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Whistles in the Wild: A Multi-Regional Assessment of Vocal Communication in Free-Ranging Bottlenose Dolphins (Tursiops truncatus)

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WHISTLES IN THE WILD: A MULTI-REGIONAL ASSESSMENT OF VOCAL COMMUNICATION IN FREE-RANGING BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*)

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ABBREVIATIONS AND ACRONYMS

ACCOBAMS	Agreement on the Conservation of Cetaceans of the Black Sea, Mediterranean Sea and Contiguous Atlantic Area
AI	Artificial Intelligence
AIC	Akaike Information Criterion
AICc	Akaike Information Criterion corrected for small sample size
ASCOBANS	Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas
BDRI	Bottlenose Dolphin Research Institute
BIC	Bayesian Information Criterion
BPs	Burst-Pulsed Sounds
CC	Creative Commons
CETMAR	Centro Tecnológico do Mar
CI	Confidence Interval
CITES	Convention on International Trade of Endangered Species
cm	Centimetre
CMS	Convention on Migratory Species
CSIC	Consejo Superior de Investigaciones Científicas
csv	Comma-Separated Values
CT	Computerized Tomography
CTD	Conductivity-Temperature-Depth
DASBR	Drifting Acoustic Spar Buoy Recorder
dB	Decibel

DHARMa	Diagnostics for HierArchical Regression Models
DSLR	Digital Single Lens Reflex
EEC	European Economic Community
ENACW	Eastern North Atlantic Central Water
EU	European Union
FAD	Fish Aggregating Device
FAO	Food and Agriculture Organisation
FFT	Fast Fourier Transformation
FNMOC	Fleet Numerical Meteorology and Oceanography Center
GAM	Generalised Additive Model
GLM	Generalised Linear Model
GLMM	Generalised Linear Mixed Model
GPS	Global Positioning System
GS	Group Size
h	Hour
ha	Hectare
HARP	High-frequency Acoustic Recording Package
HF	High Frequency
Hz	Hertz
ICI	Inter-Click Interval
ID	Identification
IEO	Instituto Español de Oceanografía
IIM	Instituto de Investigacións Mariñas
IMMA	Important Marine Mammal Areas
IRR	Incident Rate Ratio
IUCN	International Union for Conservation of Nature

kg	Kilogram
kHz	KiloHertz
kn	Knots (nautical miles/hour)
km	Kilometre
kW	Kilowatts
m	Metre
min	Minute
MAW	Modified Atlantic Water
mg	Milligram
ms	Millisecond
NAO	North Atlantic Oscillation
NOGAPS	Navy Operational Global Atmospheric Prediction System
NSW	Non-Signature Whistles
PAM	Passive Acoustic Monitoring
PCB	Polychlorinated Biphenyl
PSU	Practical Salinity Unit
QQ	Quantile-Quantile
ROCCA	Real-time Odontocete Call Classification Algorithm
ROMS	Regional Ocean Modelling System
RVI	Relative Variable Importance
s	second
SAC	Special Area of Conservation
SCI	Site of Community Importance
SD	Standard Deviation

SE	Standard Error
SIGID	Signature Identification
SNIP	Source Normalized Impact per Paper
SOFAR	Sound Fixing and Ranging
SPL	Sound Pressure Level
SPM	Suspended Particulate Matter
SPUE	Sightings Per Unit Effort
SSS	Sea Surface Salinity
SST	Sea Surface Temperature
STRAUSS	Title of Project: Effects of Ocean Waves in the Rías Baixas Upwelling System: surface dynamics on selected biological case studies
SWAN	Simulating Waves Nearshore
SWAT	Soil and Water Assessment Tool
t	Tonne
THREDDS	Thematic Real-time Environmental Distributed Data Services
TPC	Tympanoperiotic Complex
UI	Upwelling Index
USC	Universidade de Santiago de Compostela
UTC	Coordinated Universal Time
UTM	Universal Transverse Mercator
VIF	Variance Inflation Factor
WGS	World Geodesic System
°C	Degrees Celsius
λ	Wavelength
µs	Microseconds (equal to one-millionth of a second)

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RESUMO

A comunicación pode ser tan sinxela como o encontro entre dous animais que deciden reproducirse e transmitir os seus xenes, ou tan complexa como a presentación de resultados científicos en forma de tese de doutoramento. Todos os animais se comunican dalgún xeito, e estudalos axúdanos a comprender o comportamento, a ecoloxía e as experiencias vividas dos individuos. En esencia, a comunicación é a transferencia de información dun emisor a un receptor que ten o potencial de influír no estado ou no comportamento deste último, mesmo se a resposta é sutil. Os animais desenvolveron múltiples formas de producir, transmitir e percibir sinais. Estas manifféstanse a través de diversos canais sensoriais, entre eles o táctil, o visual, o químico, o eléctrico e o acústico. Cada canal presenta fortalezas e limitacións, e adoitan combinarse para asegurar que a información chegue de xeito fiable baixo condicións ambientais cambiantes. A bioacústica é o estudo do son nos sistemas biolóxicos. Integra anatomía, fisioloxía, física, cognición, comportamento e ecoloxía para analizar como os animais producen, propagan, detectan e interpretan sons. Dado que o son se transmite ben a través de distintos medios e pode empregarse sen liña de visión, constitúe unha ferramenta poderosa para a investigación, especialmente onde a observación visual é difícil. Na auga, e máis concretamente no océano, o son viaxa máis rápido ca no aire e pode propagarse a grandes distancias cando as condicións son axeitadas. O que nos parece silencioso é en realidade unha paisaxe acústica complexa, chea de sons naturais, ruído de orixe humana e vocalizacións animais. Nese mundo, os sinais acústicos sustentan funcións vitais, desde a navegación e a alimentación ata a elección de parella, os vínculos sociais e a coordinación grupal.

Os cetáceos son un bo exemplo de adaptación acústica. Os odontocetos, incluídos os golfiños, dependen en gran medida do son tanto para o biosonar como para a interacción social. Producen chasquidos de ecolocalización, sons pulsados en ráfaga e asubíos, cada un con funcións específicas. Os chasquidos empréganse para a ecolocalización e a percepción do contorno, mentres que os sons pulsados e os asubíos se utilizan para a comunicación entre individuos. Os arroaces son un modelo útil para estudar a comunicación acústica porque están amplamente distribuídos, adáptanse ben en catividade, amosan flexibilidade condutual e viven en sociedades complexas. Forman relacións a longo prazo, exhiben dinámicas de fisión–fusión, nas que os grupos se dividen e se reúnen con frecuencia, e presentan diferenzas individuais que condicionan os seus roles dentro do grupo. Como depredadores en sistemas costeiros, poden influír nas redes tróficas e adoitan empregarse como indicadores do estado dos ecosistemas. Moitas poboacións viven preto de áreas urbanas, o que xera tanto oportunidades como presións. Comprender como e por que empregan o son é interesante en si mesmo e tamén importante para a práctica da conservación.

Esta tese contribúe a ese entendemento de tres maneiras. En primeiro lugar, investiga cando e por que os golfiños producen asubíos, preguntando que factores contextuais predín taxas máis

altas de asubíos. En segundo lugar, examina unha clase particular de asubíos, os asubíos sinatura, que son sons individualmente distintivos que funcionan como sinais de identidade, para explorar como se usan dentro de interaccións grupais complexas. En terceiro lugar, aplica o seguimento acústico pasivo a un estuario para comprobar se os patróns de presenza de asubíos poden revelar como os golfiños utilizan unha parte do seu rango difícil de monitorizar visualmente. En conxunto, estes estudos vinculan a comunicación co comportamento, a organización social e o uso do hábitat, e fano con conxuntos de datos de longo prazo, comparables entre lugares e obtidos con métodos complementarios.

A investigación apóiase en dúas áreas de estudo nas que se recolleron datos a longo prazo como parte do traballo da asociación BDRI. Unha atópase en Sardeña, en Italia, no mar Mediterráneo, onde os golfiños interactúan con pesqueirías e acuicultura. A outra está en Galicia, na costa atlántica, onde vales fluviais somerxidos, coñecidos como rías, xeran hábitats altamente produtivos influídos polo afloramento e o aporte fluvial. A Ría de Arousa, a maior delas, alberga unha poboación de arroaces presente durante todo o ano que utiliza a área para alimentarse e reproducirse, e que tamén interactúa con pesqueirías e estruturas de acuicultura de moluscos (bateas). Estes escenarios brindan a oportunidade de examinar como a ecoloxía local configura o comportamento acústico. Empregáronse dous enfoques principais de recollida de datos. O primeiro utilizouse nos dous primeiros estudos desta tese e é un método convencional no que se despréga un hidrófono desde un barco de investigación, na presenza de arroaces, mentres os observadores a bordo os seguen visualmente. Isto permite recompilar datos acústicos e visuais de maneira simultánea, de modo que os sons se interpretan en relación co comportamento grupal, a composición e a identidade dos individuos observados. As gravacións obtivéronse en condicións “non invasivas” nas que se buscou minimizar calquera impacto no comportamento dos arroaces, co motor apagado durante as sesións e sen contacto directo ou captura dos animais. Observadores experimentados a bordo documentaron visualmente o tamaño do grupo, a presenza de crías, o comportamento predominante e a composición de individuos. Unha limitación práctica de traballar cun único hidrófono é que non se poden asignar con certeza os sons a individuos concretos, polo que se adoptou o enfoque de grupo focal, e os sons rexistrados atribuíronse ao conxunto do grupo seguido. Aplicáronse protocolos estritos para deter a gravación se a composición do grupo cambiaba ou se aparecían exemplares novos na área. O segundo enfoque é o seguimento acústico pasivo desde un sistema autónomo de gravación nunha plataforma fixa. No terceiro estudo desta tese, un hidrófono amarrado rexistrou de forma continua na desembocadura do río Ulla, un lugar loxísticamente complexo para os mostrexos en barco pero biolóxicamente importante porque conecta o afluente principal coa parte interna da Ría. O seguimento continuo ofrece fortalezas distintas ás do traballo con hidrófono en barco. É independente da luz diúrna e das fiestras de bo tempo, proporciona unha cobertura temporal ampla e revela patróns que poderían pasar desapercibidos en prospeccións visuais breves. Tamén presenta limitacións, xa que as gravacións pasivas detectan actividade vocal máis ca presenza física, e non se coñece o tamaño ou a composición do grupo. Polo tanto, ambos métodos complétanse: o traballo con barco vincula os sons co comportamento e o contexto social, mentres que o seguimento pasivo ofrece cobertura persistente en localizacións de difícil acceso.

