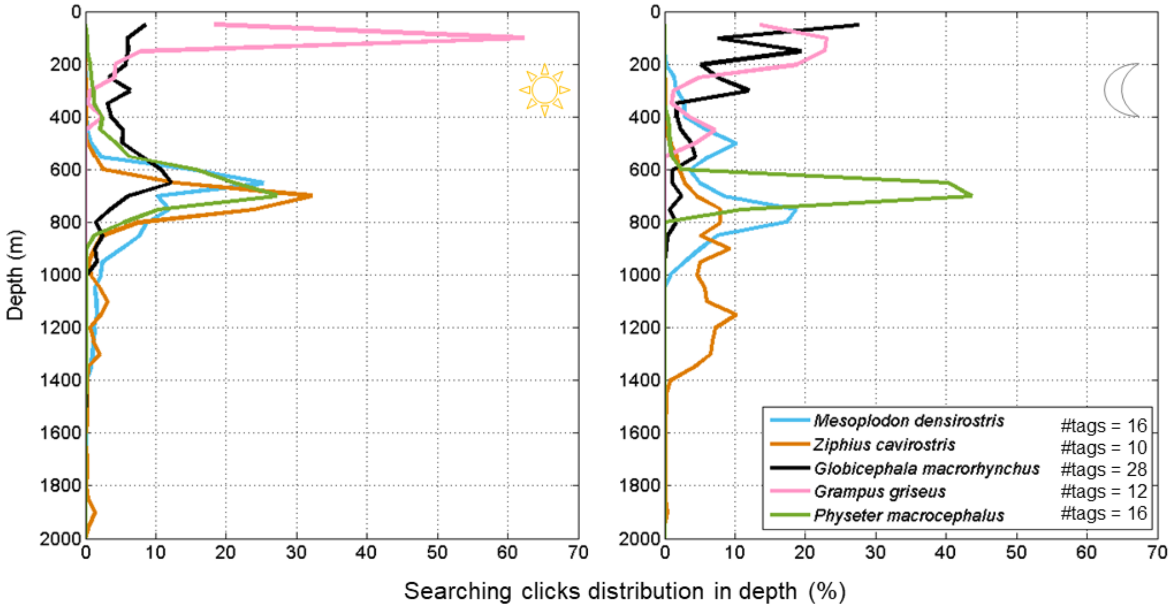

Figure 2. Distribution of searching clicks (color lines) in depth bins of 50 m from the surface to 2000 m water depth for the five study species during the day (A) and at night (B).

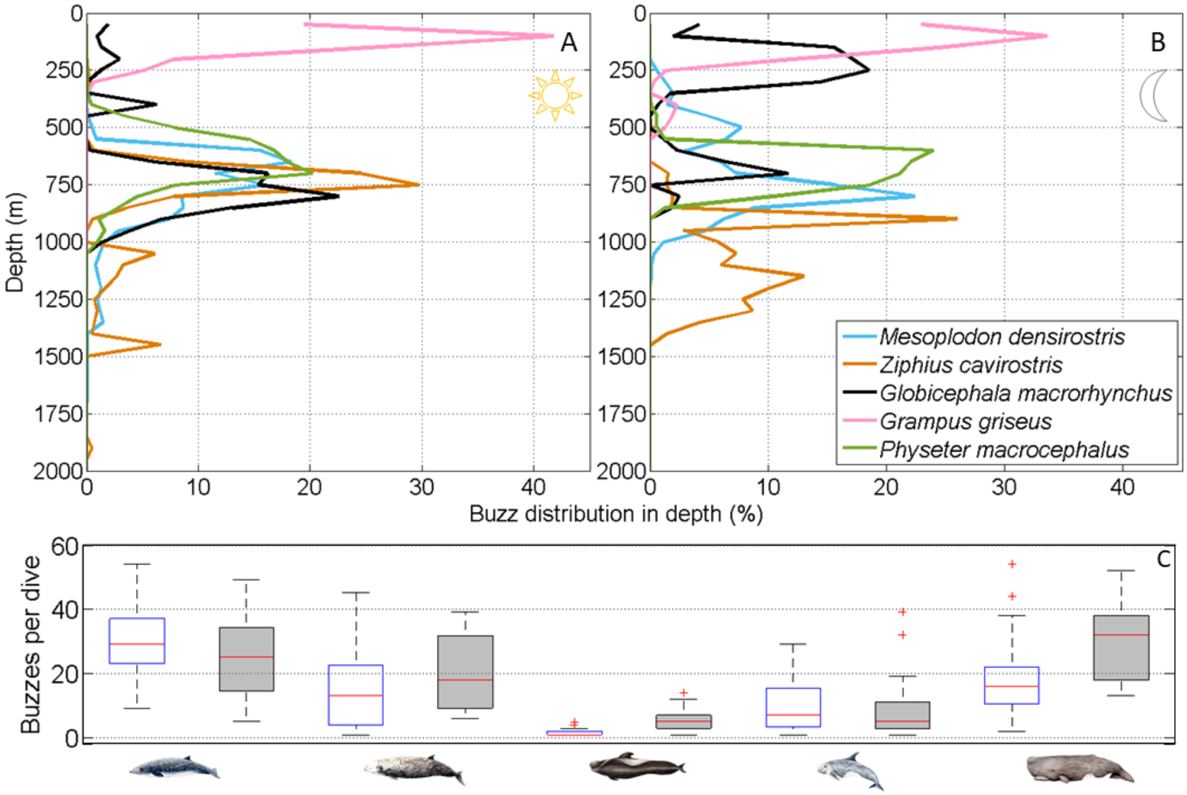

Figure 3. Distribution of buzzes (color lines) in depth bins of 50 m from the surface to 2000 m water depth for the five study species during the day (A) and at night (B). C: boxplots of the number of buzzes emitted per foraging dive during day and night periods (white and gray-coloured boxes, respectively) for each species.

Foraging altitude

Seafloor echoes were recorded for all the studied species (Figure 4-5), showing large differences in the use of benthopelagic habitat between pilot whales and the other four species (Table 2, Supplementary Figures S1-2).

Table 2. Buzz rate (number of buzzes emitted per minute of the vocal phase, i.e., the echolocating time within foraging dive), total number of buzzes and number of buzzes with seafloor echoes recorded for each species, and altitude above the seafloor estimated during buzzes with echoes, for day and night periods.

Species	**Day**		**Night**	
	bz rate = bz/min ± SD **#bz (#bz with seafloor echoes)**	**altitude (m)** **median (range)**	**bz rate =bz/min ± SD** **#bz (#bz with seafloor echoes)**	**altitude (m)** **median (range)**
Mesoplodon densirostris	1.19 ± 0.36 1178 (485)	130 (15-607)	1.31 ± 0.34 658 (212)	120 (13-707)
Ziphius cavirostris	0.42 ± 0.39 321 (39)	181 (16-687)	0.45 ± 0.17 270 (48)	155 (10-572)
Globicephala macrorhynchus	0.22 ± 0.32 138 (12)	143 (34-484)	0.39 ± 0.53 259 (2)	434 (434)
Grampus griseus	0.34 ± 0.37 432 (229)	8 (1-198)	0.92 ± 3.56 905 (207)	51 (3-422)
Physeter macrocephalus	0.49 ± 0.25 1318 (533)	123 (9-579)	0.85 ± 0.43 558 (196)	58 (9-304)

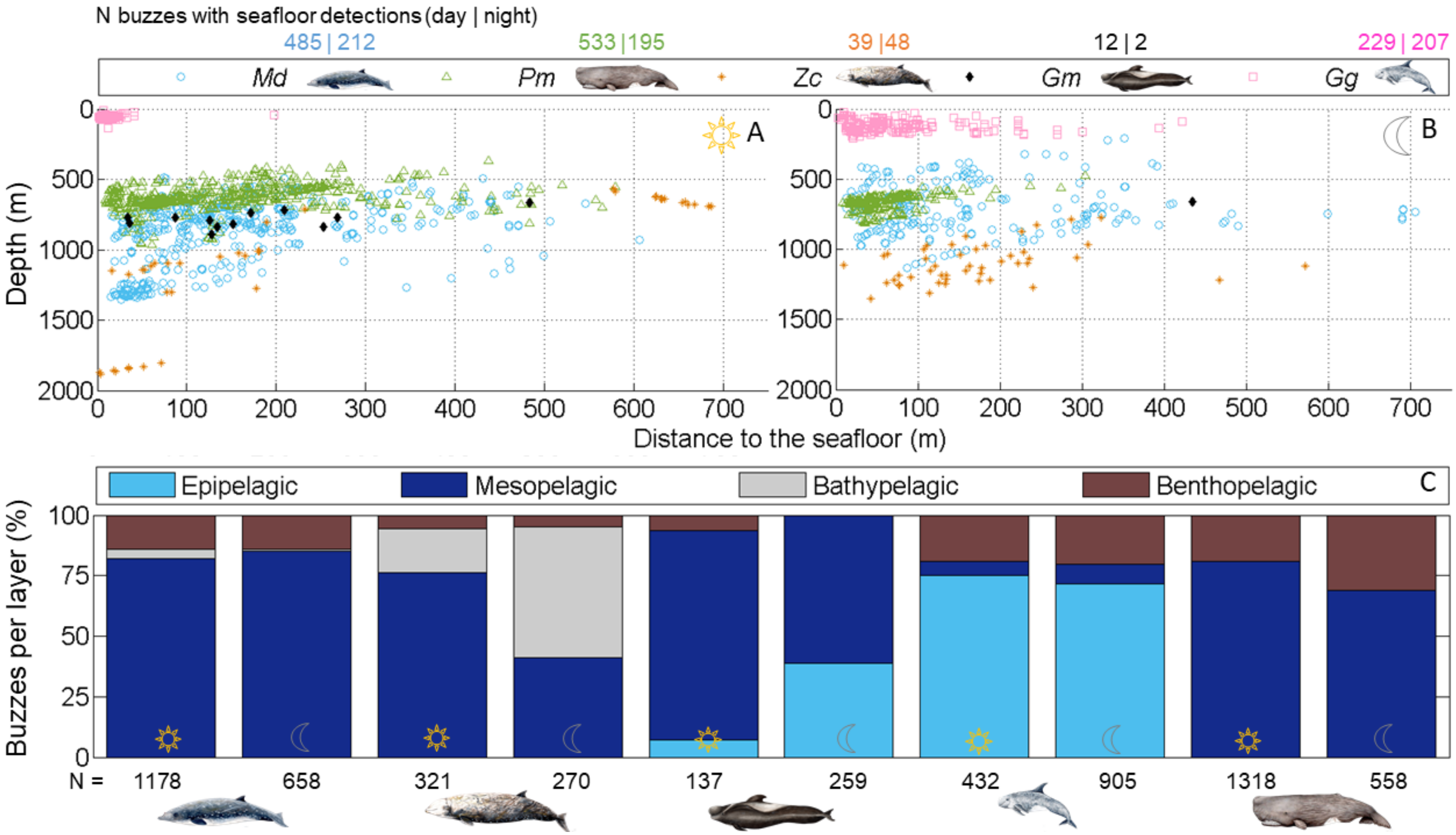

Figure 4. Depth and altitude above the seafloor of the whales while emitting buzzes that elicited seafloor echoes within 30s before or after the buzz, during the day (A) and night (B). C) Distribution of foraging during the day (sun) and night (moon) derived from all buzzes recorded for each species (N), with and without seafloor detections.

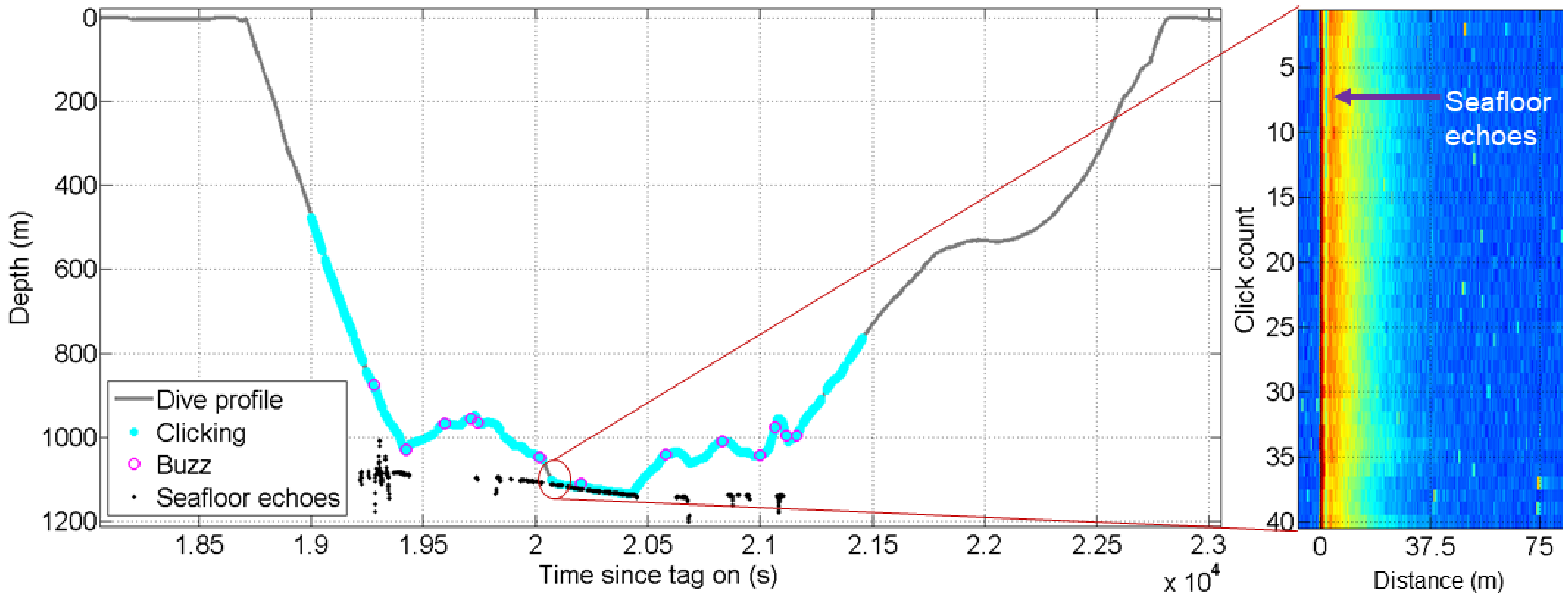

Figure 5. Dive profile showing clicking and buzzing activity for a tagged Cuvier's beaked whales (zc04_175) and the seafloor detections (left panel) and echogram showing how seafloor echoes were manually detected and the animal approaching the seafloor (right panel).

Distribution of prey capture attempts

We calculated the proportion of buzzes emitted within each depth layer from the water depth of the whale when emitting each buzz. Also, the altitude of the whale above the seafloor when emitting buzzes was calculated when seafloor echoes were received at the tag within 30 s before or after the buzz (Figure 4 and Table 3). If no echoes were received within this period, the buzz was assumed to be pelagic and allocated to the corresponding water depth layer.

Table 3. Proportion of the total # of buzzes emitted within each layer: overall (day | **night**).

Species (# bz total)	**Epipelagic (day | night)**	**Mesopelagic (day | night)**	**Bathypelagic (day | night)**	**Benthopelagic (day | night)**
***M densirostris* (n=1836)**	0 (0 | **0**)	83 (82 | **85**)	3 (4 | **1**)	14 (14 | **14**)
***Z cavirostris* (n=591)**	0 (0 | **0**)	71 (76 | **41**)	25 (18 | **54**)	4 (6 | **5**)
***G. macrorhynchus* (n=396)**	12 (7 | **39**)	82 (86 | **61**)	0 (0 | **0**)	6 (6 | **0**)
***G. griseus* (n=1337)**	69 (75 | **72**)	7 (6 | **7**)	0 (0 | **0**)	24 (19 | **21**)
***P. macrocephalus* (n=1860)**	0 (0 | **0**)	80 (81 | **69**)	0 (0 | **0**)	20 (19 | **31**)

In order to report possible individual variation, boxplots for the proportion of buzzes emitted within each layer were made using per tag deployment data (Supplementary Figure S3), showing outlier values for all the species in each layer.

Trophic niche indexes

Levin's standardized index for the foraging habitat width of the five studied species in the four water layers (Table 4) presents higher values for Risso's dolphins (0.51) while Blainville's beaked whales have the lowest value (0.36). The highest diel variation in niche width with this test is reported for the Cuvier's beaked whale (Δ 0.19) while Risso's dolphins present the lowest diel variation (Δ 0.008).

Table 4. Levin's standardized index values. For each species, the values show the niche width calculated for day vs night-time.

Species	Overall	Day	Night
Mesoplodon densirostris	0.362	0.399	0.332
Ziphius cavirostris	0.421	0.344	0.542
Globicephala macrorhynchus	0.442	0.403	0.489
Grampus griseus	0.516	0.520	0.512
Physeter macrocephalus	0.390	0.352	0.438

The results for Pianka's index of overlapping niche between pairs of the five species foraging in the four water layers (Table 5) reveal that the greatest foraging habitat overlap occurs during the day between both species of beaked whales (0.987), Blainville's and sperm whales (0.996) and Cuvier's and sperm whales (0.977). Both beaked whales and the sperm whales also overlap in foraging habitat with short-finned pilot whale (0.94), and short-finned pilot whales overlap during the night with Risso's dolphins (0.74).

Table 5. Pianka's Index values of overlapping niche between paired species for day and night (in bold) periods.

	Ziphius cavirostris	*Globicephala macrorhynchus*	*Grampus griseus*	*Physeter macrocephalus*
Mesoplodon densirostris	0.987 | **0.722**	0.94 | **0.795**	0.185 | **0.267**	0.996 | **0.963**
Ziphius cavirostris	-	0.949 | **0.574**	0.068 | **0.180**	0.977 | **0.675**
Globicephala macrorhynchus		-	0.238 | **0.741**	0.943 | **0.733**
Grampus griseus			-	0.191 | **0.312**

Discussion

Comparative trophic ecology studies of apex predators in the wild are relevant to better understand the dynamics of the ecosystem they inhabit. Exploring trophic niche width gives an idea of how generalist or specialist a species can be in relation to the available resources (Sá-Oliveira et al. 2014). Top-predator species that share adaptations to forage in similar habitats such as deep-diving odontocetes in the open-ocean could have overlapping trophic niches. Estimating this trophic niche overlap is key to understand the distribution of these species, as well as to explain interspecific agonistic behaviours that might be an evolutionary response to not overpopulate an ecosystem with apex predators exploiting either the same resources, or intertwined elements of the food webs in the deep open oceans.

Four of the five species studied here forage mostly within the same layer, the mesopelagic, while others diverge (Figures 3-4 and Table 3). Blainville's beaked whales mainly present a mesopelagic foraging, with some bathypelagic catches, and a constant use of the BBL through the day and night at seafloor depths deeper than 500 m (Figures 2-4 and Supplementary Figure S1). Cuvier's beaked whales are similar to Blainville's during the day, foraging mostly at mesopelagic depths combined with some foraging at the bathypelagic and the deep benthopelagic, but these whales forage more in the bathypelagic at night (Figure 4 and Table 3). Short-finned pilot whales are mesopelagic feeders, albeit with an important epipelagic component during the night (Figures 2-4) and very little use of the BBL. Some individual Risso's dolphins forage mostly near the seafloor (Figure 4 and Supplementary Figure S1 & S3) but the average feeding during the day in deployments on this species is epipelagic. At night, Risso's dolphins remain mostly epipelagic foragers with an important benthopelagic feeding at less than 200 m depth (Figure 4 and Table 3). Studied sperm whales behave similarly to Blainville's, being mostly mesopelagic feeders and sometimes approaching the deep seafloor, with minor differences in their diel foraging behaviour (Figure 4 and Table 3).