O primeiro obxetivo da tese formulou unha cuestión básica sobre a comunicación. Cando asubían máis os arroaces e que factores sociais ou ambientais predín taxas máis elevadas de asubíos? Os asubíos son vocalizacións que desempeñan un papel central na comunicación dos golfiños, pero as condicións que inflúen na súa frecuencia de produción seguen a estar só parcialmente comprendidas. Moitos taxóns incrementan a emisión acústica en función dos niveis de actividade e, no caso de especies altamente sociais, estas tenden a desenvolver sistemas de comunicación acústica máis amplos e complexos. Os arroaces son un exemplo claro: viven en sociedades de fisión–fusión, nas que os grupos se dividen e se reúnen con frecuencia, amosan cognición e memoria avanzadas, e presentan personalidades diversas, todo o cal se espera que configure as súas estratexias comunicativas. Estudos previos relacionaron a produción de asubíos co tamaño do grupo, o comportamento, a estación do ano, a hora do día e a localización. Con todo, a maioría realizouse en catividade ou en proxectos de campo de curta duración. Estes enfoques, aínda que valiosos, limitan a comprensión porque raramente capturan a variación a longo prazo. Ademais, as diferenzas metodolóxicas impediron a miúdo comparacións significativas entre estudos. O conxunto de datos utilizado aquí supera parte deses retos. Recompilouse durante 15 anos en dous áreas de estudo, xeograficamente distintas: Sardeña, no Mediterráneo, e Galicia, no Atlántico. En ambos casos empregouse a mesma metodoloxía de recollida de datos para garantir a comparabilidade. Esta consistencia e amplitude temporal permitiron examinar con solidez a produción de asubíos en animais en liberdade a través de contextos ecolóxicos e sociais diversos. Para abordar problemas de autocorrelación e sesgo pola duración da gravación, realizouse un submostreo do conxunto orixinal. Para cada grupo de golfiños con gravacións acústicas asociadas, seleccionáronse ao azar tres mostras dun minuto. Así obtívose un conxunto de 1119 mostras (aproximadamente 19 horas) extraídos dun total inicial de 189 horas. Cada mostra inspeccionouse visualmente e acústicamente en espectrogramas, e contáronse os asubíos para calcular a taxa de produción. Esta variable analizouse fronte a varios factores: localización, estación, parte do día (mañá, tarde, noite), comportamento do grupo, tamaño do grupo e presenza de crías. A análise baseouse en modelos lineais xeralizados mixtos (GLMM) para identificar os principais factores que influían na produción de asubíos. Os resultados indicaron que a taxa de asubíos estivo significativamente influída polo comportamento, polo tamaño do grupo, pola localización e pola interacción entre tamaño de grupo e localización. O estado condutual asociouse firmemente coa produción de asubíos, con taxas máis altas durante interaccións sociais, seguidas da alimentación e do desprazamento, e ausencia de asubíos durante o descanso. Este patrón avala a idea de que os asubíos se vinculan aos niveis de actividade e cumpren funcións sociais específicas. O tamaño do grupo tamén foi importante: os grupos grandes produciron máis asubíos, reflectindo a necesidade de maior coordinación vocal, en consonancia co observado noutros taxóns que emiten en coro, como aves e anfibios. A localización foi un preditor significativo, con golfiños en Galicia producindo case o dobre de asubíos ca os en Sardeña. A primeira vista isto suxire variación xeográfica, pero a interpretación é máis matizada. En Galicia, os arroaces observáronse en grupos máis grandes, o que explica en parte as taxas superiores de asubíos; ademais, determinadas condicións ambientais na zona de estudo poderían favorecer un maior uso das sinais acústicas para manter a cohesión grupal. Pola contra, en Sardeña, os grupos foron máis pequenos e as condicións ambientais presentes poderían reducir a necesidade de asubiar con frecuencia. Estes resultados enfatizan que as diferenzas comunicativas entre poboacións non son meramente xeográficas, senón que están modeladas polas condicións ecolóxicas, pola estrutura grupal e pola súa interacción. O estudo, por tanto, demostra a importancia de considerar variables múltiples e interactivas, subliña o valor de series longas con metodoloxías comparables para confrontar poboacións, e amosa como a produción de asubíos reflicte ao tempo a dinámica social intrínseca e as condicións ecolóxicas extrínsecas, evidenciando o papel adaptativo da comunicación en sociedades complexas.

No segundo obxetivo afóndase no uso dos asubíos centrando a atención nun tipo concreto e especialmente estudado que funciona como sinal de identidade individual: o asubío sinatura. As vocalizacións de identidade non son exclusivas dos arroaces; a codificación da identidade individual en sinais acústicas evolucionou de xeito independente en diversos taxóns. A miúdo asócianse a contextos onde os animais deben manter a cohesión ou identificar individuos concretos en entornos acústicamente complexos, como colonias ou coros, onde recoñecer á parella, ao proxenitor ou á cría resulta esencial. Os golfiños mulares ofrecen un dos exemplos mellor documentados deste fenómeno. Os asubíos sinatura descríbense por primeira vez hai máis de sesenta anos, caracterizados orixinalmente como o asubío que un individuo produce con maior frecuencia cando se atopa illado do seu grupo. Dende entón, estudáronse principalmente en catividade ou durante eventos de captura e liberación. En estudos máis recentes en poboacións silvestres, estes asubíos vinculáronse a reunións de grupo, cohesión e estrés. Os asubíos sinatura codifican a identidade mediante patróns estereotipados de modulación en frecuencia. Cada arroaz desenvolve o seu asubío nos primeiros meses de vida mediante aprendizaxe vocal, máis ca por herdanza xenética. Este proceso implica a exposición ao contorno sonoro e a creación dun asubío novedoso e distintivo. Unha vez desenvolvido, o asubío sinatura mantense estable no tempo e funciona como un “nome” acústico que outros individuos poden recoñecer. Aínda que os asubíos sinatura foron amplamente estudados en contextos de separación ou reunión, sábese menos sobre o seu uso dentro dos grupos. En particular, non está claro se os arroaces os empregan para dirixirse a individuos concretos cando os grupos son grandes ou complexos. Para abordar esta cuestión, utilizouse o conxunto descrito no primeiro obxetivo, que fornece gravacións de longo prazo con observacións visuais concurrentes. Para cada grupo, codificouse a presenza ou ausencia de asubíos sinatura inspeccionando espectrogramas e aplicando o método de identificación chamado SIGID, baseado nos patróns de repetición e nos intervalos entre asubíos. A diferenza do primeiro obxetivo, aquí a análise centrouse na presenza, xa que a natureza repetitiva dos asubíos sinatura podería introducir sesgo se se contasen repeticións. Aplicáronse modelos lineais xeralizados mixtos con distribución binomial, con localización, tamaño e composición do grupo, comportamento e factores temporais como efectos fixos, e identidade de grupo como efecto aleatorio. Os resultados indican que o comportamento tivo un efecto significativo, cunha maior probabilidade de aparición de asubíos sinatura durante as condutas sociais que durante o desprazamento, en consonancia con traballos previos que amosan unha maior produción en contextos de elevada actividade. A localización e o tamaño do grupo tamén foron factores significativos, e a interacción entre ambos mostrou que a probabilidade de aparición de asubíos sinatura aumentou en grupos máis grandes en xeral, pero a distintas taxas nas dúas áreas de estudo. Isto pon de manifesto que as diferenzas nas condicións ecolóxicas de cada rexión moldean os patróns de agrupamento, o que á súa vez inflúe en como os arroaces empregan os sinais de identidade. A complexidade ambiental e social en áreas con grupos máis numerosos resultou en maiores probabilidades de presenza de asubíos sinatura. Conxuntamente, estes achados amplían a nosa comprensión dos asubíos sinatura ao demostrar a súa función dentro dos grupos, non só durante reunións ou separacións, apoiando o seu papel no recoñecemento e na cohesión en situacións social ou acústicamente complexas. Este patrón coincide con tendencias máis amplas noutros taxóns, onde as vocalizacións individualmente distintivas evolucionan en especies que viven en grupos sociais grandes ou dinámicos. Este estudo non só afonda no coñecemento sobre a comunicación dos arroaces, senón que tamén contribúe ás teorías xerais sobre como as sociedades complexas impulsan a evolución dos sistemas de recoñecemento individual.

Como se mencionou, os datos obtidos cun hidrófono durante seguimentos focais permiten vincular a produción acústica coa composición e co comportamento do grupo. Este enfoque metodolóxico é valioso para entender as funcións sociais e condutuais dos sons, pero está condicionado pola loxística de campo, como a luz, a visibilidade, o estado do mar e o acceso físico á área de estudo, o que limita a continuidade temporal. Para complementar este enfoque e abordar preguntas máis ecolóxicas, o tercer obxetivo aplicou o seguimento acústico pasivo mediante un hidrófono fixo a unha estación para a toma de datos oceanográficos que rexistrou de maneira continua. Os estuarios considéranse áreas dinámicas e produtivas que poden servir como zonas clave de alimentación ou cría para os golfiños mulares. Ao mesmo tempo, adoitan ser focos de actividades humanas como pesqueirías, acuicultura e navegación. Dado este solapamento e a coñecida adaptabilidade dos golfiños a hábitats diversos, resulta importante avaliar o uso estuarino caso por caso para informar medidas de conservación específicas. Neste apartado, o seguimento pasivo empregouse para investigar a presenza de asubíos como indicador do uso do hábitat na parte interna da área galega de estudo, o estuario do río Ulla. Este sitio representa o límite fluvial da Ría de Arousa, onde avistamentos anecdóticos suxerían uso por golfiños, pero onde non se realizara investigación sistemática debido á dificultade das prospeccións visuais. Para este estudo, recompiláronse datos acústicos durante seis anos na desembocadura do río Ulla. En total, procesáronse máis de 330,000 arquivos acústicos que suman 22,242 horas, utilizando o software PAMGuard para a detección automática de asubíos. As deteccións agregáronse e analizáronse con modelos aditivos xeneralizados (GAMs) fronte a un conxunto de variables explicativas. Estas incluíron predictores temporais, condicións oceanográficas, indicadores de produtividade e dispoñibilidade de presas. Os resultados amosan presenza acústica regular de arroaces ao longo de todo o período de estudo, con deteccións en todos os meses mostreados e picos estacionais na primavera e no verán. Varias variables ambientais asociáronse coa presenza de asubíos, entre elas o caudal do río, a temperatura, a potencia do oleaxe, a clorofila-a, o afloramento e a presenza de lamprea e anguía. Moitas destas covariables varían estacionalmente, o que suxire que a dispoñibilidade de presas é o motor máis probable do uso do estuario. En particular, o efecto da lamprea é coherente coa súa migración estacional pola área de estudo. Aínda que especies diádromas como a lamprea e a anguía non se documentaron en estudos sobre a dieta de arroaces en augas galegas, é probable que, ao tratarse de exemplares varados, non se recolle suficiente variabilidade para reflectir o consumo neste tipo de hábitat. A evidencia anecdótica achegada por pescadores locais, incluídos os danos observados en trampas de anguías, suxire que estas especies poderían formar parte da dieta dos arroaces que utilizan o estuario, e estudos futuros centrados nestes individuos poderían confirmalo. Como acontece en estudos de seguimento pasivo, existen limitacións: as deteccións acústicas indican períodos de vocalización e poden subestimar a presenza durante comportamentos silenciosos como o descanso. Este estudo achega unha perspectiva ecolóxica sobre o uso do hábitat nun contorno complexo pero relevante. Ao demostrar un uso regular do estuario do Ulla e vinculalo a factores estacionais asociados á dispoñibilidade de presas, establece coñecementos de base sobre o uso do hábitat estuarino nunha poboación sometida a múltiples presións antrópicas. Dada a proximidade do porto de Vilagarcía, o estuario está exposto ao tráfico marítimo e ao ruído submarino, o que subliña a pertinencia destes resultados para a xestión. Unido ao recoñecemento da poboación dentro dunha área suxeita a protección baixo diferentes marcos de conservación, o estudo reforza a necesidade de medidas de conservación específicas.

Esta tese contribúe ao estudo da comunicación en golfiños ao combinar gravacións tradicionais con seguimento acústico pasivo, ofrecendo perspectivas complementarias sobre o comportamento social e o uso do hábitat. Baseada en series multianuais de dúas poboacións xeograficamente distintas, fornece ideas que transcenden o ámbito local e son relevantes para patróns máis amplos de comunicación animal e conservación. Aínda que os resultados establecen liñas de base valiosas, tamén sinalan a necesidade de continuar o traballo, desde a análise máis detallada das características e funcións dos asubíos, ata a investigación máis específica da dieta dos individuos que utilizan hábitats estuarinos e dos efectos do ruído sobre o comportamento acústico dos arroaces e o uso do hábitat. En conxunto, estes achados conforman unha plataforma para investigacións futuras e para unha planificación da conservación máis eficaz.

RESUMEN

La comunicación puede ser tan sencilla como el encuentro entre dos animales que deciden reproducirse y transmitir sus genes, o tan compleja como la presentación de resultados científicos en forma de tesis doctoral. Todos los animales se comunican de algún modo, y estudiarlos nos ayuda a comprender el comportamiento, la ecología y las experiencias vividas de los individuos. En esencia, la comunicación es la transferencia de información de un emisor a un receptor que tiene el potencial de influir en el estado o en el comportamiento de este último, incluso si la respuesta es sutil. Los animales han evolucionado múltiples formas de producir, transmitir y percibir señales. Estas se manifiestan a través de diversos canales sensoriales, entre ellos el táctil, el visual, el químico, el eléctrico y el acústico. Cada canal presenta fortalezas y limitaciones, y a menudo se combinan para asegurar que la información llegue de forma fiable bajo condiciones ambientales cambiantes. La bioacústica es el estudio del sonido en los sistemas biológicos. Integra anatomía, fisiología, física, cognición, comportamiento y ecología para analizar cómo los animales producen, propagan, detectan e interpretan sonidos. Dado que el sonido se transmite bien a través de distintos medios y puede utilizarse sin línea de visión, constituye una herramienta poderosa para la investigación, especialmente donde la observación visual es difícil. En el agua, y más concretamente en el océano, el sonido viaja más rápido que en el aire y puede propagarse a grandes distancias cuando las condiciones son adecuadas. Lo que nos parece silencioso es en realidad un paisaje acústico complejo, lleno de sonidos naturales, ruido de origen humano y vocalizaciones animales. En ese mundo, las señales acústicas sustentan funciones vitales, desde la navegación y la alimentación hasta la elección de pareja, los vínculos sociales y la coordinación grupal.

Los cetáceos son un buen ejemplo de adaptación acústica. Los odontocetos, incluidos los delfines, dependen en gran medida del sonido tanto para el biosonar como para la interacción social. Producen chasquidos de ecolocalización, sonidos pulsados en ráfaga y silbidos, cada uno con funciones específicas. Los chasquidos se emplean para la ecolocalización y la percepción del entorno, mientras que los sonidos pulsados y los silbidos se utilizan para la comunicación entre individuos. Los delfines mulares son un modelo útil para estudiar la comunicación acústica porque están ampliamente distribuidos, se adaptan bien en cautividad, muestran flexibilidad conductual y viven en sociedades complejas. Forman relaciones a largo plazo, exhiben dinámicas de fisión–fusión y presentan diferencias individuales que condicionan sus roles dentro del grupo. Como depredadores en sistemas costeros, pueden influir en las redes tróficas y suelen emplearse como indicadores del estado de los ecosistemas. Muchas poblaciones viven cerca de áreas urbanas, lo que genera tanto oportunidades como presiones. Comprender cómo y por qué utilizan el sonido es interesante en sí mismo y también importante para la práctica de la conservación.

Esta tesis contribuye a ese entendimiento de tres maneras. En primer lugar, investiga cuándo y por qué los delfines producen silbidos, preguntando qué factores contextuales predicen tasas más altas de silbidos. En segundo lugar, examina una clase particular de silbidos, los silbidos

firma, que son sonidos individualmente distintivos que funcionan como señales de identidad, para explorar cómo se usan dentro de interacciones grupales complejas. En tercer lugar, aplica el monitoreo acústico pasivo a un estuario para comprobar si los patrones de presencia de silbidos pueden revelar cómo los delfines utilizan una parte de su rango difícil de monitorear visualmente. En conjunto, estos estudios vinculan la comunicación con el comportamiento, la organización social y el uso del hábitat, y lo hacen con conjuntos de datos de largo plazo, comparables entre sitios y obtenidos con métodos complementarios.

La investigación se apoya en dos áreas de estudio donde se han recogido datos a largo plazo como parte del trabajo de la asociación BDRI. Una se encuentra en Cerdeña, en el mar Mediterráneo, donde los delfines interactúan con pesquerías y acuicultura. La otra está en Galicia, en la costa atlántica, donde valles fluviales sumergidos, conocidos como rías, generan hábitats altamente productivos influidos por el afloramiento y el aporte fluvial. La Ría de Arousa, la mayor de ellas, alberga una población de delfines presente durante todo el año que utiliza el área para alimentarse y reproducirse, y también interacciona con pesquerías y con estructuras de acuicultura de moluscos. Estos escenarios brindan la oportunidad de examinar cómo la ecología local configura el comportamiento acústico. Se emplearon dos enfoques principales de recolección de datos. El primero se utilizó en los dos primeros estudios de esta tesis y es un método convencional, en el que se despliega un hidrófono desde un barco de investigación, en presencia de delfines, mientras los observadores a bordo los siguen visualmente. Esto permite recopilar datos acústicos y visuales de manera simultánea, de modo que los sonidos se interpretan en relación con el comportamiento, la composición y la identidad de los individuos en el grupo observado. Las grabaciones se obtuvieron en condiciones “no invasivas” en las que se buscó minimizar cualquier impacto en el comportamiento de los delfines, con el motor apagado durante las sesiones y sin contacto directo o captura de los animales. Observadores experimentados a bordo de embarcaciones documentaron visualmente el tamaño del grupo, la presencia de crías, el comportamiento predominante y la composición de individuos. Una limitación práctica de trabajar con un único hidrófono es que no se pueden asignar con certeza los sonidos a individuos concretos, por lo que se adoptó el enfoque de grupo focal, y los sonidos registrados se atribuyen al conjunto del grupo, y se aplicaron protocolos estrictos para detener la grabación si la composición del grupo cambiaba o si aparecían ejemplares nuevos en el área. El segundo enfoque es el monitoreo acústico pasivo desde un sistema autónomo de grabación en una plataforma fija. En el tercer estudio de esta tesis, un hidrófono amarrado registró de forma continua en la desembocadura del río Ulla, un lugar logísticamente complejo para los muestreos en barco, pero biológicamente importante porque conecta el afluente principal con la parte interna de la Ría. El monitoreo continuo ofrece fortalezas distintas a las del trabajo con hidrófono en barco. Es independiente de la luz diurna y de las ventanas de buen tiempo, proporciona una cobertura temporal amplia y revela patrones que podrían pasar desapercibidos en prospecciones visuales breves. También presenta limitaciones, ya que las grabaciones pasivas detectan actividad vocal más que presencia física, y no se conoce el tamaño o la composición del grupo. Por tanto, ambos métodos se complementan: el trabajo con observadores a bordo de una embarcación vincula los sonidos con el comportamiento y el contexto social, mientras que el monitoreo pasivo ofrece cobertura persistente en ubicaciones de difícil acceso.