Trophic niche indices were calculated to estimate foraging habitat width and overlap between species (Tables 4-5). Attending to the results from Levin's test of niche width, both beaked whale species and the sperm whale are more restricted in terms of exploiting foraging layers during the day, while pilot whales and Risso's dolphins are more generalist in that aspect

(Table 4), as they are the only species taking advantage of the nictemeral migration of the DSL from meso to epipelagic waters. Cuvier's beaked whale is the species that presents the greatest diel variation in foraging habitat width, because they target the bathypelagic. Risso's dolphins have the least diel change for exploiting resources from the four water layers because they target mostly the epipelagic.

Our results show that the five studied species share a common foraging habitat in the mesopelagic realm, in oceanic waters between 200-1000 m depth. Both species of beaked whales and the sperm whale follow a similar foraging pattern during the day: they mostly search for prey and perform buzzes at mesopelagic depths where the DSL commonly occurs, i.e. between 400-800 m in the Canary Islands (Ariza et al. 2016) (Figures 2-4). These similarities are reflected in Pianka's index of niche overlap reporting values above 0.97 during the day when comparing the three species in pairs (Table 5). Analyses of stomach contents from stranded animals of these species reveal that the three of them share prey preferences for cephalopods within the families Cranchiidae, Histioteuthidae and Octopoteuthidae (Santos et al. 2007; Fernández et al. 2009; Foskolos et al. 2019). However, although in some cases they prey on the same species, their targeted prey size is different, i.e. the ranges of estimated dorsal mantle length for *Histioteuthis* cephalopods found in stomach contents of stranded animals in the Canary Islands was 1.5-7.5 cm in Cuvier's, 5.5 cm for a single Blainville's, and 8.5-22.9 cm in sperm whales (Santos et al. 2007; Fernández et al. 2009). This is consistent with the size difference between these predators, with the beaked whales reaching 0.8-3 tonnes (Allen et al. 1984; Mead 2002) while female sperm whales can weigh 15 tonnes (Whitehead 2018). Thus, these species hunt in part the same species, but in different ontogenetic stages, meaning that beaked whales are direct competitors for sperm whales, while sperm whales do not compete directly with beaked whales, since Ziphiids prey on earlier stages of the same prey, albeit competition could be indirect as sperm whales consume the reproductive stock of the same prey species.

During the night, these three species clearly diverge in their foraging patterns. Both beaked whales could be foraging on migrant species of the DSL during the night (Santos et al. 2007), as they abandon their preferred day-time foraging depth at night (Figures 2-3). As these animals avoid foraging at shallow waters (Aguilar de Soto et al. 2012, 2020), where part of the DSL migrates at night, they do not follow completely the vertical migration of the DSL to shallow waters after dusk, albeit Blainville´s partly shift their foraging to some 400 m depth (Baird et al. 2008; Arranz et al. 2011). Both species remain mostly mesopelagic foragers, but while Blainville's beaked whales at night concentrate their foraging just above and below their preferred day-time foraging depth, Cuvier's forage more often in deeper waters at night, reaching the bathypelagic (Figures 2-4). Both species present a consistent use of benthopelagic resources throughout the day (14 % and 6-5 % of buzzes are benthopelagic for Blainville's and Cuvier's during day and night, respectively), which could be providing them with prey which is bigger or easier to catch (i.e., less energy required to capture per unit of time). For example, some deep-waters species of fish and cephalopods present ontogenetic migration where larger organisms shift towards deeper habitats and the seafloor (Sutton 2013; Visser et al. 2021). Prey can also be easier to catch at depth due to the general trend towards a decrease in metabolism with increasing depth rendering limited evasive capacity (Seibel et al. 1997; Drazen 2007; Sutton 2013). Sperm whales feed at similar depths day and night, coinciding with the depth of the DSL, a diel behaviour similarly reported in the Bahamas (Joyce et al. 2017). This means that they prey on non-migrant species or individuals of the DSL, since not all individuals or migrant DSL species migrate every night (Ariza et al. 2016), and/or on migrant species that visit the DSL (Figures 2-3). Stomach contents found in stranded sperm whales (Fernández et al. 2009) include squid that undertake diel vertical migrations to the surface like some *Histioteuthis* (Bello et al. 2011) but also non-migrants like *Octopoteuthis* (Bush et al. 2009) or large squids that migrate but remain deeper than the epipelagic layer, like *Taningia danae* (Kubodera et al. 2007).

Studied delphinid species are more generalist, as revealed by Levin's niche width index (Table 4). Adult short-finned pilot whales are mostly mesopelagic foragers during the day (Figures 2-3). Within the mesopelagic layer, these animals perform sprints up to 9 m/s to chase their prey (Aguilar Soto et al. 2008) suggesting they are chasing rapid and highly caloric organisms. In epipelagic waters, they presumably prey on migrant DSL organisms at night. As shown with Pianka's index, these animals overlap in foraging habitat with beaked whales and the sperm whale during the daytime, and with Risso's dolphins at night (Table 5). Analyses of stomach content of stranded animals in the Canary Islands reveal a preference of short-finned pilot whales for oceanic squids within the families Cranchiidae, Cycoteuthidae and Ommastrephidae (Hernández-García & Martín 1994), similar to beaked whales and the sperm whale. Pilot whales at the Canary Islands hunt large prey probably including giant squid (Aguilar Soto et al. 2008), as sperm whales do (Fernández et al. 2009). They hunt also Ommastrephidae cephalopods, which are also found in stomach contents of Risso's dolphins (Würtz et al. 1992; Blanco et al. 2006; Luna et al. 2021). Risso's dolphins is the species that routinely forage shallower, being mostly epipelagic, with some benthic composition in their diet, and also preying on Histioteuthidae squids (Würtz et al. 1992; Blanco et al. 2006, Luna et al. 2021) as beaked and sperm whales do. Only Risso's dolphins and Cuvier's beaked whales were found to sometimes forage physically probing the seafloor (Figure 4-5 & Supplementary Figures S1-2). Since Risso's approached the seafloor in epipelagic waters were Cuvier's never forage, and Cuvier's did so in bathypelagic waters that Risso's dolphins never reach, we do not expect competition between both species regarding the benthic foraging, in an example of niche segregation between deep-diving species (Visser et al. 2021).

Our results are supported by typical prey sizes found in stomach contents of stranded whales. We find that pilot, sperm whales and Risso's dolphins prey on similar-sized individuals of the Ommastrephidae squid *Todarodes sagittatus* with Lower Rostral Lengths (LRL) between 0.8-1.1, 1-1.3 and 0.25-1 cm found in pilot, sperm whales and Risso's dolphins, respectively, and also on the Chiroteuthidae *Chiroteuthis* with LRL 0.5-0.6, 0.4-0.5 and 0.4-0.6 cm found in pilot, sperm whales and Risso's dolphins, respectively (Hernández-García & Martín 1994; Blanco et al. 2006; Fernández et al. 2009). This coincidence of prey size classes between pilot, sperm whales and Risso's dolphins could explain agonistic behaviours observed between the three species. Some short-finned pilot whale colonies are highly attached to their territories, that they usually defend from other whales as they have been observed to attack Risso's dolphins, and sperm whales react defensively to the presence of pilot whales (Shane 1995; Weller et al. 2006), which could reflect this foraging niche competition. Risso's dolphins have also been seen performing aggressive behaviour towards a group of sperm whales off Fuerteventura (Pérez et al. 2011), which may be reflecting the competition for similar-sized prey between these two species. This could happen even if Pianka's index of foraging habitat overlap between the two species is low (Table 5) if Risso's are preying on the same species as sperm whales do, but during the night at shallow waters thanks to the migration of the prey from the mesopelagic, where they are consumed by sperm whales during the day.

The partial overlap in the foraging habitat between deep-diving odontocetes could explain their geographic distribution and the rare sightings of these different species co-occurring in the same discrete area, in spite of their preference for similar prey, as well as the observations of agonistic behaviours (Weller et al. 2006; Pérez et al. 2011). However, species that usually lack aggressive behaviour and present similar predator-avoidance strategies like Blainville's and Cuvier's beaked whales (Aguilar de Soto et al. 2020) can be seen in the same area although they have overlapping niche mostly during the day, as observed off El Hierro in the Canary Islands, were both species are regularly present simultaneously in the same bay (Arranz et al. 2014). Some marine apex predators with overlapping foraging niche coexist year-round in the same area by reducing intraspecific competition as they present a diel temporal niche partitioning, e.g.: large sharks (Lear et al. 2021). However, this strategy would be inefficient in deep-diving marine mammals that have higher metabolic needs result of the extreme separation of two vital resources: the air to breath at the surface and their prey at great depths, resulting in these whales routinely performing highly energy-demanding dives. In this context, the foraging habitat segregation we report for some species is similar to that previously shown for beaked, pilot and sperm whales in the Bahamas (Joyce et al. 2017) and could be an adaptation to reduce competition for similar prey in these deep-diving apex predators. We speculate that beaked whales do not show agonistic behaviour because their small group size that allows group diving in synchrony to abate predation risk while reducing interspecific competition (Aguilar de Soto et al. 2020; Alcázar-Treviño et al. 2021) do not sustain territorial confrontations with other species, while pilot whales and Risso´s dolphins with large group sizes can use group defence both against predators and to base territorial defence.

Conclusions

The five species of deep-diving odontocetes studied here showed some level of foraging habitat overlap between them, mostly in the mesopelagic realm, foraging between 200-1000 m depth, and exploiting at some degree the highly valuable prey associated to the seafloor in the benthopelagic. However, foraging habitat segregation exists: Cuvier’s beaked whales feed more than the others in the bathypelagic, while short-finned pilot whales and Risso’s dolphins are the only species taking advantage of the migration of the DSL at night to epipelagic waters to feed. Risso´s forage more in shallow waters than the others, and also rely on benthopelagic prey.

Some of the studied species are known to rely on the strength of numbers both to mediate group defence against predators (Pitman et al. 2001; Bowers et al. 2018), or agonistic encounters (Weller et al. 2006; Pérez et al. 2011). For these species, the observed partial niche overlap could have resulted in the acquisition of agonistic behaviours to defend a territory rich in their preferred resources, e.g. the short-finned pilot whales, Risso’s dolphins and sperm whales. In contrast, beaked whales rely on different predator-avoidance tactics that do not require confrontation, such as synchronized dives and remaining silent in the epipelagic (Aguilar de Soto et al. 2020). These species would not have developed aggressive behaviours as a defence mechanism, neither against predators nor competitors, and this might explain why they can coexist in small groups in the same habitat year-round. These results on the behavioural ecology of the species are key to better understand the distribution of deep-divers and the evolutionary acquisition of agonistic behaviours between competitors.

Since all the studied species rely on mesopelagic and benthopelagic resources, they would be impacted by bottom-trawling and deep-water fisheries that operate at > 200 m (Clark et al. 2016) as well as by fisheries that target DSL resources. These fisheries would have a combined negative impact on deep-divers with the increase on macro and microplastics in the food web and in the open ocean, where these plastics remain in the water column and reach the seafloor, where it can be accidentally consumed by these whales causing them important damage and even death.

Author contributions

N.A.S., P.A., J.M. and **J.A.T.** collected the data. All authors analysed the data. **J.A.T.** wrote the paper with large contributions from N.A.S. and P.A. **[The manuscript has been sent to all coauthors for them to review and participate in the writing]**.

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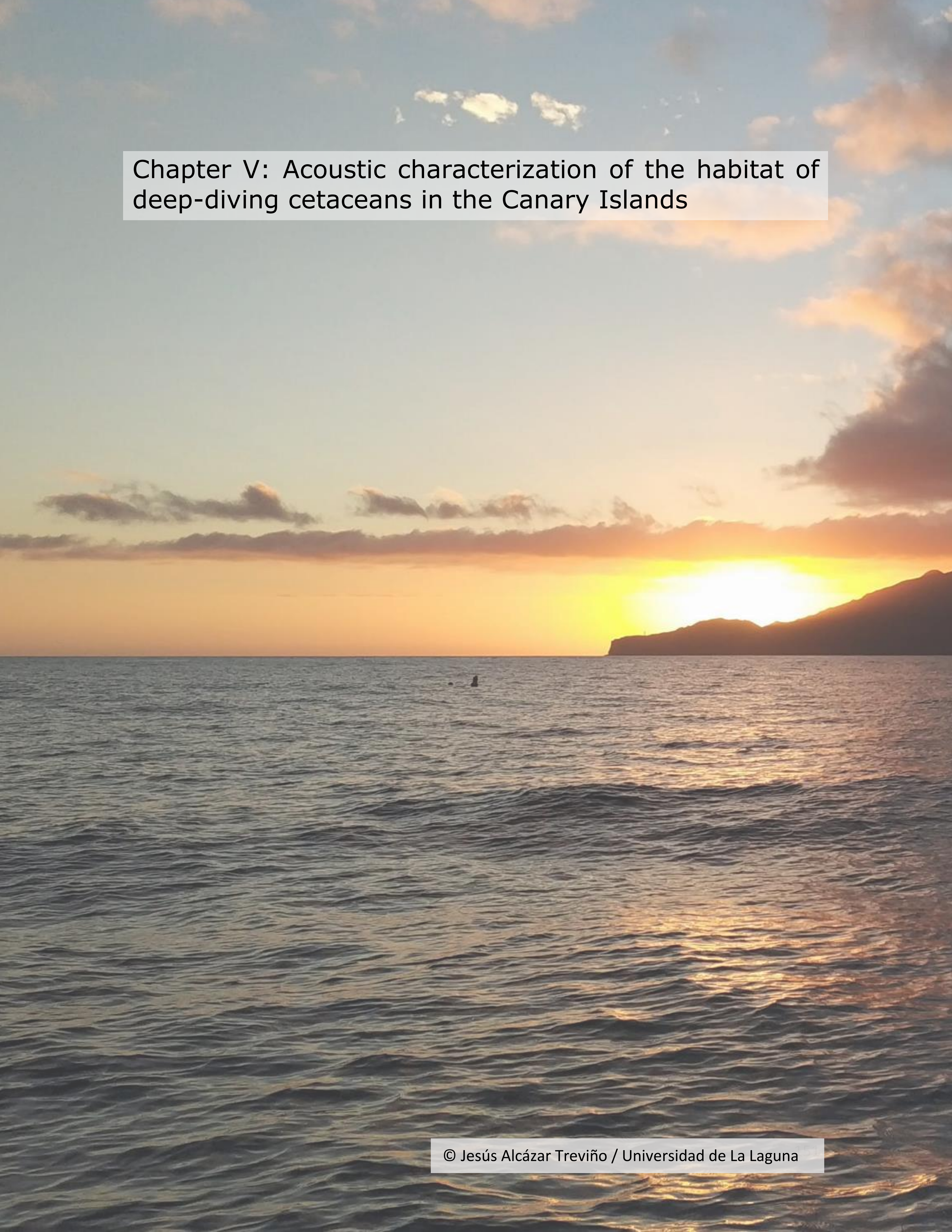
The supplementary material can be consulted in Appendix III.

Chapter V: Acoustic characterization of the habitat of deep-diving cetaceans in the Canary Islands



Drafted for the journal Ecology Letters, as

Deep conversations: Evening choruses in deep waters are associated with mesopelagic large-scale diel vertical migrations in the Canary Islands (Spain). **Alcázar-Treviño J**[1], Korneliussen R[2], Escánez A[1], Aguilar de Soto N[1].

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Abstract

Passive acoustics are used to study marine soundscapes and biodiversity. An evening chorus of uncertain origin has been found in deep waters of the Pacific and Indian Oceans. Here, we investigate the marine soundscape at 50 and 600 m depth in pelagic waters of two volcanic islands in the subtropical NE Atlantic combining passive and active acoustics. We explored chorus temporal occurrence and received level in relation with the diel migration of the Deep Scattering Layer (DSL). We report for the first time in the Atlantic Ocean a chorus that occurs concurrently with the upwards migration of the DSL at dusk. Maximum received levels of the chorus are positively correlated with the acoustic backscatter of DSL organisms that migrate to shallow waters (0-150 m depth). We propose that mesopelagic fish are most likely responsible for the chorus because these are the most abundant taxa involved in the DSL diel migration. Calibrated measures of chorus levels might thus be applicable to provide abundance estimates of migrating DSL biomass.

Introduction

Marine soundscapes comprise the combination of sounds from the geophony, produced by i.e. wind and rain, the biophony, comprising vocalizations, clicks and stridulations produced by different organisms, and in most waters, the anthrophony comprised by anthropogenic noise like boat traffic (Erbe et al. 2015; Picciulin et al. 2016). In recent years, the importance of characterizing and monitoring marine soundscapes using Passive Acoustic Monitoring (PAM) has increased due to its little to no impact on the studied ecosystems while gathering relevant biodiversity presence and abundance data (McWilliam & Hawkins 2013; Pieretti et al. 2017; Lin & Tsao 2018). Studies on specific sound sources and the soundscape can give an impression of the status of an ecosystem, i.e. the presence of top predators like marine mammals (Erbe et al. 2015; Giorli & Pinkerton 2019), soniferous invertebrates (Au & Banks 1998; Radford et al. 2008; Picciulin et al. 2016) and fish diversity (Desiderà et al. 2018; Laxminarsimha Chary et al. 2020).

There is an increasing number of studies revealing that there are more soniferous fish species than previously thought (Carriço et al. 2019). Fish use sounds to communicate (Ladich 2019), in courtship and during spawning (Rowe & Hutchings 2006; Erisman & Rowell 2017), to orientate towards preferred ecosystems like reefs (Tolimieri et al. 2000) and to startle predators (Vester et al. 2004).

A common method to study fish sounds is to isolate the fish in a pool and record all produced sounds (Vester et al. 2004). Once these sounds are identified and characterized, soniferous species can be monitored in the wild. In other cases, free-ranging soniferous fish can be studied using acoustic localization techniques (Putland et al. 2018), or combining passive acoustic recordings with concurrent active acoustic data, using scientific echosounders

(Erisman & Rowell 2017) or video recordings (Mouy et al. 2018). However, there is a group of diverse and highly abundant fishes that are still difficult to study using PAM: deep-water fish (Mann & Jarvis 2004). Some of these fish are hypothesized to produce sounds by vibrating their swimbladders, producing choruses in their diel vertical migrations, but this is still to be confirmed and the mechanism to produce these sounds and their biological function remain unclear (McCauley & Cato 2016; Lin & Tsao 2018).

Here we used a combination of active and passive acoustic techniques to study the marine soundscape in pelagic waters of Tenerife and El Hierro (Canary Islands, Spain) in the NE Atlantic Ocean, to identify and describe potential evening choruses and to investigate their source.

Material & Methods

Data collection

Experiments were conducted from a small boat drifting around the 1000 m isobath at the leeward off El Hierro and Tenerife. Passive and active acoustics were performed some 2 hours before sunset to some 2 hours post- sunset, to record data prior, during and post the upwards migration of the DSL. Surveys were conducted in last quarter moon phase to maintain similar light levels for all the deployments, as it has been proposed that lunar phase affects the depth of the migrating layer during the night (McManus et al. 2008). In one set of surveys we recorded the downwards migration, at sunrise. This was performed in second moon quarter to guarantee that the moon was below the horizon as in the other surveys.

Two SoundTrap hydrophones (http://www.oceaninstruments.co.nz) were suspended from a surface drifting buoy attached to the boat: a “shallow” unit and a “deep” unit at 50 m and 600 m water depth respectively. Both hydrophones sampled continuously at 288 kHz with 16-bit resolution. Simultaneously, the boat drifted while sampling the water column using a portable SIMRAD EK80 echosounder. The transceiver was a SIMRAD WBT Mini, and it was connected to a KODEN GPS-20A, a laptop and to the transducer. The transducer was a SIMRAD ES38-200-18C, which combines a 38 kHz split-beam transducer with a single-beam 200 kHz one, both with a 18° beamwidth. Broadband mode was employed for the surveys, emitting upsweep FM (Frequency Modulated) pulses from 34-45 kHz and 190-230 kHz, using pulse lengths of 0.512 ms and output power of 400 and 150 W for the 38 and 200 kHz frequencies, respectively. The transducer was suspended from the boat using a pole, down-looking and placed at 2 m depth. The 38 kHz frequency was calibrated using a 38.1 mm diameter Tungsten sphere following standard procedures (Demer et al. 2015). Maps for the surveys were made using ‘plot_google_map’ function (Bar-Yehuda 2021) for Matlab and the EK80-GPS data. These point data were used to calculate distances from the surveys to the coast and total drifted distance while sampling were calculated using the function ‘lldistkm’ (Sohrabinia 2021).