El primer objetivo de esta tesis planteó una cuestión básica sobre la comunicación. ¿Cuándo silban más los delfines mulares y qué factores sociales o ambientales predicen tasas más elevadas de silbidos? Los silbidos son vocalizaciones que desempeñan un papel central en la comunicación de los delfines, pero las condiciones que influyen en su frecuencia de producción siguen estando solo parcialmente comprendidas. Muchos taxones aumentan su emisión acústica en función de los niveles de actividad y, en el caso de especies altamente sociales, estas tienden a desarrollar sistemas de comunicación acústica más amplios y complejos. Los delfines son un ejemplo claro: viven en sociedades de fisión-fusión, en las que los grupos se dividen y se reúnen con frecuencia, muestran cognición y memoria avanzadas, y presentan personalidades diversas, todo lo cual se espera que configure sus estrategias comunicativas. Estudios previos han relacionado la producción de silbidos con el tamaño del grupo, el comportamiento, la estación del año, la hora del día y la ubicación. Sin embargo, la mayoría se ha realizado en cautividad o en proyectos de campo de corta duración. Estos enfoques, aunque valiosos, limitan la comprensión porque rara vez capturan la variación a largo plazo. Además, las diferencias metodológicas han impedido a menudo comparaciones significativas entre estudios. El conjunto de datos utilizado aquí supera parte de esos retos. Se recopilaron datos durante 15 años en dos áreas de estudio geográficamente distintas: Cerdeña, en el Mediterráneo, y Galicia, en el Atlántico. En ambos casos se empleó la misma metodología de recogida de datos para garantizar la comparabilidad. Esta consistencia y amplitud temporal permitieron examinar con solidez la producción de silbidos en animales en libertad a través de contextos ecológicos y sociales diversos. Para abordar problemas de autocorrelación y sesgo por duración de grabación, se realizó un submuestreo del conjunto original. Para cada grupo de delfines con grabaciones acústicas asociadas, se seleccionaron al azar tres muestras de un minuto. Así se obtuvo un conjunto de 1119 muestras (aproximadamente 19 horas) extraídas de un total inicial de 189 horas. Cada muestra se inspeccionó visual y acústicamente en espectrogramas, y se contaron los silbidos para calcular la tasa de producción. Esta variable se analizó frente a varios factores explicativos: ubicación, estación, hora del día, comportamiento del grupo, tamaño del grupo y presencia de crías. El análisis se basó en modelos lineales generalizados mixtos (GLMM), y resultados indicaron que la tasa de silbidos estuvo significativamente influida por el comportamiento, el tamaño del grupo, la ubicación y la interacción entre tamaño de grupo y ubicación. El estado conductual se asoció firmemente con la producción de silbidos, con tasas más altas durante interacciones sociales, seguidas de la alimentación y el desplazamiento, y ausencia de silbidos durante el descanso. Este patrón respalda la idea de que los silbidos se vinculan a los niveles de actividad y cumplen funciones sociales específicas. El tamaño del grupo también fue importante: los grupos grandes produjeron más silbidos, reflejando la necesidad de mayor coordinación vocal, en consonancia con lo observado en otros taxones que emiten en coro, como aves y anuros. La ubicación fue un predictor significativo, con delfines en Galicia produciendo casi el doble de silbidos que los de Cerdeña. A primera vista, esto sugiere variación geográfica, pero la interpretación es más matizada. En Galicia, los delfines mulares se observaron en grupos más numerosos, lo que explica en parte las tasas superiores de silbidos; además, ciertas condiciones ambientales en la zona de estudio podrían favorecer un mayor uso de señales acústicas para mantener la cohesión del grupo. Por el contrario, en Cerdeña, los grupos eran más pequeños y las condiciones ambientales presentes podrían reducir la necesidad de silbar con frecuencia. Estos resultados enfatizan que las diferencias comunicativas entre poblaciones no son meramente geográficas, sino que están moldeadas por las condiciones ecológicas, la estructura grupal y su interacción. El estudio, por tanto, demuestra la importancia de considerar variables múltiples e interactivas, subraya el valor de series largas con metodologías comparables para comparar poblaciones, y muestra cómo la producción de silbidos refleja a la vez la dinámica social intrínseca y las condiciones ecológicas extrínsecas, evidenciando el papel adaptativo de la comunicación en sociedades complejas.

En el segundo objetivo se profundiza en el uso de los silbidos centrándose en un tipo concreto y especialmente estudiado que funciona como señal de identidad individual: el “silbido firma”. Las vocalizaciones de identidad no son exclusivas de los delfines; la codificación de la identidad individual en señales acústicas ha evolucionado de forma independiente en diversos taxones. A menudo se asocian a contextos donde los animales deben mantener la cohesión o identificar individuos concretos en entornos acústicamente complejos, como colonias o coros, donde reconocer a la pareja, al progenitor o a la cría resulta esencial. Los delfines mulares ofrecen uno de los ejemplos mejor documentados de este fenómeno. Los silbidos firma se describieron por primera vez hace más de sesenta años, caracterizados originalmente como el silbido que un individuo produce con mayor frecuencia cuando se encuentra aislado de su grupo. Desde entonces, se han estudiado principalmente en cautividad o durante eventos de captura y liberación. En estudios más recientes en poblaciones silvestres, estos silbidos se han vinculado a reuniones de grupo, cohesión y estrés. Los silbidos de firma codifican la identidad mediante patrones estereotipados de modulación en frecuencia. Cada delfín desarrolla su silbido en los primeros meses de vida mediante aprendizaje vocal, más que por herencia genética. Este proceso implica la exposición al entorno sonoro y la creación de un contorno novedoso y distintivo. Una vez desarrollado, el silbido firma se mantiene estable en el tiempo y funciona como un “nombre” acústico que otros individuos pueden reconocer. Aunque los silbidos firma han sido ampliamente estudiados en contextos de separación o reunión, se sabe menos sobre su uso dentro de los grupos. En particular, no está claro si los delfines los emplean para dirigirse a individuos concretos cuando los grupos son grandes o complejos. Para abordar esta cuestión, utilicé el conjunto de datos descrito en el objetivo anterior, que proporciona grabaciones de largo plazo con observaciones visuales concurrentes. Para cada grupo, se codificó la presencia o ausencia de silbidos de firma inspeccionando espectrogramas y aplicando el método de identificación llamado SIGID, que se basa en los patrones de repetición y en los intervalos entre silbidos. A diferencia del primer estudio, aquí el análisis se centró en la presencia, ya que la naturaleza repetitiva de los silbidos de firma podría introducir sesgo si se contasen repeticiones. Se aplicaron modelos lineales generalizados mixtos con distribución binomial, con ubicación, tamaño y composición del grupo, comportamiento y factores temporales como efectos fijos, e identidad de grupo como efecto aleatorio. Los resultados indican que el comportamiento tuvo un efecto significativo, con una mayor probabilidad de aparición de silbidos firma durante las conductas sociales que durante los desplazamientos, en consonancia con trabajos previos que muestran una mayor producción en contextos de alta actividad. La localización y el tamaño del grupo también fueron factores significativos, y la interacción entre ambos mostró que la probabilidad de aparición de silbidos firma aumentó en grupos más grandes en general, pero a distintas tasas en las dos áreas de estudio. Esto pone de relieve que las diferencias en las condiciones ecológicas de cada región moldean los patrones de agrupamiento, lo que a su vez influye en cómo los delfines utilizan las señales de identidad. La complejidad ambiental y social en áreas con grupos más numerosos dio lugar a mayores probabilidades de presencia de silbidos firma. En conjunto, estos resultados amplían nuestra comprensión de los silbidos firma al demostrar su función dentro de los grupos, no solo durante reuniones o separaciones, apoyando su papel en el reconocimiento y la cohesión en situaciones social o acústicamente complejas. Este patrón coincide con tendencias más amplias en otros taxones, donde las vocalizaciones individualmente distintivas evolucionan en especies que viven en grupos sociales grandes o dinámicos. Este estudio no solo profundiza en el conocimiento sobre la comunicación de los delfines, sino que también contribuye a las teorías generales sobre cómo las sociedades complejas impulsan la evolución de los sistemas de reconocimiento individual.

Como se ha mencionado, los datos obtenidos con un hidrófono durante seguimientos focales permiten vincular la producción acústica con la composición y el comportamiento del grupo. Este enfoque metodológico es valioso para entender las funciones sociales y conductuales de los sonidos, pero está condicionado por la logística de campo, como la luz, visibilidad, el estado del mar y el acceso físico al área de estudio, lo que limita la continuidad temporal. Para complementar este enfoque y abordar preguntas más ecológicas, el tercer objetivo aplicó el monitoreo acústico pasivo (PAM) mediante un hidrófono fijo a una estación para la toma de datos oceanográficos que registró de manera continua. Los estuarios se consideran áreas dinámicas y productivas que pueden servir como zonas clave de alimentación o cría para los delfines mulares. Al mismo tiempo, suelen ser focos de actividades humanas como pesquerías, acuicultura y navegación. Dado este solapamiento y la conocida adaptabilidad de los delfines a hábitats diversos, resulta importante evaluar el uso estuarino caso por caso para informar medidas de conservación específicas. En este trabajo, PAM se utilizó para investigar la presencia de silbidos como indicador del uso del hábitat en la parte interna del área gallega de estudio, el estuario del río Ulla. Este sitio representa el límite fluvial de la Ría de Arousa, donde avistamientos anecdóticos sugerían uso por delfines, pero donde no se había realizado investigación sistemática debido a la dificultad de las prospecciones visuales. Para este estudio, se recopilaron datos acústicos durante seis años en la desembocadura del río Ulla. En total, se procesaron más de 330,000 archivos acústicos que suman 22,242 horas, utilizando el software PAMGuard para la detección automática de silbidos. Las detecciones se agregaron y analizaron con modelos aditivos generalizados (GAM) frente a un conjunto de variables explicativas. Estas incluyeron predictores temporales (estación y luz diurna), condiciones oceanográficas (temperatura, salinidad, velocidad de corriente, caudal del río, potencia del oleaje e índice de afloramiento), indicadores de productividad (concentración de clorofila-a) y disponibilidad de presas (desembarques comerciales de anguila y lamprea). Los resultados muestran presencia acústica regular de delfines a lo largo de todo el periodo de estudio, con detecciones registradas en todos los meses muestreados y picos estacionales en primavera y verano. Varias variables ambientales se asociaron con la presencia de silbidos, entre ellas el caudal del río, la temperatura, la potencia del oleaje, la clorofila-a, el afloramiento y la presencia de lamprea y anguila. Muchas de estas covariables varían estacionalmente, lo que sugiere que la disponibilidad de presas es el factor condicionante del uso del hábitat por parte de los delfines. Aunque especies diádromas como la lamprea y la anguila no se han documentado en estudios sobre la dieta de delfines mulares en aguas gallegas, es probable que, al tratarse de ejemplares varados, no se recoja suficiente variabilidad como para reflejar el consumo en este tipo de hábitat. La evidencia anecdótica aportada por pescadores locales, incluidos los daños observados en trampas de anguilas, sugiere que estas especies podrían formar parte de la dieta de los delfines que utilizan el estuario, y estudios futuros centrados en estos individuos podrían confirmarlo. Como ocurre en estudios similares en los que se emplea un seguimiento acústico pasivo existen limitaciones: las detecciones acústicas indican periodos de vocalización y pueden subestimar la presencia durante comportamientos silenciosos como el descanso, o la ausencia de vocalizaciones cuando hay ejemplares solitarios. Este estudio aporta una perspectiva ecológica sobre el uso del hábitat en un entorno complejo pero relevante. Al demostrar un uso regular del estuario del Ulla y vincularlo a factores estacionales asociados a la disponibilidad de presas, establece conocimientos de base sobre el uso del hábitat estuarino en una población sometida a múltiples presiones antrópicas. Dada la proximidad del puerto de Vilagarcía, el estuario está expuesto al tráfico marítimo y al ruido submarino, lo que subraya la pertinencia de estos resultados para la gestión. Unido al reconocimiento de la población dentro de un área sujeta a protección bajo diferentes marcos de conservación, el estudio refuerza la necesidad de medidas de conservación específicas.

Esta tesis contribuye al estudio de la comunicación en delfines al combinar grabaciones a bordo de embarcaciones con monitoreo acústico pasivo desde plataformas fijas, ofreciendo perspectivas complementarias sobre el comportamiento social y el uso del hábitat. Basada en series multianuales de dos poblaciones geográficamente distintas, proporciona ideas que trascienden el ámbito local y son relevantes para patrones más amplios de comunicación animal y conservación. Aunque los resultados establecen líneas de base valiosas, también señalan la necesidad de continuar el trabajo, desde un análisis más detallado de las características y funciones de los silbidos, hasta una investigación más específica sobre la dieta de los individuos que utilizan hábitats estuarinos y los efectos del ruido sobre el comportamiento acústico de los delfines mulares y el uso del hábitat. En conjunto, estos resultados conforman una base para investigaciones futuras y para una planificación de la conservación más eficaz.

SUMMARY

Communication can be as simple as two animals crossing paths and choosing to reproduce, which results in passing on their genes, or it can be as complex as presenting scientific study results in the form of a PhD thesis. All animals communicate in some way, and studying this helps us understand the behaviour, ecology and lived experiences of individuals. In its most basic form, communication is the transfer of information from a sender to a receiver with the potential to influence the receiver's state or behaviour, and elicit a response, even if subtle or non-observable. Animals have evolved many ways to produce, transmit and perceive signals, and these occur through several sensory channels, including tactile, visual, chemical, electrical and acoustic. Each channel has strengths and limitations, and different channels are often combined to ensure that information is conveyed reliably under changing environmental conditions. Bioacoustics is the study of sound in biological systems. It draws on anatomy, physiology, physics, cognition, behaviour and ecology to examine how animals produce, propagate, detect and interpret sounds. Because sound carries well through different media and can be used without line of sight, it is a powerful tool for research, especially where visual observation is difficult. In the water, and more specifically in the ocean, sound travels faster than in air and can propagate over long distances when conditions are right. Although to us it may seem a vast and quiet place, the ocean is in fact a complex soundscape filled with sounds of environmental, human, and animal origins. Under the surface, acoustic signals support fundamental life functions in a number of species, from navigation and foraging to mate choice, social bonding and group coordination.

Cetaceans are a great example of acoustic adaptation. Toothed whales, including dolphins, greatly rely on sound for both biosonar and social interaction. They produce echolocation clicks, burst-pulsed sounds and tonal whistles, each serving particular functions. Clicks are used for echolocation, to find prey, and for fine-scale sensing of the environment, while burst pulsed sounds and whistles are used for communication between individuals. Bottlenose dolphins are a particularly useful model for studying acoustic communication because they have a worldwide distribution, do well in captive and experimental environments, are behaviourally flexible and live in complex societies. They form long-term relationships, show fission–fusion dynamics, where group size changes frequently from the joining and separating of subgroups, and display individual differences that shape their roles within the group. As top predators in coastal systems, they can influence food webs and are often used as indicators of ecosystem status. Given their predominantly coastal distribution, many populations live close to urban areas, which creates both opportunities and threats. Understanding how and why they use sound is interesting in its own right and also important for conservation practice.

This thesis contributes to that understanding in three ways. First, it investigates when and why dolphins produce whistles, asking which contextual factors predict higher whistle rates. Second, it examines a particular class of whistles known as signature whistles, which are individually distinctive sounds that function as identity signals, to explore how these are used within large,

and complex group interactions. Third, it applies fixed passive acoustic monitoring to an estuarine habitat to test whether patterns in whistle presence can reveal if and how dolphins use an ecologically important part of their range that is difficult to monitor visually. Together, these studies link communication to behaviour, social organisation and habitat use, and they do so with datasets that are long-term, comparable across sites and collected with complementary methodological approaches.

The data were collected from two coastal study areas where long-term data have been collected as part of the work carried out by the Bottlenose Dolphin Research Institute (BDRI). One is located on the northeastern coast of the island of Sardinia, Italy, in the Mediterranean Sea, where resident dolphins interact with fisheries and fin-fish aquaculture. The other is in Galicia, on the Spanish Atlantic coast, where drowned river valleys, known locally as rías, create highly productive habitats influenced by upwelling and river discharge. The Ría de Arousa, the largest of these, supports a year-round dolphin population that uses the area for feeding and calving, and also interacts with fisheries and shellfish aquaculture structures. These settings provide an opportunity for examining how local ecology shapes acoustic behaviour. Two main data collection approaches were used. The first is a conventional boat-based method in which a hydrophone is deployed from a research boat in the presence of dolphins while observers on board follow the animals visually. This method was applied in the first two studies of the thesis and allows acoustic and visual data to be collected simultaneously, so sounds can be interpreted in relation to group behaviour, composition and identity. Recordings were obtained under non-invasive conditions, minimising any impact on dolphin behaviour by turning off the research vessel's engine during recording sessions, and with no direct contact or capture of the animals. Experienced observers on board visually documented group size, the presence of calves, predominant behaviour and group membership. A practical limitation of a single hydrophone is that sounds cannot be assigned to specific individuals, so the focal group approach was used. In this approach, recorded sounds are attributed to the whole group of animals being followed, and strict protocols were applied to stop recording if group composition changed or if new individuals entered the area. The second methodological approach is fixed passive acoustic monitoring from an autonomous recording station on a moored platform. In the third study of this thesis, a moored hydrophone recorded continuously at the mouth of the Ulla River, a location that is logistically difficult for boat surveys yet biologically important because it connects the main river tributary to the inner part of the ría. Continuous monitoring has different strengths from vessel work. It is independent of daylight and good weather conditions, provides long temporal coverage and reveals patterns that could be missed by short visual surveys. It also presents limitations, since passive recordings detect vocal activity rather than actual animal presence, and the group size or composition is not known. The two methods, therefore, complement one another. Recordings aboard a vessel with observers link sounds to behaviour and group context, while fixed passive monitoring delivers continuous coverage.

The first objective of this thesis addresses a basic question about communication. When do bottlenose dolphins whistle more, and which social or environmental factors predict higher whistle rates? Whistles are vocalisations that play a central role in dolphin communication, but the conditions that influence how often they are produced remain only partly understood. Many taxa increase their acoustic output depending on activity levels, and highly social species tend to develop more varied and complex communication. Dolphins are a clear example: they live in fission–fusion societies, where group size changes frequently, display advanced cognition

and memory, and show diverse personalities, all of which are expected to shape complex communication strategies. Previous research has linked whistle production to group size, behaviour, season, time of day, and location. However, most studies have been conducted in captivity or during short-term field projects. These approaches, while valuable, limit our understanding because they rarely capture long-term variation or allow for comparisons across populations. Moreover, methodological differences have often prevented meaningful comparisons between studies. The dataset used here overcomes some of these challenges, as it was collected over 15 years in two geographically distinct field sites: Sardinia in the Mediterranean and Galicia in the Atlantic. The methodology used in both sites was the same to ensure comparability. This consistency and temporal breadth allowed for a robust examination of whistle production in free-ranging animals across diverse ecological and social contexts. To address issues of autocorrelation and recording duration bias, the original dataset was subsampled. For each dolphin group with associated acoustic recordings, three one-minute samples were randomly selected. This produced a dataset of 1119 samples (about 19 h) drawn from an initial 189 h of recordings. Each minute sample was visually and acoustically inspected using spectrograms, and all whistles were counted to calculate the whistle rate of the focus group. This response variable was then tested against a suite of explanatory factors: location, season, time of day, group behaviour, group size, and calf presence. Group identity was included as a random effect to account for repeated sightings of the same individuals. Generalised linear mixed models (GLMMs) were applied, and results indicated that whistle rate was significantly influenced by behaviour, group size and location. Behavioural state was strongly associated with whistle production, with the highest rates during social interactions, followed by feeding and travelling, and no whistles were recorded during resting. This pattern supports the notion that whistles are linked to activity levels and provides further evidence for their role in social contexts. Group size was another significant predictor, with larger groups producing more whistles, reflecting the need for greater vocal coordination and consistent with findings in other chorusing species such as birds and frogs. With regards to location, dolphins in Galicia produced almost twice as many whistles as those in Sardinia. At first glance, this suggests geographical variation, but variable interactions within the model provide a more nuanced interpretation. In Galicia, dolphins were generally observed in larger groups, which partly explains the higher whistle rates. The environmental conditions in Galicia were so that dolphins may rely more on acoustic signalling to maintain cohesion; in Sardinia, on the other hand, groups were smaller, and conditions resulted in reduced need for frequent whistles. These findings emphasise that differences in communication between populations are not simply geographical but shaped by ecological conditions, group structure, and the interplay between them. The study contributes to our understanding of dolphin acoustic communication in several ways. First, it demonstrates the importance of considering multiple interacting variables when investigating dolphin communication, rather than attributing variation to a single factor. Second, it underscores the value of long-term datasets collected with a consistent methodology, which enable robust cross-population comparisons that are otherwise rare in wild dolphin studies. Finally, it shows how whistle production reflects both intrinsic social dynamics and extrinsic ecological conditions, offering insight into the adaptive role of communication in dolphin societies. By identifying the primary drivers of whistle rate across two populations, this study provides a foundation for the more focused investigations in subsequent parts of this

work. It highlights how dolphin vocal behaviour is context-dependent and shaped by both social and ecological pressures, reinforcing the idea that communication is central to survival and cohesion in complex animal societies.