Passive acoustics analyses

One-third octave band levels (TOL, dB re 1 µPa) analyses for each minute for every deployment were performed using Matlab (MathWorks). Sound samples were calibrated attending the sensitivity of each hydrophone available online at http://www.oceaninstruments.co.nz. Then, a modified version of the Matlab function ‘filtbank’ was used to calculate TOL levels of these calibrated measurements, covering center frequencies from 15 Hz to 80 kHz (Supplementary Table S1). Root-mean-square (rms) values for each band were calculated for each minute of the recordings. Median values were then calculated for the day vs night measurements. In order to identify at which TOL the chorusing occurs, these median values for each deployment were plotted, showing day vs night and shallow vs deep medians. Once the frequency band of the chorus was identified, the evolution in time of one minute received levels (RL) at that band were plotted for each deployment. Maximum RL of TOL of the chorusing event were annotated for all deployments, for the shallow and deep hydrophones.

Active acoustics analyses

Echosounder data was processed using LSSS (Large Scale Survey System) software and the KORONA preprocessor (Korneliussen et al. 2006). First, the Broadband splitter module was used to divide the 38 kHz FM data into bands with nominal frequency 36, 38, 39 and 42 kHz, respectively. Then, these bands were converted to Continuous Wave (CW) data and downsampled for a 0.1 m vertical resolution in order to reduce computation time. The bottom detection module was used after smoothing the data to detect the seafloor in the surveys, before applying the Noise quantification and Noise remover modules to improve data quality (Korneliussen 2004).

The analysis was performed for the depth ranges assigned to known backscattering acoustic layers in the Canary Islands (Ariza et al. 2016) and observed in our sampling: between 400-500 and 550-650 m depth, excluding the layer covering 700-800 m depth due to high reverberant noise because of the proximity of the seafloor. We added to our analysis a shallow layer from 15-150 m for the organisms that migrate at dusk, and another layer for the 300-400 m depth. The metric S_A or Nautical Area Scattering Coefficient (NASC) is a standardized measurement in active acoustics (MacLennan et al. 2002) and was used for the present analysis. S_A values were extracted for each of the defined water layers, for 30 min intervals before and after the diel migration. Additionally, the difference in S_A values before and after migration was calculated for all depth ranges, which should reflect the changes in organismal density in each layer after the migration occurs. We provide measures of acoustic backscatter (S_A) instead of acoustic biomass and/or density estimates since these parameters are difficult to obtain from mesopelagic fish and require a specific knowledge of the species and size classes composition of the layers that only can be acquired through concurrent net sampling. Otherwise, acoustic biomass estimates could report errors up to three orders of magnitude (Davison et al. 2015).

Exploring active-passive acoustics possible relation

Since the sample size for complete surveys was small, we explored possible relations between measured parameters (RL and S_A) using Pearson Correlation test in the software R through RStudio (R Development Core Team 2008; RStudio Team 2015). We specifically looked for a relation between maximum RL of the TOL of the chorus received at the hydrophones (passive acoustics) and acoustic backscatter in each depth layer from the echosounder (S_A, active acoustics). Differences between the S_A after and before migration in a depth layer should reflect the migration of organisms, so we investigated S_A night-day measurements for all the studied layers. We expect that the shallow layer at 15-150 m would contain most of the DSL organisms performing diel migrations, as previously observed (Ariza et al. 2016). S_A values during the night were tested against maximum RL of the TOL of the chorusing for the shallow layer (15-150 m) and for the non-migrant 300-400 m depth range.

Results

A total of 11 surveys around the 1000 m isobath included recordings from the shallow and deep hydrophone, and in 6 cruises there was a concurrent sampling of the two hydrophones and the EK80 echosounder (Figures 1-2, Table 1).

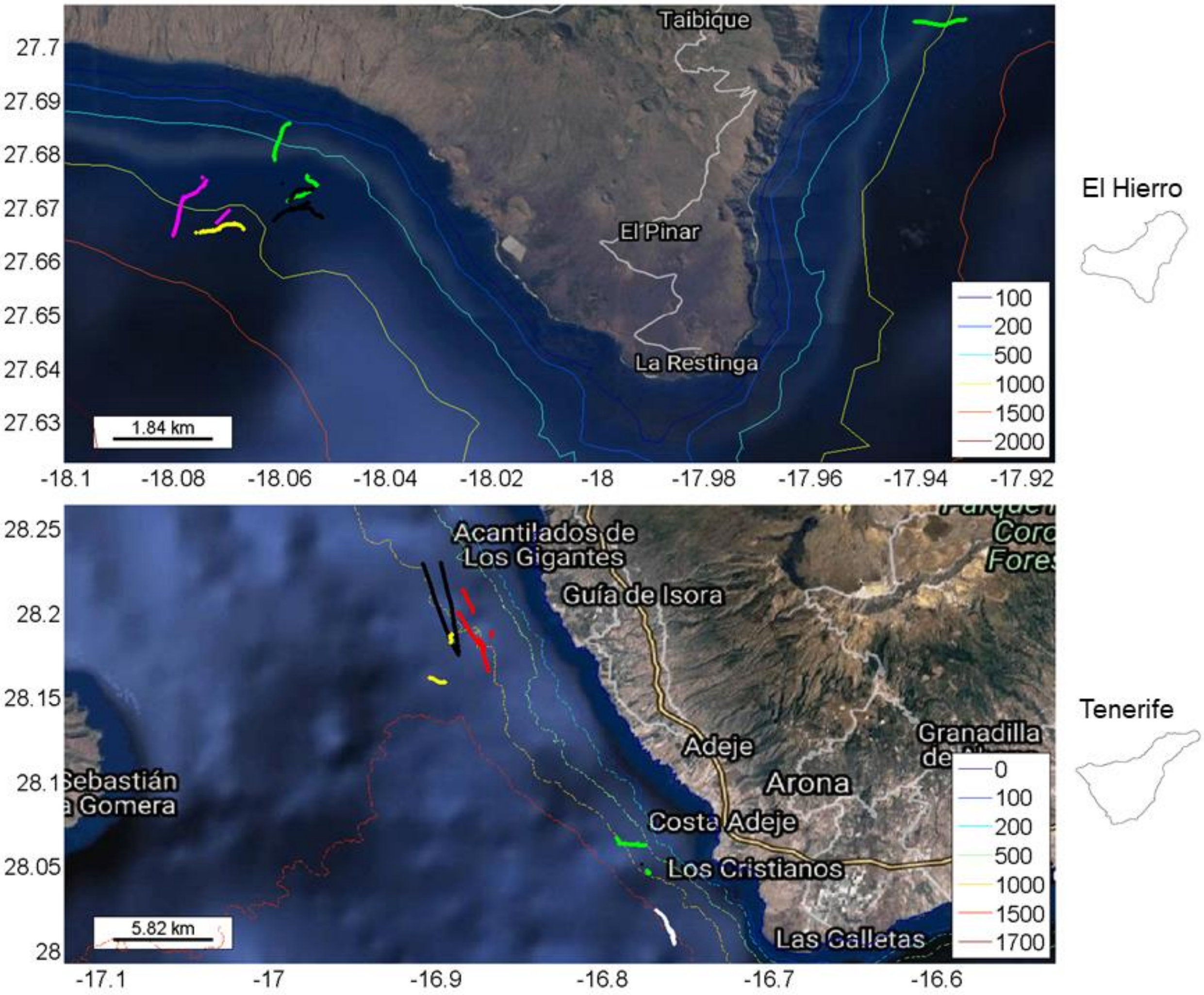

Figure 1. Survey locations for El Hierro (top map) and Tenerife (bottom map) in the Canary Islands (Spain). The thin coloured lines indicate seafloor depth in meters. The thick coloured lines show the EK80-GPS data for each survey, and the colours indicate the month of the survey: June (green), August (black), September (yellow), October (pink), November (red).

Table 1. List of surveys. Days in **bold** were used for statistical analyses, as they were complete, i.e., with all active and passive acoustic instruments functioning. Achieving complete surveys (days marked with an asterisk *) was highly dependent on sea state during the short time window of last quarter moon. In July 2019 (**) the surveys were carried out before and after sunrise instead of sunset, to explore if there was a chorus during the downwards migration of the DSL. These surveys were carried out in the second moon quarter to get the same light conditions (no moon over horizon during survey hours).

Year	**Month**	**Day**	**Location**	**Sunrise Sunset**	**Start-end hour of analysis**	**Initial position**
2019	June	**24***	El Hierro	7:16 21:11	19:30 23:00	27º 42' 18.6" N 17º 55' 52.2" W
		25			19:42 22:14	27° 38' 3.79" N 17° 58' 39.52" W
		26*			20:03 23:01	27º 40' 16.2" N 18º 3' 33" W
	July**	10*	El Hierro	7:22 21:11	5:03 7:38	27º 40' 28.2" N 18º 3' 36" W
		11*			4:56 7:46	27º 40' 16.2" N 18º 3' 31.2" W
		12*			5:30 7:48	27º 40' 12" N 18º 3' 31.2" W
		13			4:51 7:52	27º 40' 3" N 18º 3' 42" W
	September	21*	Tenerife	7:53 20:07	18:53 21:20	28º 0' 16,8" N 16º 45' 33.6" W
		22*			19:15 20:54	28º 0' 19.8" N 16º 45' 33" W
	October	19	El Hierro	8:13 19:40	19:56 21:57	27º 40' 3.6" N 18º 4' 18" W
2020	June	12	Tenerife	7:09 21:03	18:30 22:06	28° 3' 46.31" N 16° 46' 34.61" W
		13			18:49 22:01	28° 2' 47.71" N 16° 46' 29.27" W
	August	**12***	Tenerife	7:34 20:49	19:09 21:47	28° 3' 5.65" N 16° 46' 43.66" W
		13*			18:48 22:24	28° 10' 33.56" N 16° 53' 18.76" W
	September	11	Tenerife	7:49 20:17	17:20 21:30	28° 10' 59.12" N 16° 53' 34.32" W
		12*			17:36 21:10	28° 9' 44.31" N 16° 54' 20.27" W
	October	**10***	El Hierro	8:04 19:39	17:51 22:00	27° 39' 55.43" N 18° 4' 34.84" W

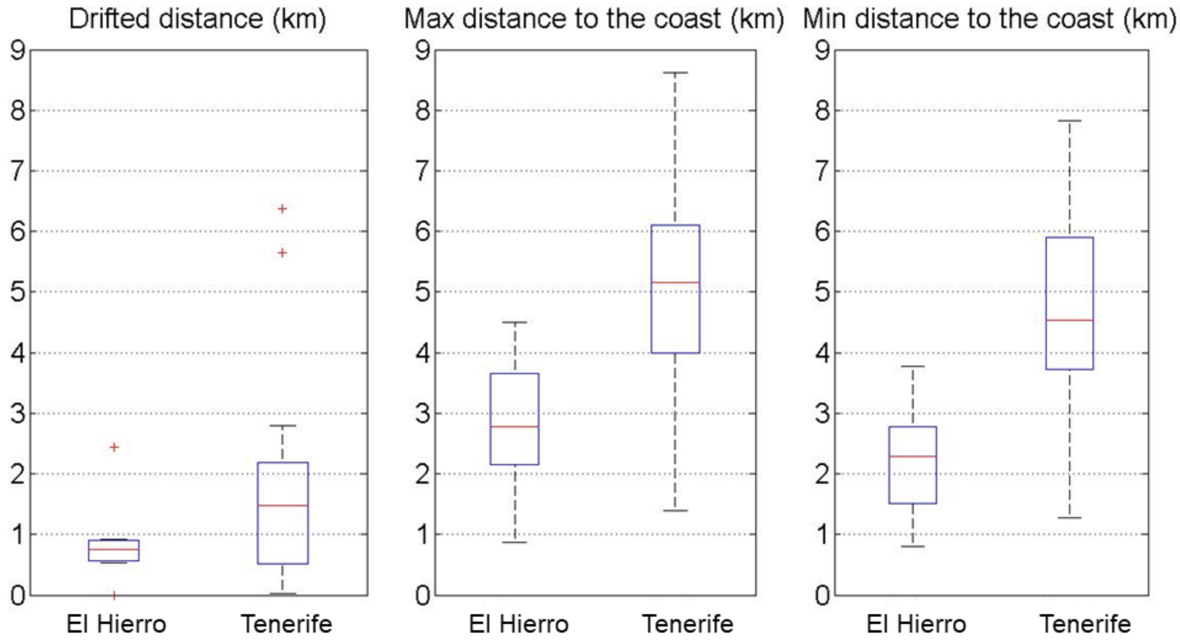

Figure 2. A) Distances drifted during the surveys in each location (km). Maximum (B) and minimum (C) distance to the coast while sampling. El Hierro and Tenerife surveys.

Figure 3 shows TOLs during day and night periods, for the deep and shallow hydrophones at Tenerife and El Hierro. There are clear trends: i) TOLs were higher at low frequencies (<1 kHz) for Tenerife compared to El Hierro, with no day/night differences; ii) Some sampling days in both locations presented an elevated RL at 500 Hz at night with respect to diurnal levels; iii) At night there is a peak centred at 2.5 kHz that is absent at day, in both islands, with a maximum RL of 98 dB re 1 µPa at 2.5 kHz. iv) Also, there is an elevated RL in the range 4-12 kHz during day and night, both in the shallow and deep hydrophones, for most of the recordings from El Hierro but just one from Tenerife.

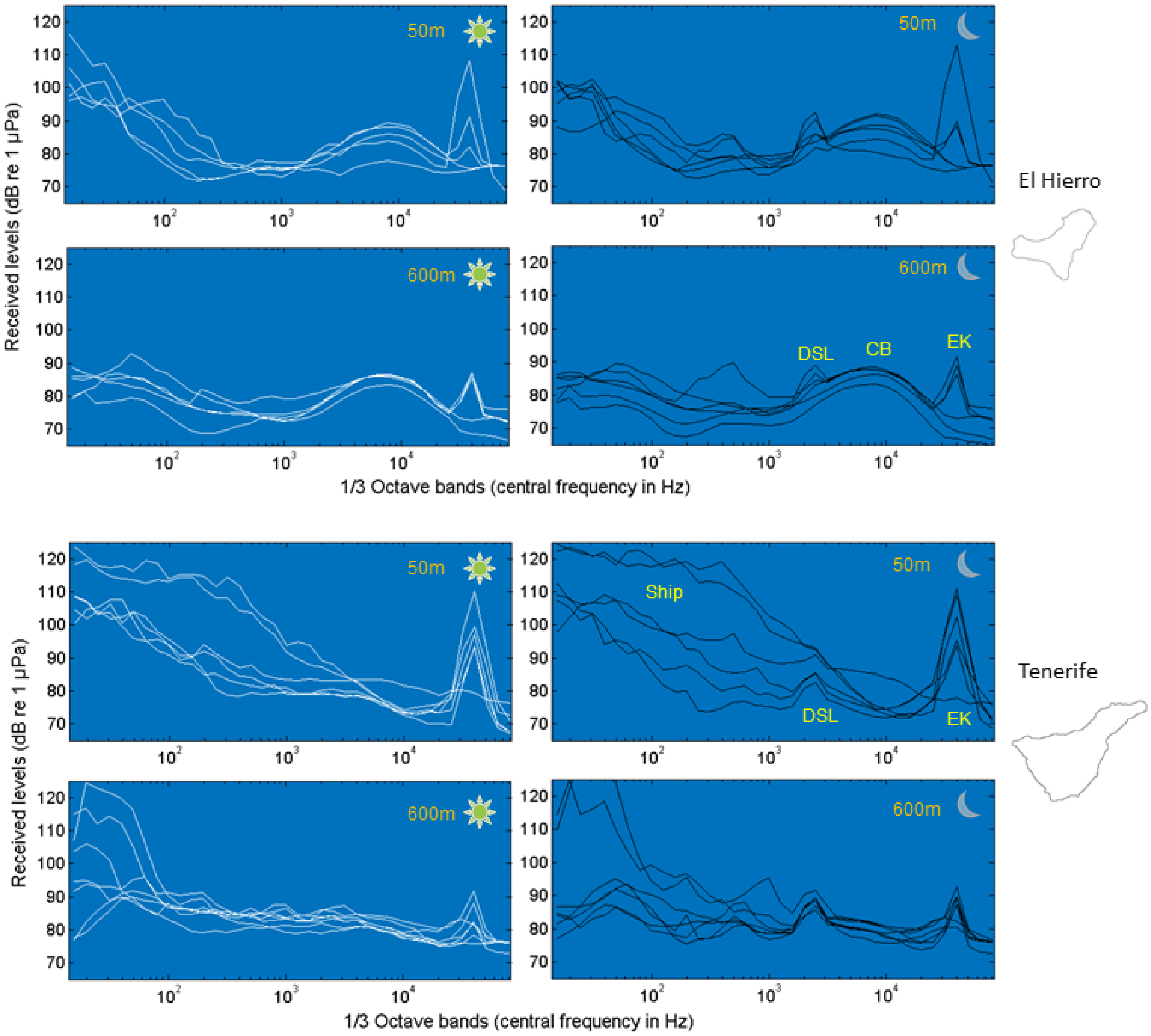

Figure 3. Absolute RL in dB re 1 µPa rms for each TOL before (left panels) and after (right panels) sunset, and from the shallow (top panels) and deep (bottom panels) hydrophones (50 and 600 m depth, respectively), for El Hierro (two first rows) and Tenerife (two last rows) surveys. Abbreviatures in yellow in the middle night panels indicate the most common detected sounds in the TOLs: Ship (shipping noise, at < 1.5 kHz), DSL (DSL chorusing at 2.5 kHz), CB (coastal biophony between 4-12 kHz) and EK (echosounder pulses at 38 kHz).

For every deployment, the evolution of RL in time for the TOL band centred at 2.5 kHz was plotted (Figure 4), revealing higher RL at dusk. This sound was consistent with choruses described for other locations. The chorus lasted a median of 1.63 hours (min 1.46, max 2.1 hours). Echograms from the EK80 data were plotted with simultaneous RL for the 2.5 kHz TOL to explore temporal coincidences of the chorus with the migration revealed by the echosounder (Figure 5 & Supplementary Figures S1-4).

To test if the DSL migration resulted in elevated RL in shallow waters, we tested correlations between the 2.5 kHz TOL at the shallow hydrophone and the increase in backscatter level (S_A) (night minus day S_A) for each depth range. The correlation was significant only for the S_A in the shallowest depth range tested between 15-150 m (Table 2). We also tested potential correlations between the maximum 2.5 kHz TOL and the absolute S_A at each depth range at night. This was significant for the 300-400 m depth range (Table 2).

Table 2. Results for Pearson Correlation tests between maximum 2.5 kHz TOL and acoustic backscatter (S_A) at different depth ranges. Tests performed for S_A increase (night minus day level) and for S_A at night. N = 6 complete surveys.