In the second objective, the study of whistle use across different populations was taken further by focusing on a specific and particularly well-studied whistle type that conveys an individual's identity: the signature whistle. Signature vocalisations are not unique to dolphins; the encoding of individual identity in acoustic signals has evolved independently across taxa. Such vocalisations are often associated with contexts where animals must maintain cohesion or identify specific individuals in acoustically complex environments, for example, in colonies or choruses, where recognising a mate, parent, or offspring is essential. Bottlenose dolphins have provided one of the best-studied examples of this phenomenon. Signature whistles were first described more than 60 years ago, originally characterised as the most common whistle contour produced by an individual when isolated from its group. Since then, these acoustic signals have been primarily studied in captivity or during capture–release events. In more recent studies of wild populations, these whistles have been linked to group reunions, cohesion, and stress, being produced at high rates in situations of separation or disturbance. Signature whistles encode identity through stereotyped frequency modulation patterns, meaning that each individual has a uniquely-shaped whistle. Every dolphin develops its whistle in the first months of life through vocal learning, rather than genetic inheritance. This process of production learning involves exposure to the vocal environment and the creation of a novel, individually distinctive whistle contour. Once developed, signature whistles are stable over time and function as acoustic "names" that can be recognised by other individuals. While signature whistles have been well studied in contexts of separation or reunion, less is known about their use within groups. In particular, it remains unclear whether dolphins use signature whistles to address specific individuals when groups are large or socially complex. To address this gap, I used the dataset described in the previous section, which provided long-term recordings with concurrent visual observations. For each acoustic sample, the presence or absence of signature whistles was determined by visually and acoustically inspecting spectrograms and applying the SIGID criteria, which identify signature whistles based on specific repetition patterns and inter-whistle intervals. Unlike in the first objective, where the number of whistles was quantified, here the analysis focused on whether signature whistles occurred in a sample, since their repeated nature could otherwise introduce bias. Generalised linear mixed models (GLMM) with a binomial distribution were applied, using location, group size, group composition, behaviour, and temporal factors as fixed effects, with group identity as a random effect. The results indicate that behaviour had a significant effect, with signature whistles more likely to occur during social behaviour than during travelling, consistent with previous work showing higher production during active contexts. Location and group size were also significant factors, and the interaction between the two showed that the probability of signature whistle occurrence increased in larger groups overall, but at different rates in the two study areas. This highlights the concept that differences in ecological conditions in each location shape grouping patterns, which in turn influence how dolphins use identity signals. The environmental and social complexity in areas with larger groups resulted in higher probabilities of signature whistle presence. Together, these findings extend our understanding of signature whistles by demonstrating their role within groups, not only during reunions or separations, supporting their role in recognition and cohesion in socially or acoustically complex situations. This pattern aligns with broader trends in other taxa, where individually distinctive calls evolve in species that live in large or dynamic social groups. This study not only deepens knowledge of dolphin communication but also contributes to general theories of how complex societies drive the evolution of individual recognition systems.

As previously outlined, data collected with boat-based hydrophone recordings during focal follows provides an effective way to link acoustic production with group composition and behaviour. This methodological approach is invaluable for understanding the social and behavioural functions of dolphin sounds, but it is also constrained by field logistics, such as daylight, good sea conditions, and physical access to the study area, meaning that temporal coverage is often discontinuous. To complement this approach and address more ecological questions, the third objective applied fixed Passive Acoustic Monitoring (PAM) by using an unsupervised hydrophone on a moored monitoring platform to collect data continuously. Estuarine habitats worldwide are recognised as dynamic, productive areas that can serve as important feeding or calving grounds for bottlenose dolphins. At the same time, they are often focal points for human activities such as fisheries, aquaculture, and shipping. Given this overlap and the known adaptability of bottlenose dolphins to diverse habitats, it is important to assess estuarine use on a case-by-case basis to inform site-specific conservation. In this section, fixed PAM was used to investigate dolphin whistle presence as a way to understand habitat use in the inner part of the Galician study area, the Ulla River estuary. This site is ecologically interesting because it represents the riverine boundary of the Ría de Arousa, where anecdotal sightings have suggested dolphin use but where no systematic research has been carried out due to the difficulty of conducting visual surveys. For this study, acoustic data from a moored hydrophone at the mouth of the Ulla River were collected over six years. In total, over 330,000 acoustic files covering 22,242 h were processed using PAMGuard software, which automatically detected the presence of whistles. Whistle detections were then aggregated and analysed with generalised additive models (GAMs) against a suite of explanatory variables. These included temporal predictors (season and daylight), oceanographic conditions (temperature, salinity, current velocity, river discharge, wave power, and upwelling index), indicators of productivity (chlorophyll-a concentration), and proxies for prey availability (commercial landings of eel and lamprey). The results show that dolphins were acoustically present in the estuary throughout the study period, with whistle detections recorded in all sampled months, and with seasonal peaks in spring and summer. Several environmental variables were significantly associated with whistle presence, including river discharge, bottom temperature, wave power, chlorophyll-a, upwelling, and fish presence. Many of these covariates vary seasonally, suggesting that prey availability is the most likely driver of dolphin use of the estuary, which is consistent with the seasonal migration of diadromous fish through the area. Although lamprey and eel specifically have not been reported in previous dietary studies of bottlenose dolphins in Galician waters, those studies sampled stranded dolphins, which did not show sufficient variability. Anecdotal reports of dolphins damaging eel traps in Galician estuaries further support the idea that diadromous species may form part of the diet of estuary-using groups, and future diet studies on these individuals could confirm this. In a similar way to other studies employing passive acoustic methodologies, this study presents some limitations. For example, acoustic detections can only indicate periods when dolphins are vocalising and thus may underestimate presence during silent behaviours such as resting or when solitary non-vocalising individuals may be present. This study builds upon the behavioural focus of the previous studies by providing an ecological perspective on habitat use in a challenging but ecologically important environment. By demonstrating consistent dolphin use of the Ulla River estuary and linking it to seasonal drivers of prey availability, it establishes baseline knowledge of estuarine habitat use in a population already subject to multiple anthropogenic pressures. Located adjacent to Vilagarcía harbour, this estuary is exposed to vessel traffic and underwater noise, highlighting the relevance of these findings for management. Combined with the population's recognition as part of an area under a number of international protection frameworks, the study reinforces the need for site-specific conservation measures.

This thesis contributes to the study of dolphin communication by combining boat-based recordings with visual observations, and long-term fixed passive acoustic monitoring, offering complementary perspectives on social behaviour and habitat use. By drawing on multi-year datasets from two geographically distinct populations, it provides insights that extend beyond local contexts, with relevance for broader patterns of animal communication and conservation. While the findings establish valuable baselines, they also highlight the need for continued work, from further work into whistle characteristics and use to further investigating the diet of estuarine-dwelling individuals and understanding the impact of anthropogenic noise on dolphin acoustic behaviour and habitat use. Together, these results form a platform for future research and more effective conservation planning.


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CHAPTER 1:
GENERAL INTRODUCTION

The following chapter provides the immediate relevant context for the three research studies presented within this thesis. A broader, more descriptive overview of animal communication, marine bioacoustics, and the study species is provided in Annex III. This introduction begins by outlining the importance of sound in the marine environment, and how bioacoustics research can provide insights into both behavioural and ecological knowledge of species by outlining some of the main methodological approaches. The role of sounds for communication within dolphin highly social societies is explored, and then how whistles specifically can be used as the tool to do that given their great variability and main conservation outlooks. The thesis structure and objectives are then outlined in the last section.

1.1 SOUNDS IN THE OCEAN

The ocean is a dense, visually limited medium in which light attenuates over tens of metres, chemical cues dilute rapidly, and tactile signals require immediate proximity, whereas sound travels around five times faster in water than in air and with comparatively low attenuation (Bass and Clark, 2003; Erbe *et al.*, 2025). Vertical gradients in temperature, salinity, and pressure generate spatially variable sound-speed profiles, creating features such as the SOFAR channel that allow low-frequency sounds to propagate over hundreds to thousands of kilometres (Bass and Clark, 2003; Au and Hastings, 2008; Erbe *et al.*, 2025). For many marine organisms, acoustic signals therefore constitute the primary means of sensing and interacting with their environment, supporting navigation, prey detection, predator avoidance, and social communication (Au, 2000; Herzing, 2000; Gordon and Tyack, 2002b; Amorim *et al.*, 2006; Schärer *et al.*, 2012; Hadjiaghai and Ladich, 2015; Parmentier and Fine, 2016).

To understand these animals, it is necessary to consider not only the physical properties of underwater sound and its propagation, but also the sensory space within which acoustic information is actually usable. The concept of "acoustic active space" provides such a framework, describing the dynamic three-dimensional sensory space around an individual in which signals from the environment or from other animals can be detected, interpreted, and acted upon (Tervo *et al.*, 2012; Burnham and Duffus, 2023). Active space, with respect to acoustic signals, encompasses both actively produced sounds (e.g. vocalisations, echolocation clicks) and passively received cues (e.g. environmental sounds, conspecific calls or eavesdropped signals), representing the scale over which effective acoustic communication and sensing occur (Tervo *et al.*, 2012; Burnham and Duffus, 2023) (Figure 1.1), and providing an effective framework for a better understanding of the ecology of a species (Miller, 2006).

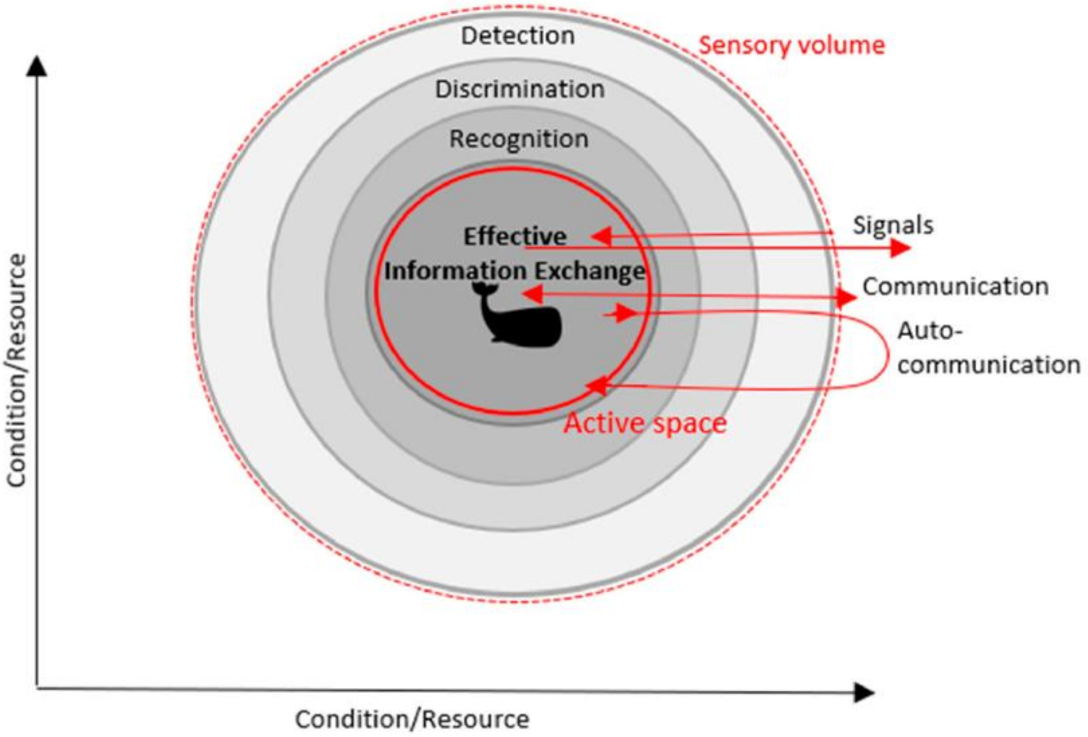


Figure 1.1 A theoretical schematic depicting how active space differs from sensory volume. The conditions or resources on the axes could be environmental conditions, resource/prey abundance, or a condition of the morphology, genotype or phenotype of the organism at the centre of the concentric circles. Adapted from Burnham and Duffus, 2023, MDPI, under the terms of the Creative Commons Attribution 4.0 International License (CC BY 4.0)

The extent of an animal's active space depends on a combination of physical and biological factors (Burnham and Duffus, 2023). Signal frequency, amplitude, and directionality, together with propagation conditions and background noise, constrain the distance over which sounds can travel and remain above masking levels (Janik, 2000; Au and Hastings, 2008; Clark *et al.*, 2009; Tervo *et al.*, 2012; Burnham and Duffus, 2023). At the same time, the receiver's auditory sensitivity, attention, experience, location, and motivational state determine whether those sounds are detected and how they are interpreted (Miller, 2006; Burnham and Duffus, 2023; Erbe *et al.*, 2025).

Among marine sound producers, marine mammals, and particularly cetaceans, are the most extensively studied contributors to biophony (Herzing, 2000; Sayigh, 2013; Duarte *et al.*, 2021; Erbe *et al.*, 2025). All cetacean species investigated so far rely heavily on sound, and have evolved specialised anatomical and physiological adaptations for sound production and reception that are closely tied to their ecology, social structure, and life history (Herzing, 2000; Ketten, 2000; Brill *et al.*, 2001; Gordon and Tyack, 2002b; Cranford, Krysl and Amundin, 2010; Erbe *et al.*, 2025). Sound frequencies are related to body size (Fletcher, 2004; May-Collado, Agnarsson and Wartzok, 2007), so large species using predominantly low-frequency calls, such as many mysticetes (Mellinger and Clark, 2003; Fletcher, 2004; May-Collado, Agnarsson and

Wartzok, 2007), tend to have larger active spaces, as these sounds propagate omnidirectionally and can travel over great distances (Au, Fay and Popper, 2000; Burnham, 2020; Burnham and Duffus, 2023; Erbe *et al.*, 2025). In contrast, the smaller odontocetes use higher-frequency signals and highly directional echolocation clicks that support fine-scale spatial resolution but usually operate over shorter ranges (Au, Fay and Popper, 2000; Janik, 2000; Lammers and Au, 2003; Miller, 2006; Branstetter *et al.*, 2012; Erbe *et al.*, 2025).

1.1.1 Bioacoustics as a Window into Behaviour and Ecology

Cetacean research is intrinsically challenging: these animals inhabit vast, dynamic, and often remote habitats, spend most of their time underwater, and are only intermittently available to visual observation (Tyack, 1998; Mann *et al.*, 2000; Montgomery and Radford, 2017). Because sound is the dominant sensory channel in the marine environment, acoustic methods partly overcome these constraints by exploiting the efficiency of sound transmission in water and the central role of vocalisations in cetacean communication (Gordon and Tyack, 2002a; Au and Hastings, 2008; Janik, 2009). However, the practical challenges of accessing the marine environment, together with the technological demands and specialised equipment required, have made marine bioacoustics research particularly demanding (Pavan *et al.*, 2022). While the physics of underwater sound are relatively well established, our understanding of how sound is employed by animals in behavioural and ecological contexts is still developing (Montgomery and Radford, 2017).

By recording and analysing vocalisations, researchers can infer species presence, relative occurrence, and aspects of behaviour and habitat use over a range of spatial and temporal scales (Barlow and Taylor, 2005; Tellechea, 2014; Carmen, Berrow and O'Brien, 2021; Fleishman *et al.*, 2023; Ross *et al.*, 2023). The strength of these inferences, however, depends on how acoustic data are collected and contextualised. While there are numerous ways to study cetacean sounds in the marine environment (Hopp, Owren and Evans, 1998; Gordon and Tyack, 2002a; Mellinger *et al.*, 2007; Erbe, 2022; Pavan *et al.*, 2022) for the purposes of this thesis, I focus on two overarching methodological approaches: First, contextualised studies, in which vocalisations are recorded alongside direct observations (Section 1.1.1.1), and second, passive acoustic monitoring (PAM), providing information by recording continuously in the absence of observers (Section 1.1.1.2).

1.1.1.1 Boat-Based Hydrophone Recordings

The first approach for collecting cetacean bioacoustics data in the field involves deploying a hydrophone from a research vessel while in the presence of the dolphins being recorded, allowing for simultaneous acoustic and visual data collection (Owren and Bernacki, 1998; Díaz López, 2011, 2022; Pavan *et al.*, 2022). This method has its challenges, as it depends on field logistics and environmental conditions, with high-quality recordings requiring both close proximity to the animals and favourable sea states (Herzing, 2000; National Research Council, 2003). Despite the limitations, linking acoustic information to observed behaviours, group composition, age, sex, and identity of the individuals provides important context for interpreting sound production (Owren and Bernacki, 1998; Herzing, 2000). This approach provides a foundational knowledge of species or population repertoires and an understanding of fundamental social and ecological context for sound production (Quick and Janik, 2008; Hawkins and Gartside, 2010; Hernandez, Solangi and Kuczaj, 2010; Díaz López, 2011). It is also an approach used for assessing the effects of anthropogenic stressors, such as noise pollution or vessel presence on acoustic behaviour (Buckstaff, 2004; Heiler *et al.*, 2016; Perez-Ortega *et al.*, 2021). Long-term acoustic datasets paired with visual observations are therefore considered important for studying cetacean sounds, as they provide a strong basis for understanding their communication (Barlow and Taylor, 2005; Rankin *et al.*, 2007; Jacobson, Forney and Barlow, 2017; Jolliffe *et al.*, 2025).

1.1.1.2 Fixed Passive Acoustic Monitoring

Passive Acoustic Monitoring (PAM) refers broadly to any technique that records underwater sounds without actively emitting signals, in contrast to “active” methods such as sonar (Zimmer, 2011; Erbe *et al.*, 2025). In the literature, this umbrella term encompasses a wide range of approaches, including boat-based hydrophones, drifting recorders and acoustic tags (Zimmer, 2011; Van Parijs *et al.*, 2021; Ross *et al.*, 2023) In this thesis, the term Fixed PAM refers specifically to autonomous, moored recording systems that operate without concurrent visual observation. This system continuously records underwater sounds over extended temporal and spatial scales, independent of daylight, visibility, or sea state, making it valuable for detecting and analysing cetacean vocalisations, revealing diel, seasonal, and interannual patterns in acoustic activity (Mellinger *et al.*, 2007; Zimmer, 2011; Fleishman *et al.*, 2023; Ross *et al.*, 2023).

Passive acoustic monitoring methods have become widespread in cetacean research because they overcome the main limitations of visual surveys, which only allow the detection of animals during brief surfacing periods, in good weather, and in daylight (Mann *et al.*, 2000; Redfern *et al.*, 2006; Mellinger *et al.*, 2007). In contrast, acoustic methods can detect one to 10 times more groups than visual surveys, and can continue at night and under poor weather conditions or difficult-to-access areas (McDonald and Moore, 2002; Barlow and Taylor, 2005; Rankin *et al.*, 2007; Ross *et al.*, 2023). Fixed PAM is also quite cost-effective when compared to data collection with a research vessel and team (Zimmer, 2011). Despite these strengths, fixed PAM also has intrinsic limitations, as it cannot detect individuals if they are not producing sounds, infer group size from sounds alone, or reliably link calls to specific behaviours without auxiliary data (Zimmer, 2011). Overall, fixed PAM complements visual surveys rather than replacing them (Simard *et al.*, 2015; Thompson, Brookes and Cordes, 2015; Frasier *et al.*, 2021). Boat-based hydrophone methods remain essential for collecting demographic, social, and contextual data, while fixed PAM provides the temporal and spatial coverage to capture broader trends in the acoustic landscape. Combining the two methods increases the interpretative power of both and supports a broader understanding of cetacean communication and social structure (Herzing, 2000; Jacobson, Forney and Barlow, 2017; Akkaya *et al.*, 2023).