S_A at 38 kHz (post-processed)	**15-150 m night – day**	**200-300 m night - day**	**400-500 m night - day**	**550-650 m night - day**	**15-150 m night**	**300-400 m night**
p-value	**0.019**	0.56	0.97	0.65	0.25	**0.048**
R	0.88	0.27	-0.016	-0.21	0.5	0.76
R^2	0,77	0,07	0,0002	0,04	0,25	0,58
Equations for significant corelations	y (RL) = 0.0061 * x (S_A) + 80.914					y (RL) = 0.0104 * x (S_A) + 87.976

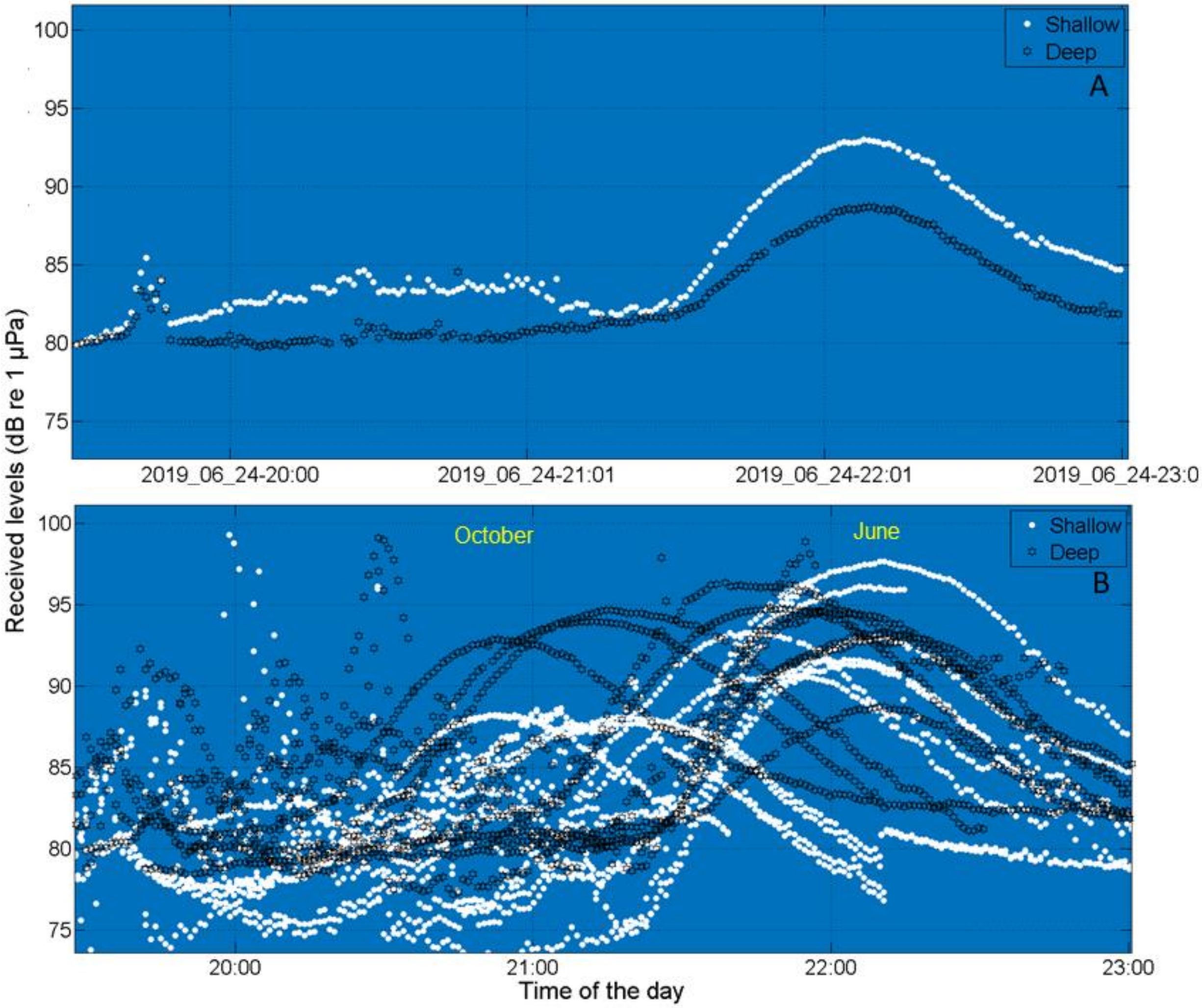

Figure 4. Evolution of RL in time at TOL 2.5 kHz for the shallow and deep hydrophones (50 and 600 m depth, respectively). A) An example of a single deployment (24th June 2019). B) Pooled data from 11 deployments. The hour of maximum TOL for the chorus is displaced in time among surveyed months, consistently with the delay in sunset timing, i.e. earlier in October and later in June.

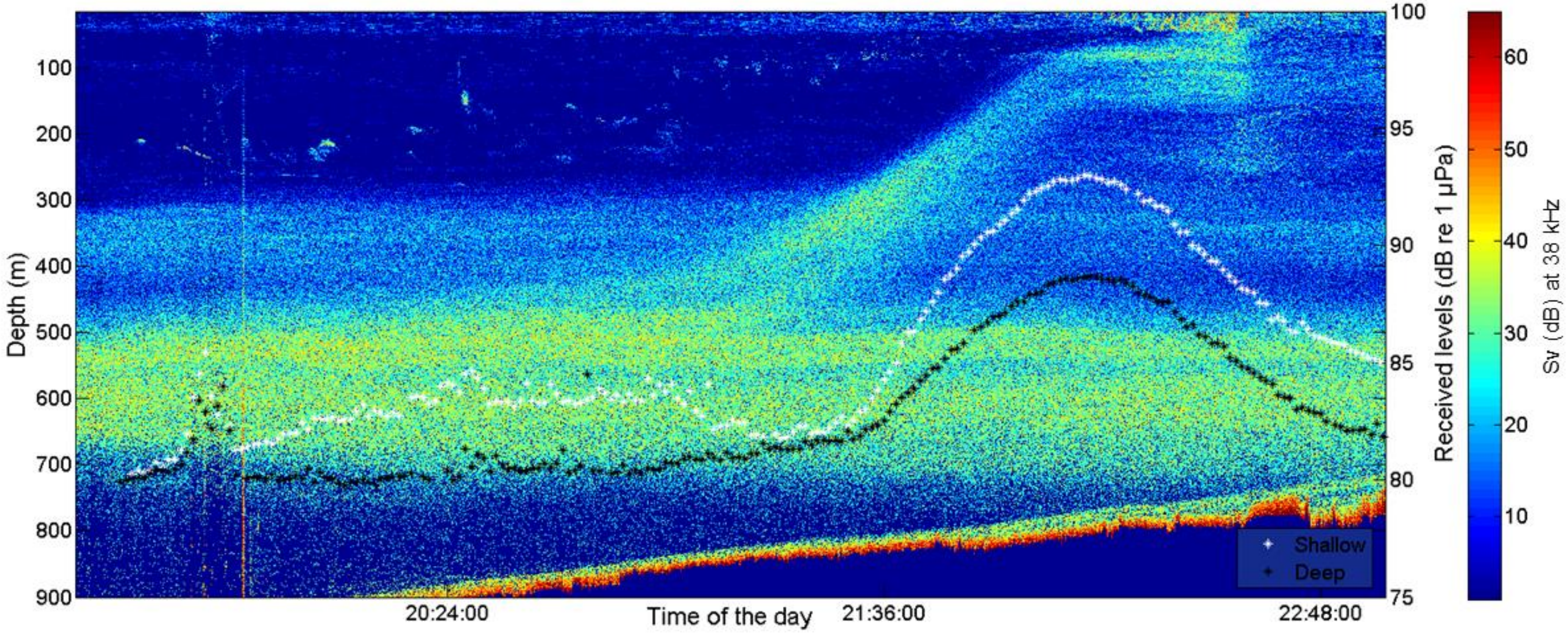

Figure 5. Echogram for the EK80 data taken the 24th June 2019, using Sv data processed by KORONA in LSSS at 38 kHz. The superposed asterisks (*) represent the received levels at TOL 2.5 kHz at the shallow (white) and deep (black) hydrophones at the same time.

Discussion

Passive Acoustic Monitoring (PAM) is an emerging tool to assess biodiversity and to detect biological processes like aggregations of foraging or reproducing animals (Rowe & Hutchings 2006; Erisman & Rowell 2017). Here we studied the marine soundscape at the leeward of two volcanic islands in the NE Atlantic and used a combination of active and passive acoustic techniques in order to identify and explore the origin of deep-water evening choruses as in McCauley & Cato (2016) and Lin & Tsao (2018).

Deep-waters soundscape off Tenerife and El Hierro islands

In pristine areas, the low and mid-frequencies of the marine soundscape are typically occupied by the geophony, i.e. wind and waves, and the biophony formed by marine mammal sounds, i.e. calls from baleen whales, and fish sounds (Erbe et al. 2015). However, long term recordings in some areas have detected an increase of 3 dB per decade in low frequency sound levels attributable to shipping noise (McDonald et al. 2006). We contribute here a further example of how similar habitats present different soundscapes that can be attributed to human activities introducing the anthrophony in the soundscape. In our results, TOL frequencies < 1 kHz are up to 24-36 dB higher at Tenerife compared to El Hierro (Figure 3), which probably reflects the higher vessel traffic off SW Tenerife. This is consistent with observations that in high shipping areas engine noise dominates the soundscape at frequencies < 1.5 kHz (Laxminarsimha Chary et al. 2020). Boat noise can produce masking reducing the active acoustic space of fish and cetaceans e.g. orcas and humpback whales (Holt & Noren 2009; Fournet et al. 2018; Bolgan et al. 2020), can negatively affect hearing and communication in soniferous fish species (Codarin et al. 2009) as well as orientation behaviour of fish larvae (Holles et al. 2013).

There was another visible difference between the two studied islands. In most surveys off El Hierro there was a curve of higher RL between 4-12 kHz that was absent in the recordings of Tenerife except for one occasion (Figure 3). We attribute this curve to coastal biophony, probably produced by snapping shrimp and foraging sea urchins that produce sounds at these frequencies (Radford et al. 2008; Picciulin et al. 2016). This interpretation is consistent with the drifting hydrophone being closer to the coast in El Hierro compared to Tenerife (Figure 2) and with the absence of this signal in reports of other studies that needed to get far from the coast to study the soundscape of deep waters (McCauley & Cato 2016).

In both islands we observed a peak of higher TOL at 2.5 kHz after sunset (Figure 3). The temporal evolution of TOL 2.5 kHz in each survey (Figure 4) supports that this is an evening chorus. This is similar to choruses previously detected in deep waters of the Pacific (Taiwan) and Indian Ocean (Perth Canyon) (McCauley & Cato 2016; Lin & Tsao 2018; Id et al. 2021). To our knowledge, this is the first report of the occurrence of such chorus in Atlantic waters. Moreover, the timing of this chorus concurrent with the upwards vertical migration of the DSL indicate a relation between these two events (Figure 5). However, the small differences found in received levels for the chorus at the shallow and deep hydrophones makes it difficult to identify the source of the chorus.

Deep-waters chorus

The origin of the chorus is still enigmatic and we explored coincidences in frequencies with the vocalizations of different marine taxa. Some marine mammals present in the Canary Islands produce calls at similar frequencies, such as the short-finned pilot whale off Tenerife (Jensen et al. 2011; Pérez et al. 2017), but we were unable to distinguish isolated signals in the chorus resembling marine mammal vocalizations described in the literature. Dugongs make mastication sounds when foraging, with peak frequencies between 1.4-3.2 kHz (Tsutsumi et al. 2006), within the range of the 2.5 kHz chorus, but these mammals are absent in the Canary Islands.

Another possible source for the chorus could be migrating mesopelagic fish, such as myctophids, as previously hypothesized for the Pacific and Indic choruses (McCauley & Cato 2016; Lin & Tsao 2018). This would be supported by the correlation found between TOL 2.5 kHz and the increase in S_A from day to night in the shallowest depth range tested between 15-150 m. However, the small differences of TOL 2.5 kHz received in shallow and deep hydrophones suggests that the source of the chorus is located either at both depths simultaneously, or somewhere in between them, i.e. at some 300-400 m depth. This is consistent with the relation between TOL 2.5 kHz and the absolute S_A at night at 300-400 m depth. At this estimated depth range the source of the chorus could be fish at the non-migrant upper DSL.

We investigated other fish taxa potentially producing the chorus and found that Syngnathids (seahorses) emit at 2.65-3.43 kHz and 1.96-2.37 kHz while foraging (Colson et al. 1998). Then, the chorus might be due to foraging fish present in the Perth Canyon (McCauley & Cato 2016), Taiwan (Lin & Tsao 2018), and the Canary Islands. However, to produce the choruses we found would require large aggregations of foraging fishes and it seems unlikely that seahorses aggregate at 300-400 m depth. A different sygnathid is frequent at the Canary Islands, the longspine snipefish *Macroramphosus scolopax.* This fish inhabits waters from 25 to 600 m depth (May & Maxwell 1986). However, we have no knowledge about the behavior of this species that might explain why it should be soniferous only at dusk and at this depth range. Potential explanations would be that these fishes have adapted their behavior to start feeding on migrating organisms like zooplankton. The chorusing might be then a by-product of their foraging mechanisms as in seahorses (Colson et al. 1998), and chorus levels would fade when most of the migrating organisms have reached shallow waters or have been consumed by these mesopelagic predators.

Although we cannot exclude the above explanation, it seems more plausible that the source of the chorus is mesopelagic fish. In this case the sound could be originated by different behaviours. It could be related with communication, but this behaviour seems unlikely as it would be risky to attract acoustic predators during the migration event. Also, most fishes use lower frequencies when communicating (Ladich 2019; Bolgan et al. 2020). Sounds could be also a by-product of physiological phenomena, i.e. degasification of upwards migrating fish with gas-filled swimbladders as hydrostatic pressure decreases and swimbladder gas expands This could explain the highly conservative chorus levels in all the surveys reported from different locations (McCauley & Cato 2016; Lin & Tsao 2018). Sounds could be produced by different migrating species with gas-bearing swimbladders in different geographic areas. This interpretation is consistent with the absence of chorus during the downwards migration at sunrise (Supplementary Figure S5), because fishes would reabsorbe gas while descending to compensate shrinking of their swimbladders (Butler & Pearcy 1972).

Given that chorus TOL levels are similar in both shallow and deep hydrophones, this would imply that fishes degasify at all depths, or at 300-400 m, broadly coinciding with the depth where gas volumes double for fish ascending from 600-800 m depth. Alternatively, bubble expulsion could not associate with a physiological need, but rather with a behavioural response (e.g. startling predators), as it has been proposed for herring emitting bubbles that produce sounds at similar frequencies (Wahlberg & Westerberg 2003).

With the limitations of a small sample size, the observed relation between the chorus TOL at the shallow hydrophone (50 m depth) and the acoustic backscatter (S_A) of migrating organisms that reach shallow waters of 15-150 m (Table 2) underlines the need to further augment the sample size and perform calibrating experiments to further confirm and model this correlation. This preliminary result is exciting as it suggests that it might be possible to estimate migrating biomass in the future from PAM data by deploying a hydrophone at 50 m depth for 1-2 hours at sunset.

Also, if the chorus is a signature of the migrating DSL, it could provide acoustic cues to acoustic-guided oceanic predators. Same that some oceanic predators seem to follow chemical cues such as DMS gradients indicating biomass concentration (Owen et al. 2021), predators with hearing capabilities at 2.5 kHz could orient towards high chorusing levels if these reflect higher organismal density. It has been observed that deep-sea zooplankton biomass can be used as a proxy of primary production (Hernández-León et al. 2020). Seemingly, predators could target areas of high-level chorus even if they do not prey directly on the soniferous organisms if these are indicators of higher overall biomass. Thus, acoustic cues could help ranging apex predators to find oases of enhanced resources in the wide 3D blue water desert.

Conclusions

Applying passive acoustic monitoring techniques at SW Tenerife and El Hierro (Canary Islands) reflects human influence in the marine soundscape, with vessel traffic reducing acoustic space for vocal communication, orientation and foraging in soniferous species inhabiting these waters.

At dusk, concurrently to the large-scale diel vertical migration of some DSL organisms to shallow waters, there is an evening chorus with high TOL at 2.5 kHz. This is similar to chorus reported for deep waters of the Pacific and Indian Oceans (McCauley & Cato 2016; Lin & Tsao 2018; Id et al. 2021). The chorus is possibly produced by mesopelagic migrating fish as a result of degasification during the upwards migration. With the limitations of a discrete sample size, there seems to be a relation between chorusing levels and the acoustic backscatter, opening future research avenues to expand the dataset and model the possibility of estimating migrating biomass using PAM. Further, acoustic-guided predators might be using chorus levels to find richer foraging patches.

A coastal biophony at 4-12 kHz is detectable in oceanic recordings both at shallow and deep waters when performed relatively close to shore. This biophony is probably originated by snapping shrimp and foraging sea urchins as reported for coastal biophonies in other areas. The simultaneous recording of coastal biophonies and chorus apparently atributable to the migration of the DSL is possible thanks to the steep bathymetry of El Hierro, the youngest of the Canary Islands (Guillou et al. 1996; Acosta et al. 2005). Some animals could be using this complex soundscape to orientate. We believe that it is important to continue monitoring these habitats using the novel combination of passive and active acoustic techniques used here, to assess the origin of the chorus in order to improve monitoring of deep water ecosystems and contribute information to base conservation management measures in areas impacted by anthropogenic noise.

Author contributions

N.A.S., A.E. and **J.A.T.** collected the data. All authors analysed the data. **J.A.T.** wrote the paper with contributions from N.A.S. and R.K. **[The manuscript has been sent to all coauthors for them to review and participate in the writing]**

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The supplementary material can be consulted in Appendix IV.

GENERAL CONCLUSIONS

The conclusions of this thesis are:

i) Groups of tagged Blainville’s and Cuvier’s beaked whales show an extreme diving synchronicity. Group members overlap vocal foraging time for long periods and this synchronicity disappears when group members disperse. Vocal synchronisation reduces group temporal availability for acoustic detection by killer whales. Groups also perform a coordinated silent ascent in an unpredictable direction. This tactic sacrifices foraging time but reduces by an order of magnitude the risk of interception by killer whales.

ii) The strategy of “acoustic hiding” shown by studied beaked whale is borne out in their responses to sonar and killer whale experimental playbacks: silencing and avoidance. Evolution of their behaviour in a “soundscape of fear” therefore offers a mechanistic explanation for why beaked whales respond so strongly to sonar and killer whale sounds at barely audible levels. As such, a successful predator abatement strategy shaped by natural selection has become maladaptive in the face of novel human activities.

iii) Given the vast zones over which mid-frequency navy sonars are audible and so may impact the behaviour of beaked whales, large-scale spatial avoidance of beaked whale habitats when mid-frequency sonar is used should provide the most effective mitigation measure for these cryptic species.

iv) Blainville’s and Cuvier’s beaked whales foraging in groups do not modify individual rates of echolocation and prey capture attempts in relation to group size. This indicates that sensory interference or competition from group members is unlikely to occur while hunting. Individuals are also unlikely to benefit from local enhancement directly by sharing information of echo arrivals from conspecific clicks.

v) However, tagged whales were in acoustic contact with other group members via eavesdropping almost all their vocal (foraging) time. This presumably aids coordination of the timing and mean direction of their synchronized dives while they separate to hunt independently.

vi) Blainville's and Cuvier's beaked whales do not behave as cooperative hunting predators, but more like social foraging herbivores and frugivores such as ungulates and primates that coordinate group movements but forage independently. These collective behavioural tactics reduce intra-group competition allowing individuals to maintain foraging efficiency while gaining the social and predation risk abatement benefits of group living.

vii) Small group sizes in these species of beaked whales might thus be related to the foraging footprint of the group. Their independent but coordinated foraging suggests dependence upon a reliable foraging niche and sets an upper limit to the number of whales that can efficiently forage simultaneously.

viii) The five studied species of deep-diving odontocetes tagged in warm-temperate areas showed some level of vertical niche overlap among them. Both Cuvier´s and Blainville´s beaked whales, short-finned pilot whales and sperm whales forage mostly in the mesopelagic during the day, while pilot whales and Risso's dolphins are the only species foraging in the epipelagic at night. The five species exploit prey associated to the seafloor, albeit benthopelagic foraging is rarest in short-finned pilot whales. All species exploit the DSL or predators associated to the DSL.

ix) Niche overlap might explain observations of agonistic behaviours between short-finned pilot whales, Risso’s dolphins and sperm whales if these species tend to defend a territory rich in their preferred resources. Knowledge about the behavioural ecology of deep-divers is key to understand their spatial distribution. For example, these species show segregated distributions within the same archipelago of the Canary Islands and this might be partly explained by a strategy of conflict avoidance in addition to prey distribution.

x) Acoustic habitat quality is important for acoustic-guided deep diving whales. Applying passive acoustic monitoring techniques at SW Tenerife and El Hierro in the Canary Islands reflects human influence on the marine soundscape, with vessel traffic potentially reducing acoustic space for low-frequency communication, orientation and foraging in soniferous species inhabiting these waters.

xi) At dusk, concurrently to the large-scale diel vertical migration of DSL organisms between meso- and epipelagic waters, there is an evening chorus centred at 2.5 kHz. This is consistent with a chorus described in deep waters of the Pacific and Indian Oceans.

xii) The chorus is possibly produced by mesopelagic fish, and it could be used for communication, be a by-product of foraging, a tactic to startle predators, or most probably the result of degasification for pressure adjustments during migration.

xiii) There seems to be a positive correlation between received sound levels of the chorus recorded passively and the acoustic backscatter of migrant organisms to shallow waters detected with active acoustics. This pioneering result requires more sampling to confirm and quantify this relationship, with potential applications towards developing the use of passive acoustics to quantify migrant biomass of the DSL.

CONCLUSIONES GENERALES

Las conclusiones de esta tesis son las siguientes:

i) Los grupos de zifios de Blainville y Cuvier marcados mostraron una extrema sincronización en sus inmersiones. Los miembros del grupo solapan el tiempo vocal de alimentación por largos periodos, y esta sincronización desaparece cuando los miembros del grupo se separan. La sincronización vocal reduce la disponibilidad temporal del grupo a ser detectados acústicamente por orcas. Además, los grupos realizan un ascenso coordinado en silencio en dirección impredecible. Esta táctica sacrifica tiempo de alimentación pero reduce en un orden de magnitud el riesgo de intercepción por orcas.

ii) La estrategia de los zifios de "esconderse acústicamente" observada en los zifios estudiados puede apreciarse en sus respuestas en experimentos donde son expuestos a sonidos de sonares y orcas: silencio y evitación. La evolución de su comportamiento en un ambiente sonoro con ese miedo a la depredación ofrece una explicación de por qué los zifios presentan respuestas tan fuertes a los sonidos de sonares y orcas incluso a niveles apenas perceptibles. De esta manera, una estrategia tan exitosa de evitación de la depredación fomentada por la selección natural se convierte en desventajosa de cara a las actividades humanas.

iii) Dado que el sonar naval de media frecuencia puede ser escuchado en una gran zona alrededor de donde se emite y puede afectar al comportamiento de los zifios, la medida mitigadora más efectiva debería ser evitar estas prácticas navales en un área grande alrededor de los hábitats ocupados por estas crípticas especies.

iv) Los zifios de Blainville y de Cuvier alimentándose en grupos no modifican sus tasas de ecolocalización ni de intentos de captura de presas en relación al tamaño de grupo. Esto indica que no es probable que ocurra una interferencia sensorial o competición entre miembros del mismo grupo durante la alimentación. No parece probable que los ejemplares se beneficien de compartir información de los ecos provocados por chasquidos de conspecíficos.

v) Los animales marcados permanecían en contacto acústico con otros miembros del grupo gracias a la detección de sonidos producidos por otros ejemplares durante casi todo su tiempo de alimentación. Este hecho ayudaría a la coordinación en los tiempos y dirección de sus buceos sincronizados, mientras los ejemplares se separan para cazar eficientemente.

vi) Los zifios de Blainville y de Cuvier no se comportan como depredadores cooperativos, sino como herbívoros y frugívoros sociales como algunos ungulados y primates, que coordinan sus movimientos pero se alimentan independientemente. Estas tácticas de comportamiento colectivo reducen la competencia dentro del mismo grupo, permitiendo a los ejemplares mantener la eficiencia en la alimentación pero al mismo tiempo ganando las ventajas sociales y de reducción del riesgo de depredación que les otorga vivir en grupo.

vii) Los pequeños tamaños de grupo en estas especies de zifio podrían estar relacionados con la huella depredadora del grupo. Su alimentación, independiente aunque a la vez coordinada, sugiere la dependencia de estos animales sobre un nicho trófico y recursos estables, imponiendo un límite máximo de número de zifios que pueden alimentarse eficientemente de manera simultánea

viii) Las cinco especies de odontocetos de buceo profundo marcadas en aguas templado-cálidas mostraron algún nivel de solapamiento vertical en su nicho trófico entre ellas. Los zifios de Blainville y de Cuvier, el calderón tropical y el cachalote se alimentan principalmente en la capa mesopelágica durante el día, mientras que los calderones tropical y gris son las únicas especies que se alimentan en el epipelágico durante la noche. Las cinco especies depredan sobre las presas de alto valor asociadas al fondo marino en la zona bentopelágica, aunque los calderones tropicales lo hagan en mucha menor medida. Todas las especies depredan sobre la DSL o depredadores de la DSL.

ix) El solapamiento de nicho podría explicar las observaciones de comportamientos agonísticos entre los calderones tropical y gris, y los cachalotes si estas especies tienden a defender un territorio rico en recursos. El conocimiento acerca la ecología del comportamiento de los buceadores profundos es clave para entender mejor su distribución espacial. Por ejemplo, estas especies muestran una distribución segregada en el mismo archipiélago en las Islas Canarias y esto podría estar explicado en parte por una estrategia de evitación del conflicto además de por la distribución de las presas.

x) La calidad acústica de un hábitat es importante para los cetáceos de buceo profundo, que son depredadores acústicos. Aplicar técnicas de monitoreo acústico pasivo en el suroeste de Tenerife y El Hierro en las Islas Canarias refleja la influencia humana sobre el ambiente acústico marino, con el tráfico de barcos potencialmente reduciendo el espacio acústico para comunicación a bajas frecuencias, orientación y alimentación en animales vocales que habitan estas aguas.

xi) Al anochecer, coincidiendo con la migración vertical a gran escala de algunos organismos de la DSL a aguas entre el meso- y el epipelágico, hay un coro sonoro detectado a 2.5 kHz de frecuencia. Este coro es similar al que ha sido previamente grabado en aguas profundas de los océanos Pacífico e Índico.

xii) El coro es probablemente producido por peces mesopelágicos, y podría ser usado para comunicarse, ser un efecto de su alimentación, o para desconcertar depredadores, o más probablemente ser un resultado de desgasificación debido a ajustes de presión de estos peces durante la migración.

xiii) Parece existir una correlación positiva entre el nivel sonoro del coro al emplear acústica pasiva y los datos de dispersión acústica de organismos migrantes a aguas someras detectada por la acústica activa. Este resultado pionero necesita aumentar el tamaño muestral con el fin de confirmar y cuantificar esta relación, con potenciales aplicaciones en el empleo de la acústica pasiva para cuantificar la biomasa migrante de la DSL.

APPENDIX I: Other publications

Besides the manuscripts from the presented chapters, this thesis has contributed to the following publications.

Conference Communications

Alcázar-Treviño J, Johnson M, Arranz Alonso P, Aguilar de Soto N. Sincronización acústica en grupos de zifio de Blainville (*Mesoplodon densirostris*) en El Hierro. IX Congreso Anual de la Sociedad Española de Cetáceos (SEC). Las Palmas de Gran Canaria, Spain, October 2016.

Alcázar-Treviño J, Johnson M, Madsen PT, Aguilar de Soto N. Every beaked whale for itself: individual foraging activity in social groups of Blainville's beaked whale (*Mesoplodon densirostris*). 31st Annual Conference of the European Cetacean Society (ECS). Middelfart, Denmark, May 2017.

Aguilar de Soto N, Visser F, Madsen PT, Tyack P, Ruxton G, **Alcázar-Treviño J**, Arranz Alonso P, Johnson M. Animals can abate acoustic predation risk by using collective behaviour: The Killer Whale-Beaked Whale Example. African Bioacoustics Community Conference. Cape Town, South Africa, December 2018.

Arranz Alonso P, Aguilar de Soto N, Johnson M, Thomas L, Gkikopoulou K, **Alcázar-Treviño J**, Cardona A, Miranda D, Marques T. Estimating beaked whale density from passive acoustic recordings: case example in El Hierro, Canary Islands. African Bioacoustics Community Conference. Cape Town, South Africa, December 2018.

Alcázar-Treviño J, Johnson M, Arranz Alonso P, Marrero Pérez J, Madsen PT, Aguilar de Soto N. A whale bio-echosounder tell-tale of niche diversification in deep-diving beaked and pilot whales. World Marine Mammal Conference, Barcelona, December 2019.

Arranz Alonso P, Aguilar de Soto N, Johnson M, Thomas L, Gkikopoulou K, **Alcázar-Treviño J**, Cardona A, Miranda D, Marques T. Estimating beaked whale density from passive acoustic recordings. World Marine Mammal Conference, Barcelona, December 2019.

Aguilar de Soto N, Visser F, Madsen PT, Tyack P, Ruxton G, **Alcázar-Treviño J**, Arranz Alonso P, Johnson M. Fear of killer whale predation drives extreme collective behaviour in beaked whales. World Marine Mammal Conference, Barcelona, December 2019.

Marín Delgado O, Madsen PT, Johnson M, **Alcázar-Treviño J**, Aguilar de Soto N. The role of sperm whales as benthopelagic predators. World Marine Mammal Conference, Barcelona, December 2019.

Alcázar-Treviño J, Johnson M, Arranz P, Warren VE, Pérez-González CJ, Marques T, Madsen PT, Aguilar de Soto N. Deep-diving beaked whales dive together but forage apart. ECS Webinar, March 2021.

Journal papers

Lozano-Bilbao E, **Alcázar-Treviño J**, Alduán M, Lozano G, Hardisson A, Rubio C, González-Weller D, Paz S, Carrillo M, Gutiérrez A. 2021. Metal content in stranded pelagic vs deep-diving cetaceans in the Canary Islands. *Chemosphere* 285: 131441.

Arranz P, Miranda D, Gkikopoulou P, Cardona A, **Alcazar, J**, Aguilar de Soto N, Thomas L, Marques T. Estimating beaked whale density from passive acoustic recordings – a comparison with independent visual data. Submitted to Applied Acoustics.

Arranz P, Aguilar de Soto N, Madsen PT, Sprogis KR. 2021. Whale-watch vessel noise levels with applications to whale-watching guidelines and conservation. *Marine Policy* 134: 104776. Collaboration acknowledged: ‘We greatly appreciate the field assistance of Dani Miranda, **Jesús Alcazar**’.

Pedersen MB, Tønnesen P, Malinka CE, Ladegaard M, Johnson M, Aguilar de Soto N, Madsen PT. 2021. Echolocation click parameters of short-finned pilot whales (*Globicephala macrorhynchus*) in the wild. *The Journal of the Acoustical Society of America* 149: 1923. doi: 10.1121/10.0003762. Collaboration acknowledged: ‘Thanks to Jacobo Marrero Pérez (Asociacion TONINA) for his contribution of clicks extracted from DTAGs deployed in pilot whale (pw) in 2004 and to **Jesús Alcázar** for clicks of 2019’.

Technical reports

Fraile Nuez E, Santana-Casiano JM, Aguilar de Soto N, Herrera I, Presas-Navarro C, Castro-Álamo A, Lozano Bilbao E, **Alcázar Treviño J**, Moreno Aguilar J, Burgos E, Somínguez-Yanes JF. INFORME CAMPAÑA VULCANO-II-1017 Physico-chemical, biological and geological study of an underwater volcano in a degassing stage: Island of El Hierro, VULCANO-II (CTM2014-51837-R). Canary Islands, Spain, 2017.

Escánez A, Marrero J, **Alcázar J**, Aguilar de Soto N. Informe intermedio Plan Nacional de I+D+i Proyecto: Comunidades biológicas de aguas profundas mesopelágicas de Canarias (DeepCom). Canary Islands, Spain, 2017.

APPENDIX II: Supplementary Material Chapter III

Electronic Supplementary Material

Deep-diving beaked whales dive together but forage apart.

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[7]Zoophysiology, Department of Biology, Aarhus University, C.F. Moellers Allé 3, DK-8000, Aarhus C, Denmark.

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<u>Content</u>

Figures

Figure S1. 3D reconstruction of the dead-reckoned track of two Blainville's tagged in the same social group during a coordinated foraging dive. Northing is shown in the x-axis, Easting in the y-axis and depth in the z-axis. The start of the dive is marked with a dark asterisk (*) for both whales. Buzzes marking prey capture attempts are shown as circles throughout the vocal foraging phase of the dive of each whale. Start of clicking is shown as a green diamond, and end of clicking as a red square. The color scale shows the separation distances in meters between tagged whales.

Figure S2. Boxplots showing the estimated minimum number of animals vocalizing per minute in 29 foraging dives from 9 tags deployed on Blainville's beaked whales off El Hierro. The boxes represent the acoustically estimated group size, including the tagged whale, while the visually assessed group size is shown in the top of the figure. Each box extends from the lower to upper quartile. The dark line is the median and the whiskers show the min and max values excepting 6 outliers represented with circles. N: number of foraging dives per tag deployment. Tag deployments are coded by the initials of the Latin name of the species (md) and two digits indicating the year of the deployment, followed by the Julian day of the year and a letter for the consecutive tag deployment of the day.

Figure S3. Distances between pairs of whales as a function of time within coordinated foraging dives: Blainville's beaked whales (above), and Cuvier's beaked whales (below). Distances between the whales in each pair are estimated from the time delay between the emission of echolocation clicks (recorded by the tag attached to the emitting animal) and their reception by the tag carried by the second whale of the pair. Within the limitations of the sample size, notice that whales spread at variable distances during the vocal (foraging) phase of the dive and tend to approach each other towards the end of the vocal phase, before initiating the silent ascent to the surface. We interpret this behaviour as serving to facilitate group cohesion and coordinated surfacing of group members after a deep foraging dive in spite of maintaining silence from a mean depth of 700 m in the ascent.

Tables

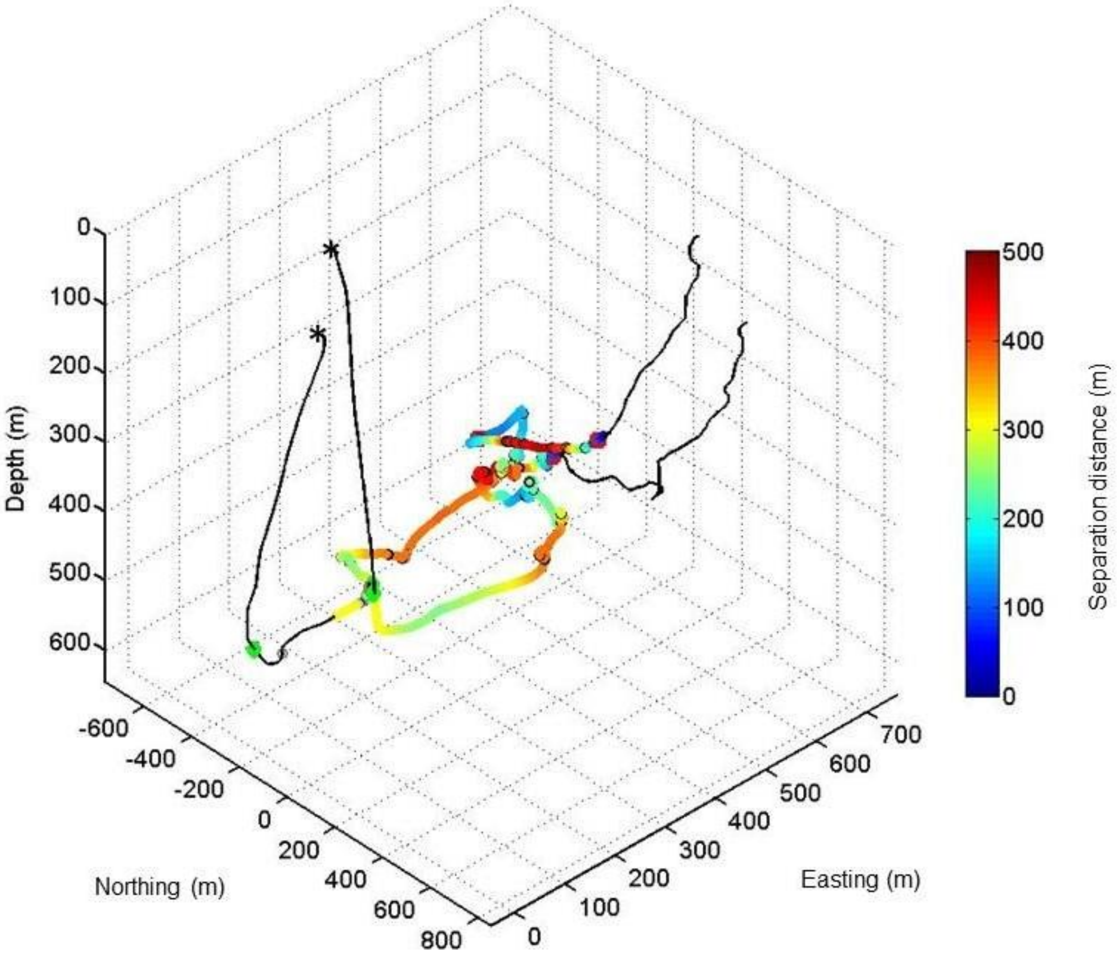
Table S1. Fitted GEE models for 50 Blainville’s dives, with tag deployment as a random grouping factor, using group size to predict mean click or buzz rate averaged over each dive.

Table S2. Fitted GEE models for 29 Blainville’s dives, with dive of each tag deployment as a random grouping factor, testing the relationship between apparent source level (ASL) of focal clicks and length of pauses in clicking and the minute-averaged animal counts over each minute of foraging dives.

Table S3. Individual dive parameters for the tagged Blainville’s and Cuvier’s beaked whales analysed in this study.

Table S4. Per-minute data of a coordinated dive performed by two Blainville´s tagged in the same social group (tags ‘a’ and ‘b’) while both whales were vocal. ICI = inter-click-interval.

Table S5. Per-minute data of a coordinated dive performed by two Cuvier´s tagged in the same social group (tags ‘a’ and ‘b’) while both whales were vocal. ICI = inter-click-interval.



0
100
200
300
400
500
600
Depth (m)
-600
-400
-200
0
200
400
600
800
Northing (m)
0
100
200
300
400
500
600
700
Easting (m)
500
400
300
200
100
0
Separation distance (m)

Figure S1.

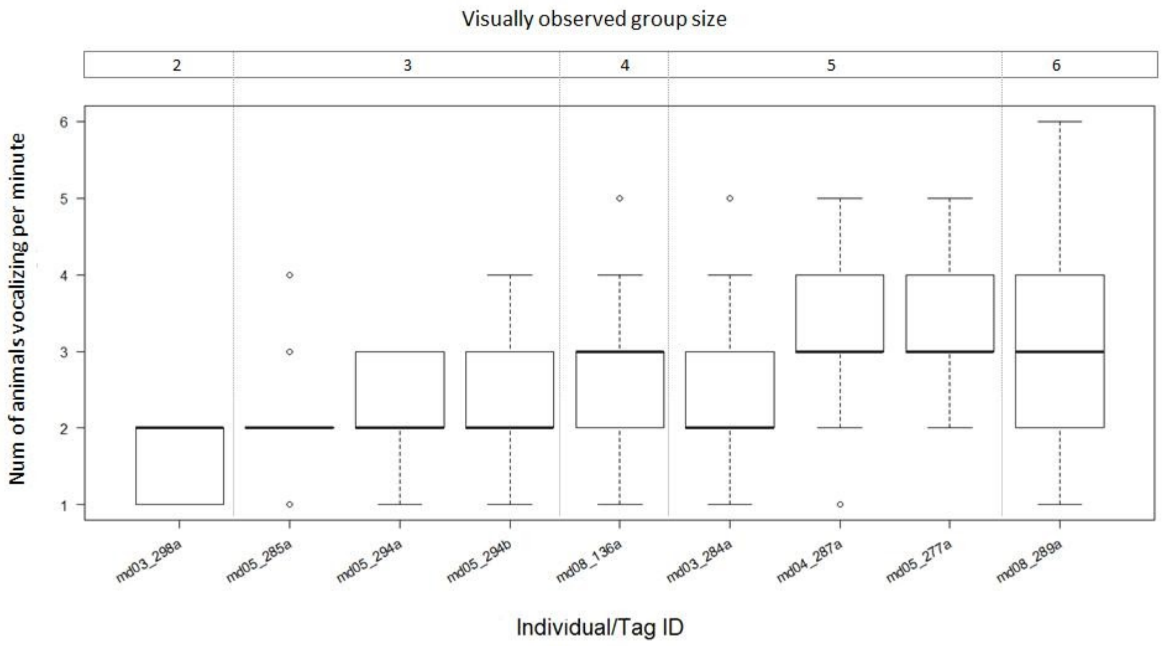


Figure S2.

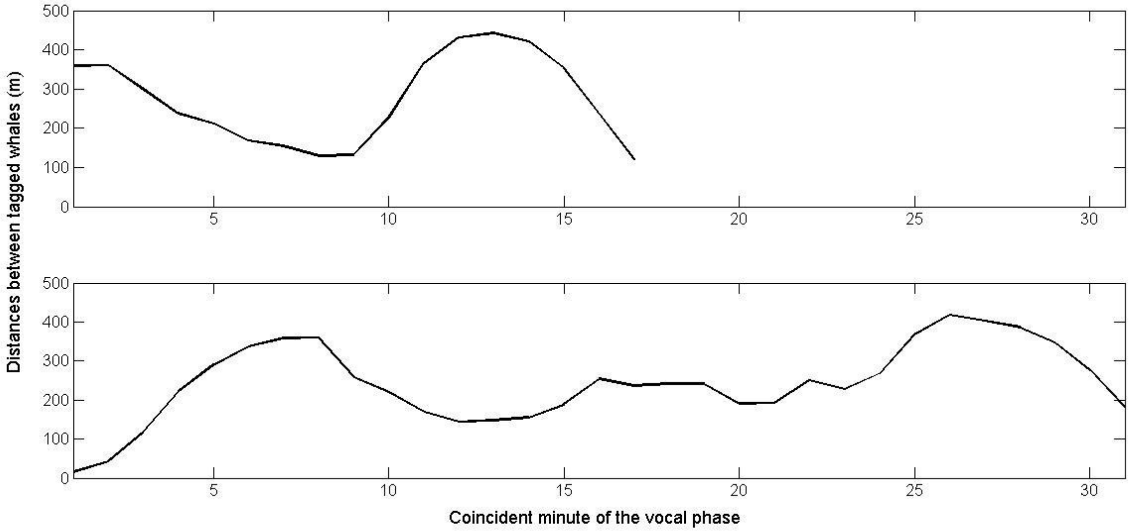


Figure S3.

Table S1.

Generalized Estimating Equations				
Click rate				
Factors	**Coefficients**			
Term	Estimate	Std. error	Wald	p-value
(Intercept)	2.55	0.17	222.92	<0.001
Group size	-0.04	0.03	1.11	0.29
Buzz rate				
Factors	**Coefficients**			
Term	Estimate	Std. error	Wald	p-value
(Intercept)	0.02	0.00	37.27	<0.001
Group size	0.00	0.00	0.37	0.54

Table S2.

Generalized Estimating Equations				
Vocalizing animals count				
Factors	**Coefficients**			
Term	Estimate	Std. error	Wald	p-value
(Intercept)	2.43	0.13	338.26	<0.001
Focal ASL	13.68	7.78	3.09	0.079
Pauses duration	0.004	0.01	0.3	0.58

Table S3.

Species	*Tag ID*	*Individual*	*Sex*	*Dive number*	*Vocal time (s)*	*Focal clicks*	*Click rate (clicks/s)*	*Group size (visual)*	*Group size (acoustic)*	*Buzzes*	*Buzz rate (buzzes/min)*
Mesoplodon densirostris	md03_284a	MDH1	♂	1	1673	4206	2.51	5	4	29	1.04
				2	1749	4254	2.43	5	5	26	0.89
				3	1836	4208	2.29	5	4	47	1.54
				4	1091	2216	2.03	5	4	12	0.66
				5	1519	3476	2.29	5	4	19	0.75
	md03_298a	MdH15	I	1	1356.8	3177	2.34	2	2	20	0.88
				2	1617.7	3816	2.36	2	2	28	1.04
	md04_287a	MdH22	♀	1	1531	3781	2.47	5	5	32	1.25
			♀	2	1687	3710	2.20	5	5	36	1.28
			♀	3	1398	3500	2.50	5	5	26	1.12
			♀	4	1986	4196	2.11	5	4	37	1.12
	md05_277a	MdH6	♂	1	1517	3518	2.32	5	5	27	1.07
			♂	2	1720	3611	2.10	5	4	37	1.29
			♂	3	1331	3367	2.53	5	-	25	1.13
	md05_285a	MdH43	♀	1	1553	4109	2.65	3	4	54	2.09
			♀	2	1479	3390	2.29	3	4	38	1.54
			♀	3	1488	3468	2.33	3	3	41	1.65
			♀	4	1831	4096	2.24	3	3	35	1.15
	md05_294a	MdH22	♀	1	1262.4	3638	2.88	3	3	18	0.86
	md05_294b	MDH1	♂	1	1086	2587	2.38	3	4	19	1.05
			♂	2	1333	3472	2.60	3	4	20	0.90

		♂	3	1337	3503	2.62	3	4	28	1.26
		♂	4	920.9	2101	2.28	3	4	13	0.85
md08_136a	MdH6	♂	1	1600.2	4171	2.61	4	4	22	0.82
		♂	2	1317.7	3053	2.32	4	5	31	1.41
md08_137a	MDH1	♂	1	1809	3876	2.14	4	-	48	1.59
		♂	2	1265	3046	2.41	4	-	32	1.52
		♂	3	1752	3542	2.02	4	-	48	1.64
		♂	4	1243	3372	2.71	4	-	18	0.87
		♂	5	1610	3920	2.43	4	-	27	1.01
md08_142a	MdH74	♂	1	1208.9	3047	2.52	4	-	12	0.60
md08_148a	MdHC1	♂	1	1430	2641	1.85	2	-	37	1.55
		♂	2	1832	4311	2.35	2	-	32	1.05
md08_289a	MdH22	♀	1	2054	4992	2.43	6	4	39	1.14
		♀	2	1899	4425	2.33	6	6	29	0.92
		♀	3	1609	3868	2.40	6	6	30	1.12
		♀	4	1820	4552	2.50	6	6	34	1.12
		♀	5	1044	2488	2.38	6	-	10	0.57
		♀	6	529	1213	2.29	6	-	5	0.57
		♀	7	1512	3580	2.37	6	-	20	0.79
md10_163a	md10_163a	♂	1	933	3863	4.14	3	-	21	1.35
		♂	2	1360	2691	1.98	3	-	18	0.79
		♂	3	1276	1933	1.51	3	-	19	0.89
		♂	4	1700	3245	1.91	3	-	20	0.71
		♂	5	1096	3039	2.77	3	-	12	0.66

			♂	6	1016	3953	3.89	3	-	14	0.83
	md17_168a	md17_168a	♂	1	1393	3348	2.40	6	-	28	1.21
			♂	2	1675.4	3809	2.27	6	-	24	0.86
	md18_297b	MdH23	♀	1	1458.5	3315	2.27	6	-	29	1.19
Ziphius cavirostris	zc03_263a	zc03_263a	I	1	2626	4347	1.66	4	-	33	0.75
			I	2	2663	4044	1.52	4	-	29	0.65
			I	3	2116	3368	1.59	4	-	44	1.25
			I	5	1017	2428	2.39	4	-	23	1.36
			I	6	1415	3332	2.35	4	-	36	1.53
			I	7	1770	3160	1.79	4	-	34	1.15
			I	8	1769	3080	1.74	4	-	32	1.09
	zc04_160a	zc04_160a	♂	1	2822	6003	2.13	3	-	52	1.11
			♂	2	2679	2438	0.91	3	-	*	*
	zc04_161a	zc04_161a	I	1	1936	3604	1.86	5	-	45	1.39
			I	2	1967	3782	1.92	5	-	*	*
			I	3	1953	3337	1.71	5	-	*	*
	zc04_161b	zc04_161b	I	1	1916.4	4074	2.13	5	-	*	*
			I	2	1967	3362	1.71	5	-	*	*
			I	3	2057	4419	2.15	5	-	*	*
			I	4	1279	1387	1.08	5	-	*	*
			I	5	1826	2794	1.53	5	-	*	*
			I	6	1755	2896	1.65	5	-	*	*
			I	7	2235	2866	1.28	5	-	*	*
			I	8	1620	3232	2.00	5	-	*	*

zc04_175a	zc04_175a	I	1	2592	3902	1.51	1	-	25	0.58
		I	2	2128	3498	1.64	1	-	21	0.59
		I	3	2456	3704	1.51	1	-	13	0.32
zc04_179a	zc04_179a	I	2	1725	3644	2.11	4	-	34	1.18
		I	3	2073	3484	1.68	4	-	37	1.07
zc05_167a	zc05_167a	♂	1	2317	3599	1.55	5	-	13	0.34
		♂	2	2272	3511	1.55	5	-	17	0.45
		♂	3	2268	3492	1.54	5	-	10	0.26
zc05_170a	zc05_170a	I	1	2597	3943	1.52	4	-	*	*
		I	2	2122	2589	1.22	4	-	*	*
		I	3	2385	3580	1.50	4	-	*	*
		I	4	2097	3032	1.45	4	-	*	*
		I	5	1622	2600	1.60	4	-	*	*
zc06_204a	zc06_204a	I	1	2335	4169	1.79	4	-	22	0.57
		I	2	2037	362	0.18	4	-	15	0.44
zc06_205a	zc06_205a	I	1	1799	2763	1.54	4	-	*	*
		I	2	1464	2528	1.73	4	-	*	*
		I	3	2067	3160	1.53	4	-	*	*
		I	4	1655	2932	1.77	4	-	*	*

Table S4.

Coincident minute	***ICI a (s)***	***ICI b (s)***	***Buzz rate a (buzzes/min)***	***Buzz rate b (buzzes/min)***	***Heading a (º)***	***Heading b (º)***	***Mean depth a (m)***	***Mean depth b (m)***	***Estimated separation (m)***	***Pauses a (count)***	***Pauses a (summed duration) (s)***	***Pauses b (count)***	***Pauses b (summed duration) (s)***
1	0.350	0.426	1	0	67.45	124.98	621.77	569.97	359.25	5	5.15	1	6.70
2	0.340	0.388	1	1	65.71	102.19	599.50	595.02	360.93	5	5.3	1	6.38
3	0.375	0.374	0	0	134.44	114	611.74	608.17	298.48	5	3.11	4	3.99
4	0.333	0.378	2	0	20.07	66.13	603.27	612.11	237.61	5	2.71	3	3.09
5	0.370	0.249	0	5	4.83	0.92	611.97	595.35	211.27	7	3.63	1	4.20
6	0.242	0.291	2	0	-59.99	112.95	580.25	591.81	168.57	5	4.26	7	3.97
7	0.398	0.366	0	0	-9.89	-39.7	589.80	599.16	154.38	5	4.58	7	3.90
8	0.310	0.389	1	1	16.45	-34.53	602.47	593.92	129.71	4	4.60	2	4.33
9	0.368	0.353	0	1	-151	34.18	600.15	597.87	132.32	3	6.27	4	3.74
10	0.338	0.370	1	0	-113.33	81.47	606.16	620.44	226.74	4	5.88	6	4.38
11	0.411	0.365	0	2	-153.53	66.55	607.47	628.4	366.19	3	4.85	4	4.87
12	0.276	0.375	3	1	-34.01	63.17	581.10	597.02	431.07	2	4.44	4	3.70
13	0.297	0.267	1	2	29.81	4.58	584.63	581.56	442.40	6	3.80	5	3.61

14	0.423	0.322	0	1	109	88.55	599.74	587.34	421.65	9	4.60	7	3.38
15	0.381	0.298	1	3	74.11	44.37	594.14	603.35	352.84	4	5.10	7	3.90
16	0.368	0.365	2	0	34.25	147.18	601.16	595.87	235.14	5	4.08	6	5.39
17	0.401	0.320	1	2	8.28	12.71	587.46	578.19	120.13	6	4.39	5	5.22

Table S5.

Coincident minute	*ICI a (s)*	*ICI b (s)*	*Buzz rate a (buzzes/min)*	*Heading a (º)*	*Heading b (º)*	*Mean depth a (m)*	*Mean depth b (m)*	*Estimated horizontal distance (m)*	*Pauses a (count)*	*Pauses a (summed duration) (s)*	*Pauses b (count)*	*Pauses b (summed duration) (s)*
1	0.44	0.42	0	-82.72	50.66	516.75	536.85	15.32	1	6.05	1	12.80
2	0.43	0.41	1	-46.72	83.85	590.37	603.39	42.24	2	4.54	1	27.60
3	0.41	0.37	3	-57.85	90.63	659.17	655.36	117.37	3	7.61	0	0.00
4	0.40	0.38	1	26.65	23.58	655.92	646.19	221.60	5	8.31	1	6.10
5	0.40	0.38	0	151.11	57.4	623.9	648.55	290.07	4	7.25	2	7.00
6	0.40	0.40	2	2.61	140.44	628.87	645.63	337.09	3	6.60	1	6.40
7	0.39	0.42	3	153.21	103.35	641.57	661	358.88	5	4.21	3	5.10
8	0.41	0.40	1	104.91	32.45	640.68	663.95	359.23	5	4.50	1	4.10
9	0.41	0.41	3	54.28	131.14	646.1	667.11	257.69	6	5.51	2	23.70
10	0.41	0.43	2	58.37	56.17	644.6	677.11	219.96	4	3.97	0	0.00
11	0.41	0.41	1	18.7	81.25	644.07	689.84	169.61	3	4.90	2	4.00
12	0.41	0.44	2	89.54	144.96	655.01	686.66	143.89	5	7.10	0	0.00
13	0.44	0.43	1	28.18	131.55	637.78	713.46	147.88	3	7.11	1	4.00

14	0.40	0.39	2	28.63	132.42	635.19	690.25	155.74	4	4.91	2	4.50
15	0.41	0.36	1	-115.99	61.58	640.95	668.77	188.95	6	6.46	3	4.17
16	0.44	0.38	1	-148.72	35.62	673.13	671.13	253.90	5	5.97	1	2.80
17	0.43	0.36	2	-67.19	-88.38	667.8	647.38	237.10	4	3.76	3	4.30
18	0.42	0.37	1	-49.52	-98.79	649.91	704.27	242.12	3	2.93	2	6.90
19	0.42	0.40	1	-41.44	-41.57	649.67	712.42	242.17	3	3.63	1	2.70
20	0.42	0.41	3	-19.23	7.62	654.12	678.31	190.48	5	4.32	2	13.00
21	0.42	0.35	1	-50.85	70.57	653.81	675.94	191.82	5	4.28	1	52.00
22	0.41	0.43	2	118.52	125.05	646.61	669.64	251.30	3	5.32	0	0.00
23	0.41	0.38	2	73.46	87.24	629.3	682.08	228.39	3	8.08	1	4.80
24	0.47	0.36	0	61.87	61.18	640.57	669.76	267.68	2	10.18	2	3.90
25	0.49	0.38	2	85.7	43	678.19	639.74	366.96	2	7.45	2	7.05
26	0.48	0.38	1	66.66	51.12	715.43	650.28	418.44	4	14.88	2	5.75
27	0.47	0.39	1	27.29	6.63	688.27	708	402.28	2	16.33	2	3.10
28	0.46	0.40	2	2.68	-5.94	690.11	711.93	386.30	4	5.25	2	7.00
29	0.46	0.35	1	46.07	-49.59	665.76	674.1	347.67	4	5.41	2	4.75

30	0.45	0.41	0	16.81	-68.05	644.83	648.22	276.78	1	4.34	1	9.70
31	0.41	0.35	1	31.13	-77.76	646.49	658.33	182.51	1	12.22	2	5.40

APPENDIX III: Supplementary Material Chapter IV

Digital tags (DTAGs, Johnson & Tyack 2003) were deployed in five deep diving odontocete species in subtropical and warm temperate waters of the North Hemisphere. Two beaked whale species, Blainville's and Cuvier's beaked whales (*Mesoplodon densirostris* and *Ziphius cavirostris*, respectively) were instrumented in El Hierro (Canary Islands) and Liguria (Mediterranean Sea) between 2003-2018 and 2003-2006, respectively. Two deep-diving delphinids, short-finned pilot whales and Risso's dolphins (*Globicephala macrorhynchus* and *Grampus griseus*, respectively) were instrumented off Tenerife (Canary Islands) and Santa Catalina (Southern California Bight) in 2003-2019 and 2011-2013 respectively. Sperm whales (*Physeter macrocephalus*) were instrumented in Liguria and the Gulf of Mexico in 2002-2003 (Figure 1, Supplementary Table S1).

DTAGs were attached to the back of the whales using suction cups and delivered with a long pole after approaching slowly the animal from a small boat. Once detached from the whales, tags were recovered with the aid of VHF tracking. Acoustic data were recorded from one or two hydrophones that sampled from 32 kHz to 576 kHz, depending on the DTag version (version 1 to 4 were used). DTAGs also registered depth and acceleration at sampling rates of 50 Hz and 50–250 Hz, respectively (Johnson & Tyack 2003). The Dtag toolbox (Johnson 2014, www.soundtags.org) was used to analyse tag data in Matlab (The MathWorks Inc.).

Supplementary Table S1. DTAG deployments analysed for this study, indicating sex when known and the number of dives and buzzes (total, day and night) per tag, along with the geographic location of the deployment. Indet (indeterminate) refers to whales of adult size and unknown sex (adult or subadult males or females). The code of the name of each deployment shows the species, the year and the the julian day of deployment, followed by a letter indicating the order of tagging within the same day. **ΦΨ***Codes referring to the same individuals when tagged more than once (MdH1, MdH6 and MdH22, respectively).

Species	Tag	Sex	n dives	n dives day	n dives night	n buzzes	n buzzes day	n buzzes night	Location
Blainville´s beaked whale ***Mesoplodon densirostris*** n=16 tags 10 whales	md03_284a **Φ**	Male	6	3	3	137	60	77	El Hierro
	md03_298a	Indet	2	2	0	48	48	0	El Hierro
	md04_287a*****	Female	4	4	0	131	131	0	El Hierro
	md05_277a **Ψ**	Male	3	3	0	87	87	0	El Hierro
	md05_285a	Female	4	2	2	166	91	75	El Hierro
	md05_294a*****	Female	1	1	0	18	18	0	El Hierro
	md05_294b **Φ**	Male	4	2	2	80	44	36	El Hierro
	md08_136a **Ψ**	Male	2	2	0	53	53	0	El Hierro
	md08_137a **Φ**	Male	9	3	6	271	127	144	El Hierro
	md08_142a	Male	1	1	0	12	12	0	El Hierro
	md08_148a	Male	2	2	0	69	69	0	El Hierro
	md08_289a*****	Female	7	3	4	167	98	69	El Hierro
	md10_146a	Indet	1	1	0	36	36	0	El Hierro
	md10_163a	Male	7	3	4	107	58	49	El Hierro
	md17_168a	Male	8	5	3	241	142	99	El Hierro
	md18_297b	Female	8	4	4	213	104	109	El Hierro
Total	**16**		**69**	**41**	**28**	**1836**	**1178**	**658**	

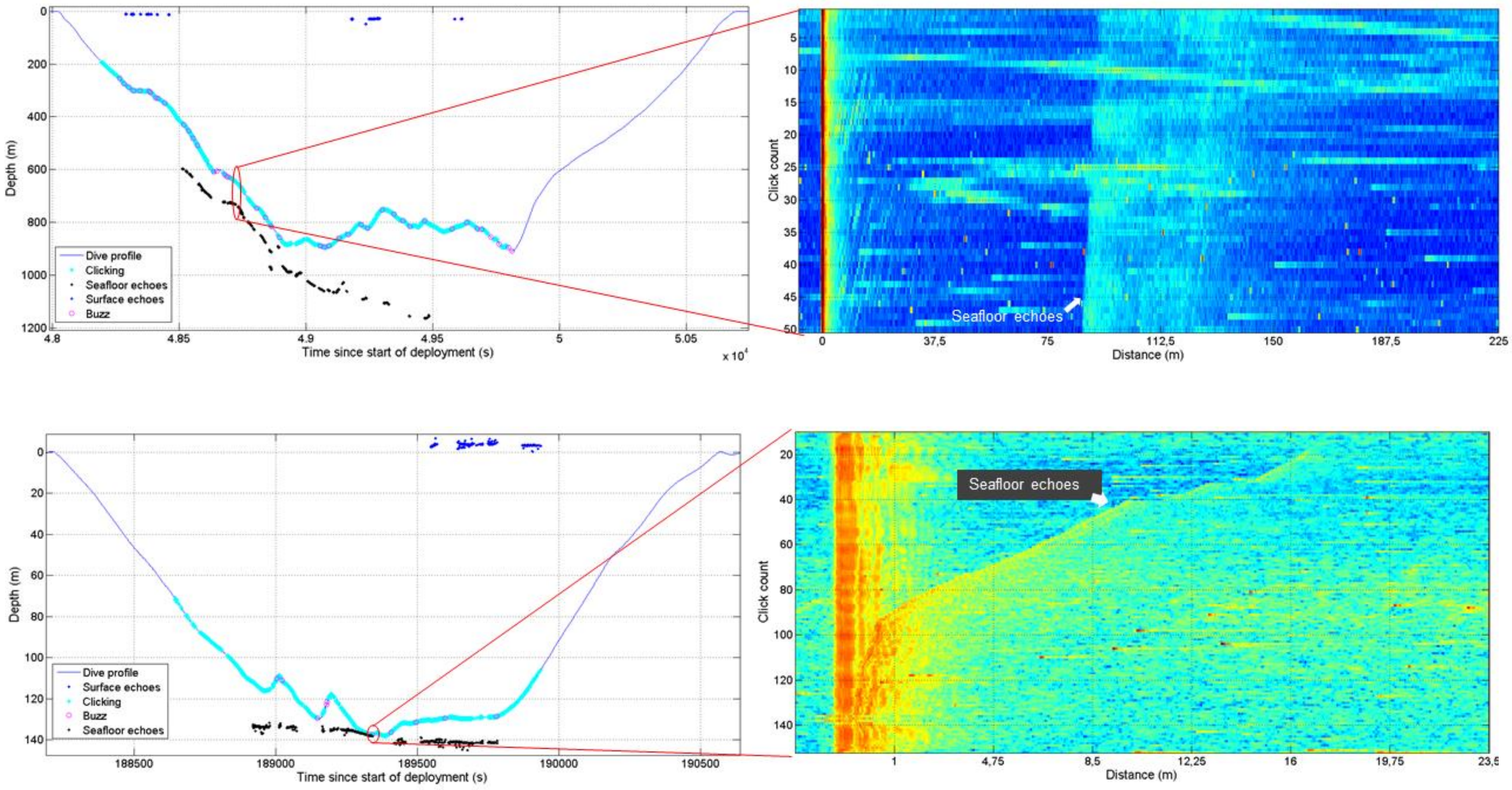
Species	Tag	Sex	n dives	n dives day	n dives night	n buzzes	n buzzes day	n buzzes night	Location
Cuvier´s beaked whale ***Ziphius cavirostris***	zc03_263a	Indet	8	1	7	221	24	197	Liguria
	zc04_160a	Male	2	2	0	62	62	0	Liguria
	zc04_161a	Indet	4	4	0	60	59	1	Liguria
	zc04_161b	Indet	1	1	0	6	6	0	Liguria
	zc04_175a	Indet	4	2	2	73	43	30	Liguria
	zc04_179a	Indet	3	3	0	68	68	0	Liguria
	zc05_167a	Male	3	1	2	41	13	28	Liguria
	zc05_170a	Indet	4	2	2	20	6	14	Liguria
	zc06_204a	Indet	2	2	0	36	36	0	Liguria
	zc06_205a	Indet	1	1	0	4	4	0	Liguria
Total	**10**		**32**	**19**	**13**	**591**	**321**	**270**	

Species	Tag	Sex	n dives	n dives day	n dives night	n buzzes	n buzzes day	n buzzes night	Location
Short-finned pilot whale ***Globicephala macrorhynchus***	pw03_306a		3	3	0	6	6	0	Tenerife
	pw03_306b		14	5	9	57	8	49	Tenerife
	pw03_306d		18	6	11	100	14	86	Tenerife
	pw03_307a		4	2	2	18	5	13	Tenerife
	pw03_307c		4	1	3	36	19	17	Tenerife
	pw03_308b		1	1	0	2	2	0	Tenerife
	pw04_295a		2	2	0	3	3	0	Tenerife
	pw04_295b		4	4	0	8	8	0	Tenerife
	pw04_295f		5	5	0	6	6	0	Tenerife
	pw04_296a		9	9	0	15	15	0	Tenerife
	pw04_296b		1	1	0	2	2	0	Tenerife
	pw04_296d		9	9	0	14	14	0	Tenerife
	pw04_297a		2	2	0	3	3	0	Tenerife
	pw04_297e		1	1	0	2	2	0	Tenerife
	pw04_297f		5	3	2	10	6	4	Tenerife

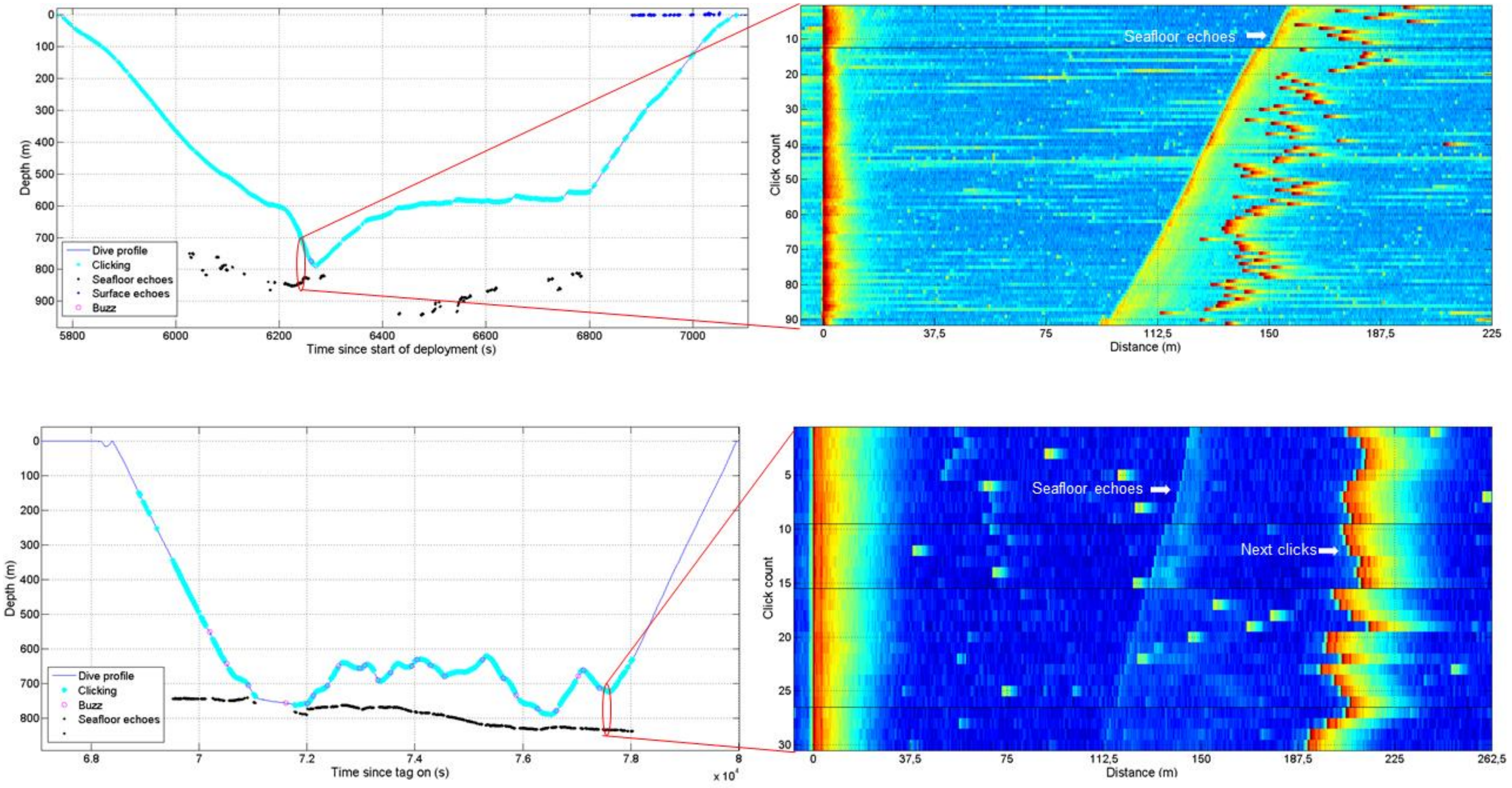
	pw04_297h		17	3	14	61	5	56	Tenerife
	pw04_297i		1	0	1	3	0	3	Tenerife
	pw04_297k		1	1	0	1	1	0	Tenerife
	pw04_299b		1	1	0	1	1	0	Tenerife
	pw04_299c		8	1	7	32	1	31	Tenerife
	pw08_108d		2	2	0	2	2	0	Tenerife
	pw08_110b		2	2	0	3	3	0	Tenerife
	pw08_110d		1	1	0	1	1	0	Tenerife
	pw08_112a		1	1	0	1	1	0	Tenerife
	pw08_112b		1	1	0	1	1	0	Tenerife
	pw08_112e		1	1	0	1	1	0	Tenerife
	pw08_113c		7	7	0	7	7	0	Tenerife
Total	**27**		**125**	**75**	**49**	**396**	**137**	**259**	
Species	**Tag**	**Sex**	**n dives**	**n dives day**	**n dives night**	**n buzzes**	**n buzzes day**	**n buzzes night**	**Location**
Risso's dolphin ***Grampus griseus***	gg11_216a		37	0	33	313	0	313	Santa Catalina
	gg11_265a		36	0	36	200	0	200	Santa Catalina
	gg11_269a		3	0	3	13	0	13	Santa Catalina
	gg13_190a		2	4	2	14	12	2	Santa Catalina
	gg13_204b		1	0	1	2	0	2	Santa Catalina
	gg13_255a		3	0	3	14	0	14	Santa Catalina
	gg13_261a		10	9	1	48	42	6	Santa Catalina
	gg13_262a		18	17	1	275	272	3	Santa Catalina
	gg13_262b		28	3	25	338	61	277	Santa Catalina

	gg13_262c		9	0	9	46	0	46	Santa Catalina
	gg13_264a		6	6	0	18	18	0	Santa Catalina
	gg13_266b		12	5	7	56	27	29	Santa Catalina
Total	**12**		**165**	**44**	**121**	**1337**	**432**	**905**	
Species	**Tag**	**Sex**	**n dives**	**n dives day**	**n dives night**	**n buzzes**	**n buzzes day**	**n buzzes night**	**Location**
Sperm whale ***Physeter macrocephalus***	sw02_239a		12	9	3	222	172	51	Gulf of Mexico
	sw02_240a		1	1	0	8	9	0	Gulf of Mexico
	sw02_249a		2	2	0	36	37	0	Gulf of Mexico
	sw02_253a		2	2	0	36	36	1	Gulf of Mexico
	sw02_254a		11	9	2	166	114	53	Gulf of Mexico
	sw02_254b		7	7	0	69	70	0	Gulf of Mexico
	sw02_254c		8	8	0	86	87	0	Gulf of Mexico
	sw03_156a		5	5	0	113	114	0	Gulf of Mexico
	sw03_165a		12	4	8	440	153	288	Gulf of Mexico
	sw03_165b		8	4	4	232	97	136	Gulf of Mexico
	sw03_167a		2	2	0	26	27	0	Gulf of Mexico
	sw03_197a		2	2	0	37	38	0	Gulf of Mexico
	sw03_247a		4	2	2	60	32	29	Liguria
	sw03_249a		3	3	0	66	67	0	Liguria
	sw03_249b		8	8	0	128	129	0	Liguria

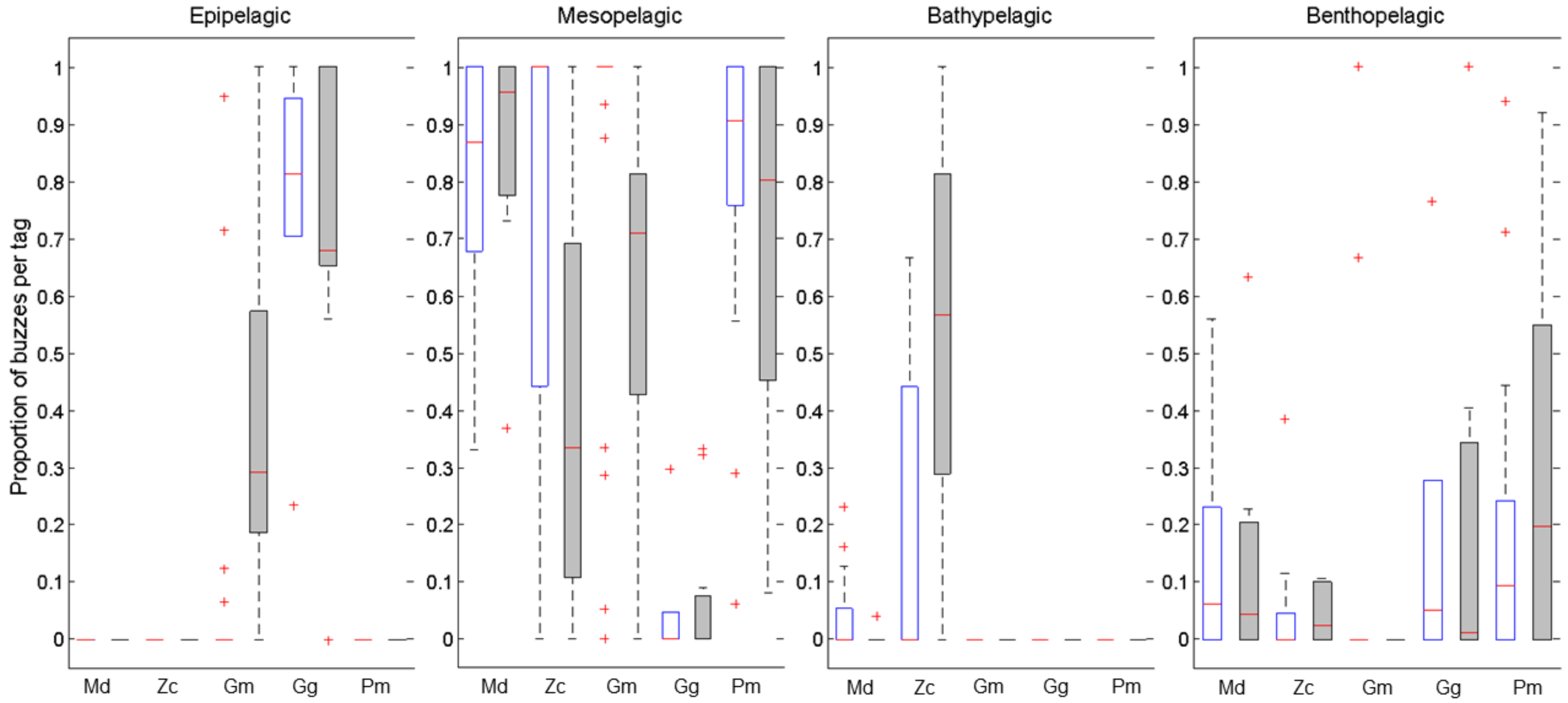
	sw03_249c		7	7	0	135	136	0	Liguria
Total	**16**		**94**	**75**	**19**	**1860**	**1318**	**558**	
Total all species	**81**		**485**	**254**	**230**	**6020**	**3386**	**2650**	



Supplementary Figure S1. Dive profiles showing clicking and buzzing activity for the tagged whales, and the surface and seafloor detections (left panels) and echograms showing how seafloor echoes were manually detected. The upper panel shows a Blainville's beaked whale



Supplementary Figure S2. Dive profiles showing clicking and buzzing activity for the tagged whales, and the surface and seafloor detections (left panels) and echograms showing how seafloor echoes were manually detected. The upper panel shows a pilot whale deployment (pw08_110b), and the bottom panel



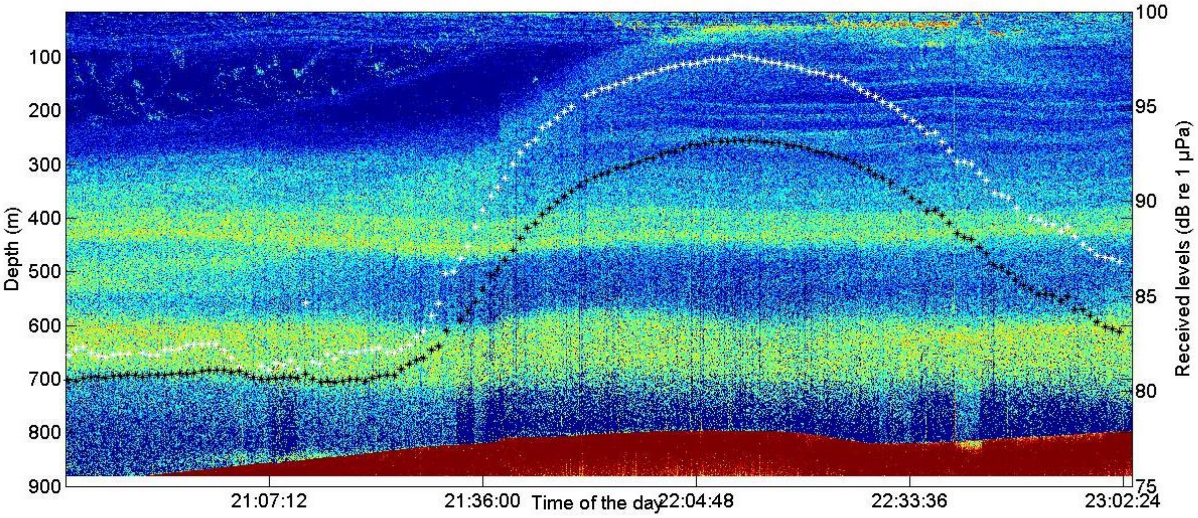
Supplementary Figure S3. Boxplots showing individual variation in the proportion of buzzes emitted within each pelagic layer for the 5 species: Md for M. densirostris, Zc for Ziphius cavirostris, Gm for Globicephala macrorhynchus, Gg for Grampus griseus and Pm for Physeter macrocephalus. The boxes are coloured white or gray to indicate day or night values, respectively. Median values are indicated with red lines and outliers are marked as red crosses. Note that the DTAG deployments analysed here range in duration

APPENDIX IV: Supplementary Material Chapter V

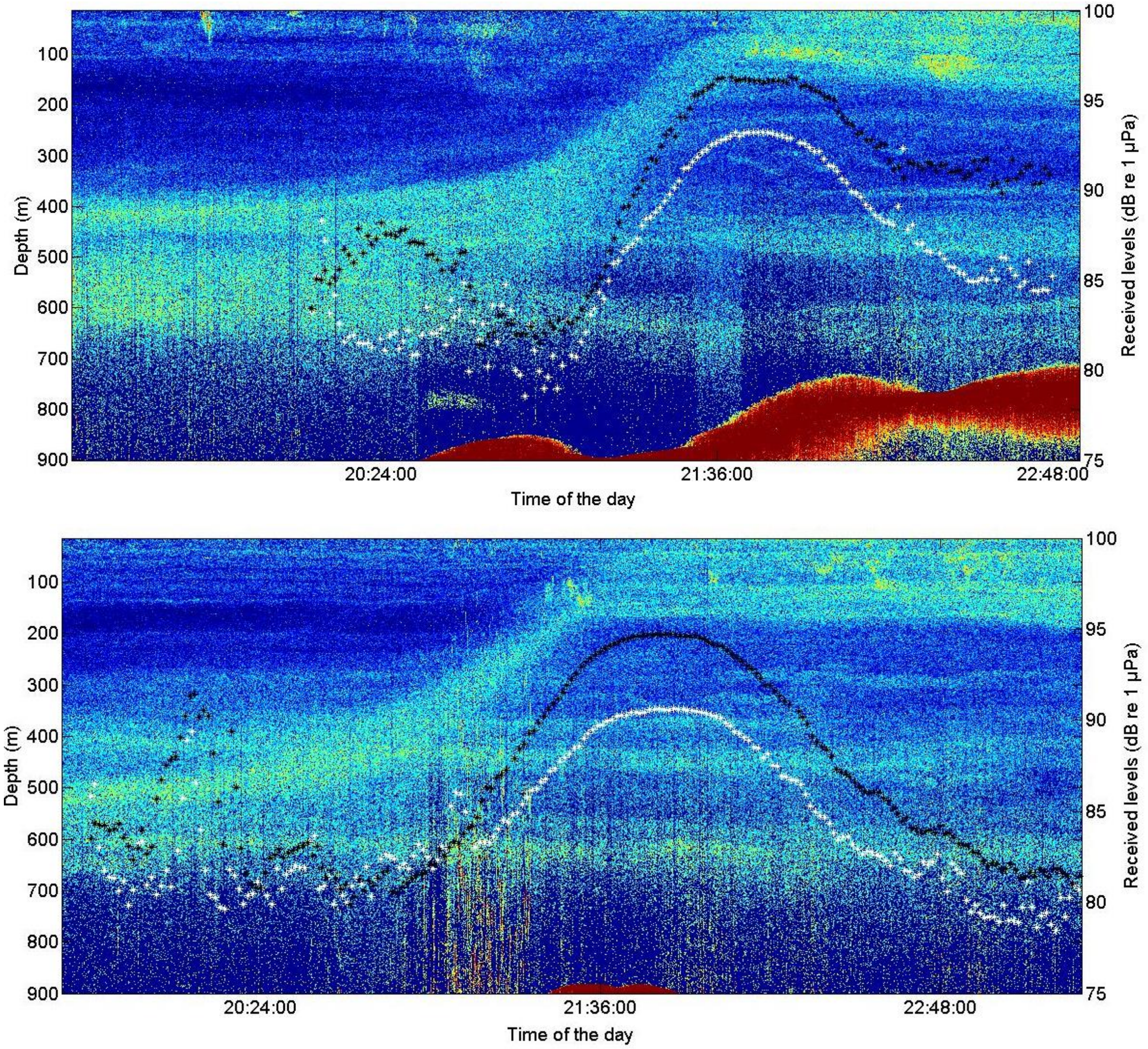
Supplementary Table S1. 1/3 octave (TOL) bands used in the analyses: exact center frequencies and lower and upper band limits.

Lower Band Limit (Hz)	**Center Frequency (Hz)**	**Upper Band Limit (Hz)**
13,93	15,63	17,53
17,55	19,69	22,09
22,11	24,80	27,83
27,85	31,25	35,06
35,09	39,37	44,18
44,21	49,61	55,66
55,70	62,50	70,13
70,18	78,75	88,35
88,42	99,21	111,32
111,41	125,00	140,25
140,36	157,49	176,71
176,85	198,43	222,64
222,81	250,00	280,50
280,73	314,98	353,41
353,69	396,85	445,27
445,63	500,00	561,01
561,45	629,96	706,83
707,39	793,70	890,55
891,25	1000,00	1122,02
1122,91	1259,92	1413,65
1414,77	1587,40	1781,09
1782,50	2000,00	2244,04
2245,81	2519,84	2827,31
2829,55	3174,80	3562,19
3565,00	4000,00	4488,07
4491,62	5039,68	5654,62
5659,09	6349,60	7124,37
7130,01	8000,00	8976,15

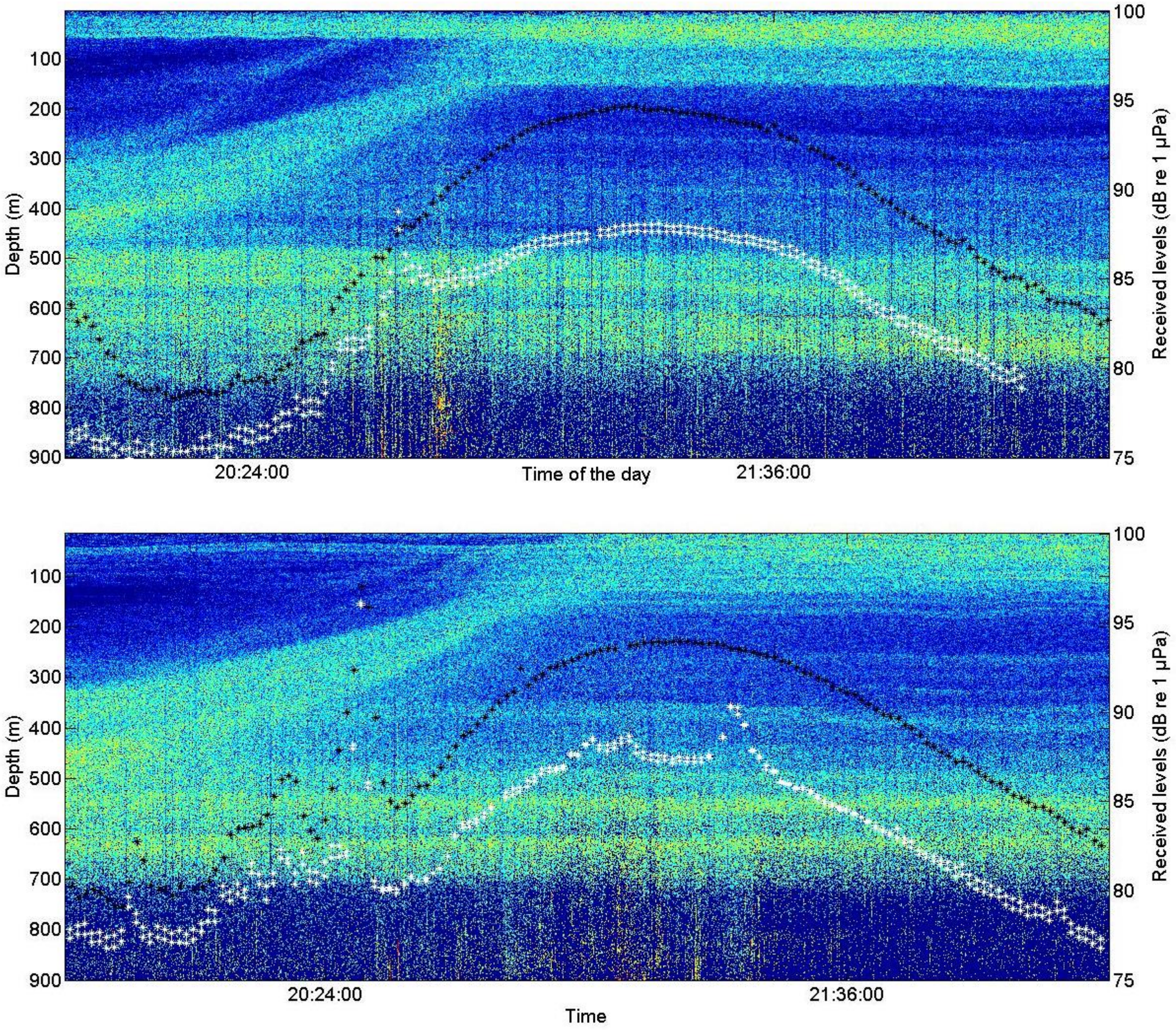
8983,25	10079,37	11309,24
11318,18	12699,21	14248,75
14260,02	16000,00	17952,30
17966,49	20158,74	22618,47
22636,36	25398,42	28497,49
28520,03	32000,00	35904,59
35932,99	40317,47	45236,95
45272,73	50796,83	56994,98
57040,06	64000,00	71809,18
71865,97	80634,95	90473,90



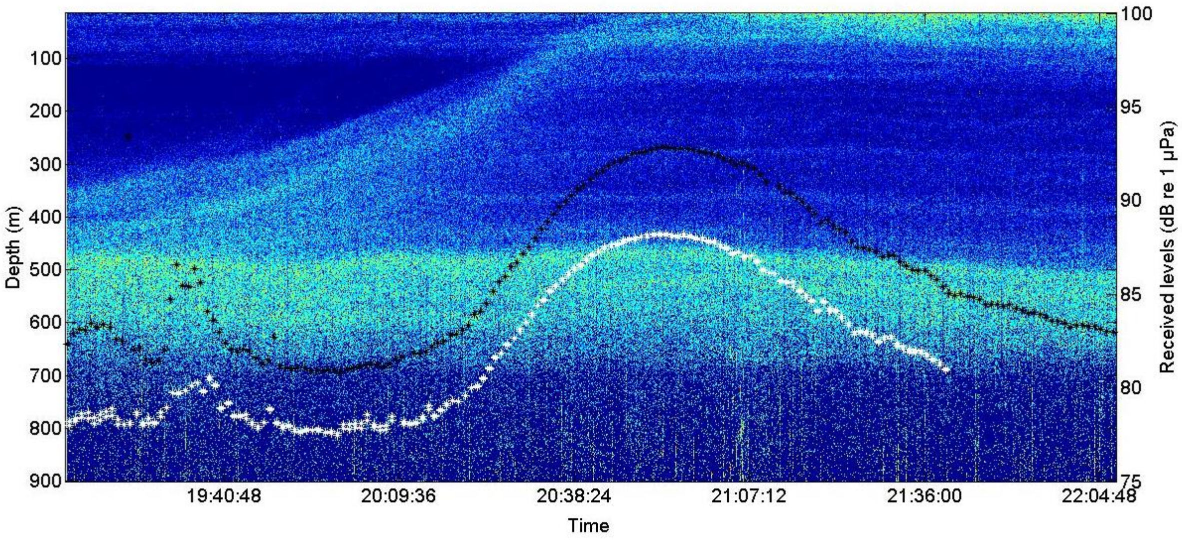
Supplementary Figure S1. Echogram for the EK80 data taken the 26th June 2019 at El Hierro island, using Sv data processed by KORONA in LSSS at 38 kHz. The superposed asterisks (*) represent the received levels at the shallow (50 m, white asterisks) and deep (600 m, black aserisks) hydrophones at the same time.



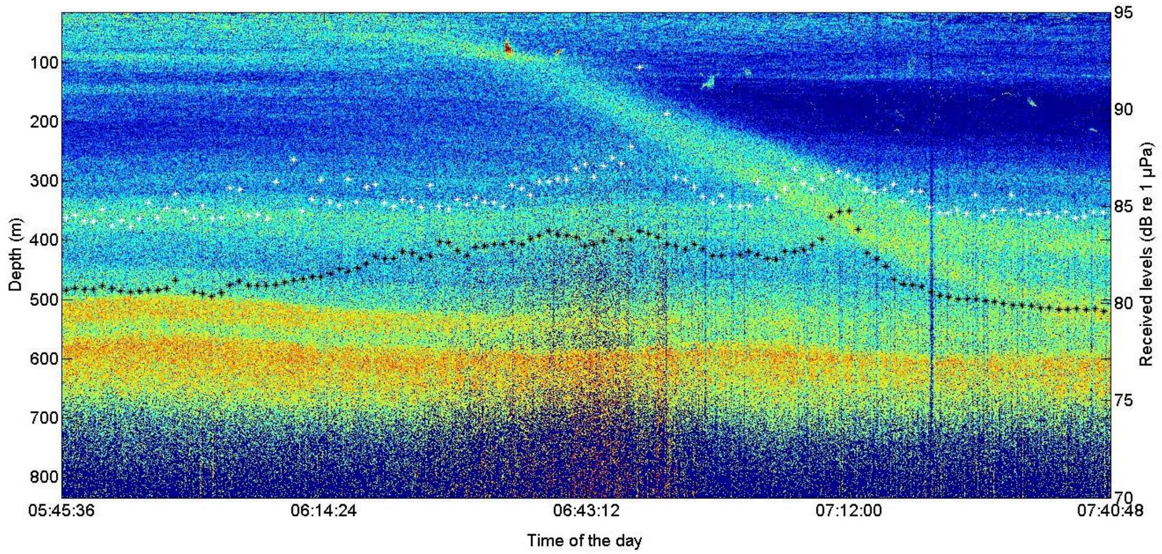
Supplementary Figure S2. Echogram for the EK80 data taken the 12th and 13th August 2020 (upper and lower panels, respectively) at Tenerife island, using Sv data processed by KORONA in LSSS at 38 kHz. The superposed asterisks (*) represent the received levels at the shallow (white) and deep (black) hydrophones at the same time.



Supplementary Figure S3. Echogram for the EK80 data taken the 11th and 12th September 2020 (upper and lower panels, respectively) at Tenerife island, using Sv data processed by KORONA in LSSS at 38 kHz. The superposed asterisks (*) represent the received levels at the shallow (white) and deep (black) hydrophones at the same time.



Supplementary Figure S4. Echogram for the EK80 data taken the 10th October 2020 at El Hierro island, using Sv data processed by KORONA in LSSS at 38 kHz. The superposed asterisks (*) represent the received levels at the shallow (white) and deep (black) hydrophones at the same time.



Supplementary Figure S5. Echogram for the EK80 data taken the 12th July 2019 at El Hierro island (sunrise surveys), using Sv data processed by KORONA in LSSS at 38 kHz. The superposed asterisks (*) represent the received levels at the shallow (white) and deep (black) hydrophones at the same time.

APPENDIX V: New holistic analyses

After the results we obtained for this thesis regarding the foraging behaviour of deep diving whales and the migrating and vocal behaviour of some of their potential prey in the DSL (Deep Scattering Layer), we are approaching a multi-disciplinary and concurrent analysis of how these predators and their prey behave in the Canary Islands. These analyses will include data from DTAGs deployed while simultaneously sampling the water column with the EK80 echosounder and using PAM (Passive Acoustic Monitoring) with drifting hydrophones. We aim to better understand and quantify how much of the DSL and BBL (Benthic Boundary Layer) resources are deep diving whales extracting during day and night, and how these predator & prey adapt to each other i.e., pilot whales foraging more in the epipelagic when the DSL migrates to shallow waters at night, or Cuvier's beaked whales exploiting more deep scattering layers at night due to their avoidance of foraging in the epipelagic, and if we can see evasion tactics of the prey like avoiding the depths were the whales are foraging, or tighten organismal aggregations shown in the acoustic backscatter.

So far, we have gathered some of the data to make a promising pilot study. In the Figure 1 of this appendix, a Blainville's beaked whale and a short-finned pilot whale were tagged off El Hierro and Tenerife island, respectively. At similar locations, EK80 active acoustic sampling was conducted, although at different moments, so this only serves as a guidance to prepare the holistic study.

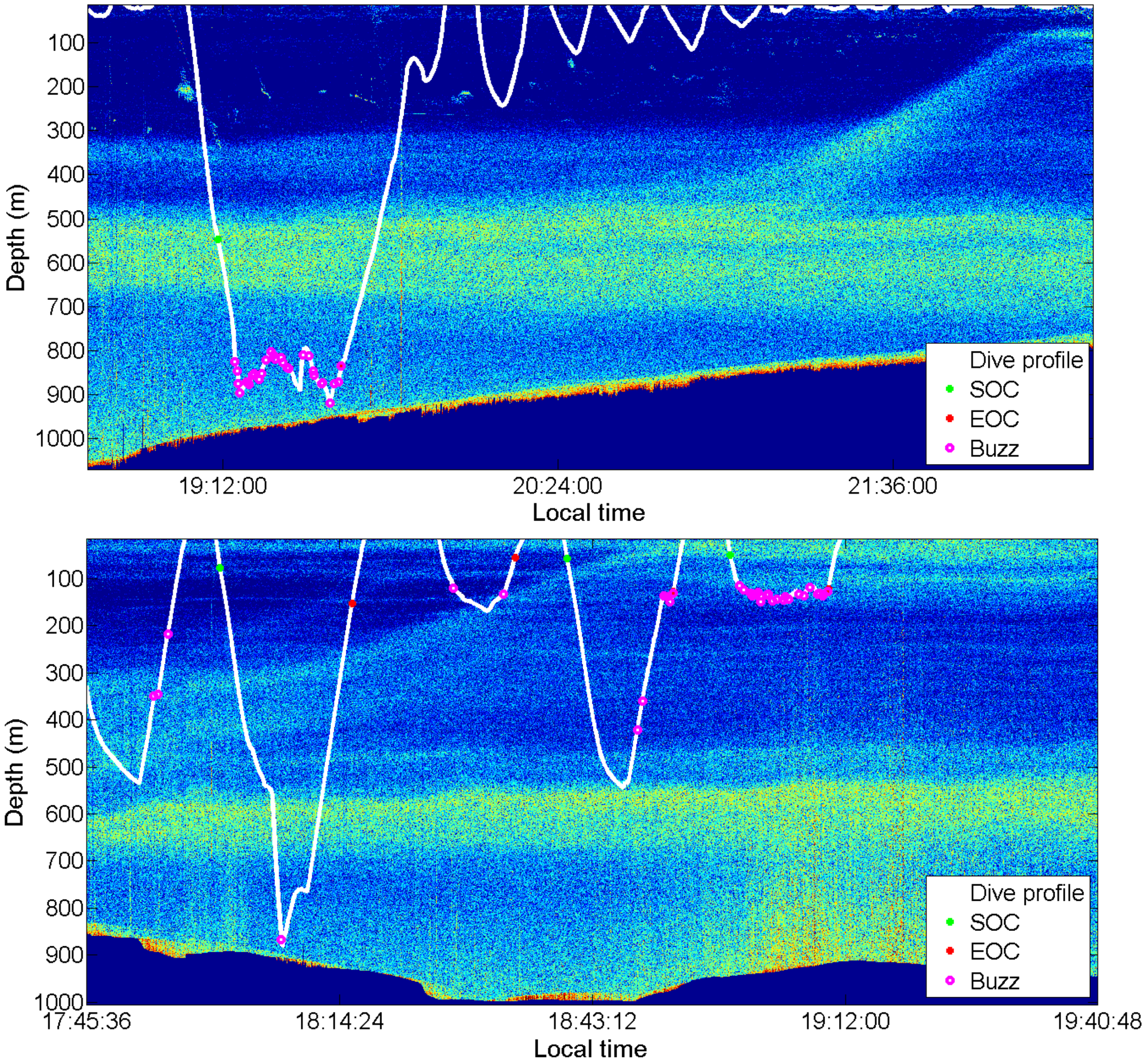


Figure 1. Dive profiles superposed to echograms. Dive profiles (white lines) were extracted from DTAG deployments of a Blainville's beaked whale off El Hierro island (md17_168a) and a short-finned pilot whale off Tenerife (pw19_080b). Magenta circles show buzzes, and the start and end of clicking (SOC & EOC, respectively) is shown in green and red circles. Echograms were made from EK80 data taken off El Hierro in June 2019 and Tenerife in September 2020. Although at different years, local hour in the x axes was matched between DTAG and EK80 data.