1.2 COMMUNICATION AND SOCIAL DYNAMICS IN DOLPHINS

Communication is a fundamental feature of life, allowing organisms to exchange information that affects survival and reproduction (Martinelli, 2017; Rossano And Kaufhold, 2021), and is therefore central to the study of animal behaviour (Naguib and Price, 2013). Animal communication can be broadly defined as the intentional or unintentional transmission of signals from a sender to a receiver, with the potential to alter the receiver's behaviour or internal state (Megela Simmons, Popper and Fay, 2003; Martinelli, 2017; Rossano and Kaufhold, 2021). Studying communication thus involves understanding not only the signals themselves, but also how individuals perceive and interpret them within their ecological and social context (Martinelli, 2017).

The social complexity hypothesis proposes that increasing social complexity selects for more elaborate communication systems (Freeberg, Dunbar and Ord, 2012; Bouchet, Blois-Heulin and Lemasson, 2013; King, Connor and Montgomery, 2022). Species living in structured groups, with differentiated roles, long-term relationships, and frequent changes in association patterns, are expected to rely on a larger and more flexible communicative repertoire and on enhanced cognitive capacities (Freeberg, Dunbar and Ord, 2012). Within such systems, communication occurs within networks (Templeton and Carlson, 2019), and signals serve to maintain social bonds, coordinate activities, and mediate competition and cooperation, highlighting the role of communication as a system that adapts and evolves to meet the demands of living in structured, dynamic groups (Freeberg, Dunbar and Ord, 2012; King, Connor and Montgomery, 2022).

Bottlenose dolphins exemplify these principles, as they live in societies with fission-fusion dynamics, where group composition changes frequently, individuals form long-term alliances, and associations are influenced by ecological conditions and social relationships (Connor *et al.*, 2000; Aureli *et al.*, 2008). This social complexity is also reflected in their acoustic communication, which developed as a result of advanced cognitive and behavioural capacities, including long-term memory, conspecific recognition, problem solving, and the ability to integrate information across sensory modalities (Herzing, 2000; Janik, 2009, 2013; Wiley, 2013; Bruck, Walmsley and Janik, 2022). Certain acoustic social signals, in fact, are used to mediate interactions and convey emotional states in contexts of aggression and competition (Caldwell and Caldwell, 1966; Overstrom, 1983; Herzing, 2000), disciplinary signals between mothers and calves (McCowan and Reiss, 1995) or mating and mate guarding (Herzing, 2000; King *et al.*, 2019; Díaz López, 2022). Dolphins also exhibit vocal learning, both in the production of novel sounds and in the modification of existing signals according to social context (Tyack and Sayigh, 1997; Herzing, 2000; Janik, 2009). This ability is clearly illustrated by the development of individualised frequency-modulated signals (known as signature whistles), which function as acoustic identifiers and can be used to address specific conspecifics, analogous to the use of names (Tyack and Sayigh, 1997; Janik and Slater, 2000; Janik and Sayigh, 2013a; Sayigh *et al.*, 2022).

1.2.1 Whistles and their Variability as Analytical tools

Within the broader acoustic repertoire of dolphins, whistles are the most frequently studied vocalisation, largely because they are relatively easy to record with good signal quality and allow for detailed acoustic measurements compared to other sound types (Caldwell, Caldwell and Tyack, 1990; Boisseau, 2005; Janik, 2009). Whistles are also useful analytical tools for the study of bioacoustics, as their presence, production rate, and spectral characteristics vary greatly across behavioural and ecological contexts (May-Collado and Wartzok, 2008; La Manna *et al.*, 2022; Pace *et al.*, 2025).

Whistles serve several well-documented social functions, including maintaining group cohesion (Janik and Slater, 1998), mediating mother–calf contact (Sayigh *et al.*, 1990; Smolker, Mann and Smuts, 1993; Fripp and Tyack, 2008), and occurring in a range of emotional contexts (Herzing, 2000; Janik, 2009; Janik and Sayigh, 2013a; Sayigh *et al.*, 2022). Whistle production also varies according to activity levels (Quick and Janik, 2008; Hawkins and Gartside, 2010; Hernandez, Solangi and Kuczaj, 2010; Díaz López, 2011), making them sensitive indicators of behavioural dynamics.

Whistle variability also mirrors broader ecological differences, as they vary with group size and composition patterns (Quick and Janik, 2008; Hawkins and Gartside, 2010; Pace *et al.*, 2025), and can be used for habitat use monitoring (Gregorietti *et al.*, 2021) reflecting influences of habitat-specific characteristics across populations inhabiting distinct environments (Jones and Sayigh, 2002; Morisaka *et al.*, 2005; May-Collado and Wartzok, 2008; Luís *et al.*, 2021; Patiño-Pérez *et al.*, 2024).

Signature whistles, the individually distinctive subset of the whistle repertoire (Caldwell and Caldwell, 1965; Caldwell, Caldwell and Tyack, 1990; Janik and Sayigh, 2013a), have also been extensively studied over several decades, and their production rates and spectral features show meaningful variability across behaviours, social contexts, and populations (Janik, Todt and Dehnhardt, 1994; Cook *et al.*, 2004; Kriesell *et al.*, 2014; La Manna *et al.*, 2022; Sayigh *et al.*, 2022; Akkaya *et al.*, 2023), providing a sensitive indicator of how dolphins adjust their use of identity signals. Because this signal type combines individual specificity with contextual flexibility, signature whistles offer a powerful means of investigating how dolphins organise their social relationships and how communication patterns vary across environments (Romeu *et al.*, 2024).

Because variability in whistles and signature whistles reflects both social dynamics and ecological pressures, understanding these patterns is particularly valuable for drawing broader biological inferences and for generating practical information relevant to conservation and management.

1.3 FROM WHISTLES TO CONSERVATION

Anthropogenic presence and human reliance on the ocean and its resources are increasing, leading to a greater overlap with dolphin habitats (López *et al.*, 2004; Díaz López, Marini and Polo, 2005; Díaz López and Methion, 2017; Barnhill *et al.*, 2022). Anthropogenic noise has increased drastically over the past century and has now been recognised as a pervasive pollutant in marine ecosystems, with documented physiological and behavioural impacts on marine mammals, fish, invertebrates, and seabirds (Duarte *et al.*, 2021). These acoustic disturbances, along with climate-driven alterations in water properties, are causing changes in underwater soundscapes, which can alter the perceptual active space in which animals communicate (Duarte *et al.*, 2021; Burnham and Duffus, 2023).

Efforts to understand how noise affects cetacean communication have expanded rapidly (Buckstaff, 2004; Brumm, 2013; Erbe *et al.*, 2025). Numerous studies show that dolphins adjust call amplitude, frequency, or timing in response to elevated background noise, with potential energetic or information-transfer costs (Buckstaff, 2004; Gillooly and Ophir, 2010; Heiler *et al.*, 2016; Dey *et al.*, 2019; Pellegrini *et al.*, 2021; G. La Manna *et al.*, 2023). These findings highlight the urgency of characterising how communication interacts with changing soundscapes and of identifying ways to mitigate these impacts (Weilgart, 2007).

As marine top predators, dolphins act as key elements of the marine ecosystem, exerting a top-down effect on other species within the ecosystem (Heithaus *et al.*, 2008; Kiszka, Heithaus and Wirsing, 2015), and can serve as indicators of ecosystem health (Bowen *et al.*, 2006). Ensuring their proper conservation and management may therefore also benefit other species (Hooker and Gerber, 2004). Many cetacean species worldwide, including dolphins, are often protected by law, requiring local research efforts to understand the status, behaviour, and habitat use of each population to inform effective conservation practices (Convention on the Conservation of Migratory Species of Wild Animals (CMS), 1979; Council of Europe, 1979; Council of the European Communities, 1992; Marine Mammal Protected Areas Task Force, 2024).

Within this conservation context, acoustic signals, and especially whistles and signature whistles, can provide valuable information. Their structure and use vary among populations, offering cues about social organisation and potentially identifying distinct management units (Papale *et al.*, 2021). Patterns of whistle occurrence can reveal how dolphins use specific habitats, including estuaries and coastal zones with intense human activity (Marley *et al.*, 2017; Carmen, Berrow and O'Brien, 2021). Moreover, detections from passive acoustic monitoring offer practical indices of presence, seasonality, and habitat association, especially in conditions where visual surveys are limited or impractical (Frasier *et al.*, 2021; Ross *et al.*, 2023).

1.4 THESIS STRUCTURE AND OBJECTIVES

1.4.1 Thesis Structure

This thesis aims to advance the understanding of acoustic behaviour and vocal communication in common bottlenose dolphins (*Tursiops truncatus*) across a range of ecological contexts and social environments. It draws on long-term acoustic and visual datasets collected from two distinct populations inhabiting Galicia (Spain, Atlantic Ocean) and Sardinia (Italy, Mediterranean Sea). The work explores both the overall use of whistles and the contextual drivers behind different whistle types, including signature whistles. In addition, it evaluates the potential of fixed Passive Acoustic Monitoring (PAM) to enhance our understanding of dolphin presence in remote or logistically challenging habitats by applying this method in a river estuary to examine how environmental variables influence acoustic presence. Built on extensive, multi-year datasets that are rarely available due to the logistical constraints of fieldwork, this research provides valuable comparative insights across regions, methods, and population contexts. Collectively, the three main objectives seek to clarify how dolphins use tonal vocal signals in relation to their social structure, behaviour, and environment, and how these patterns differ across populations and monitoring approaches.

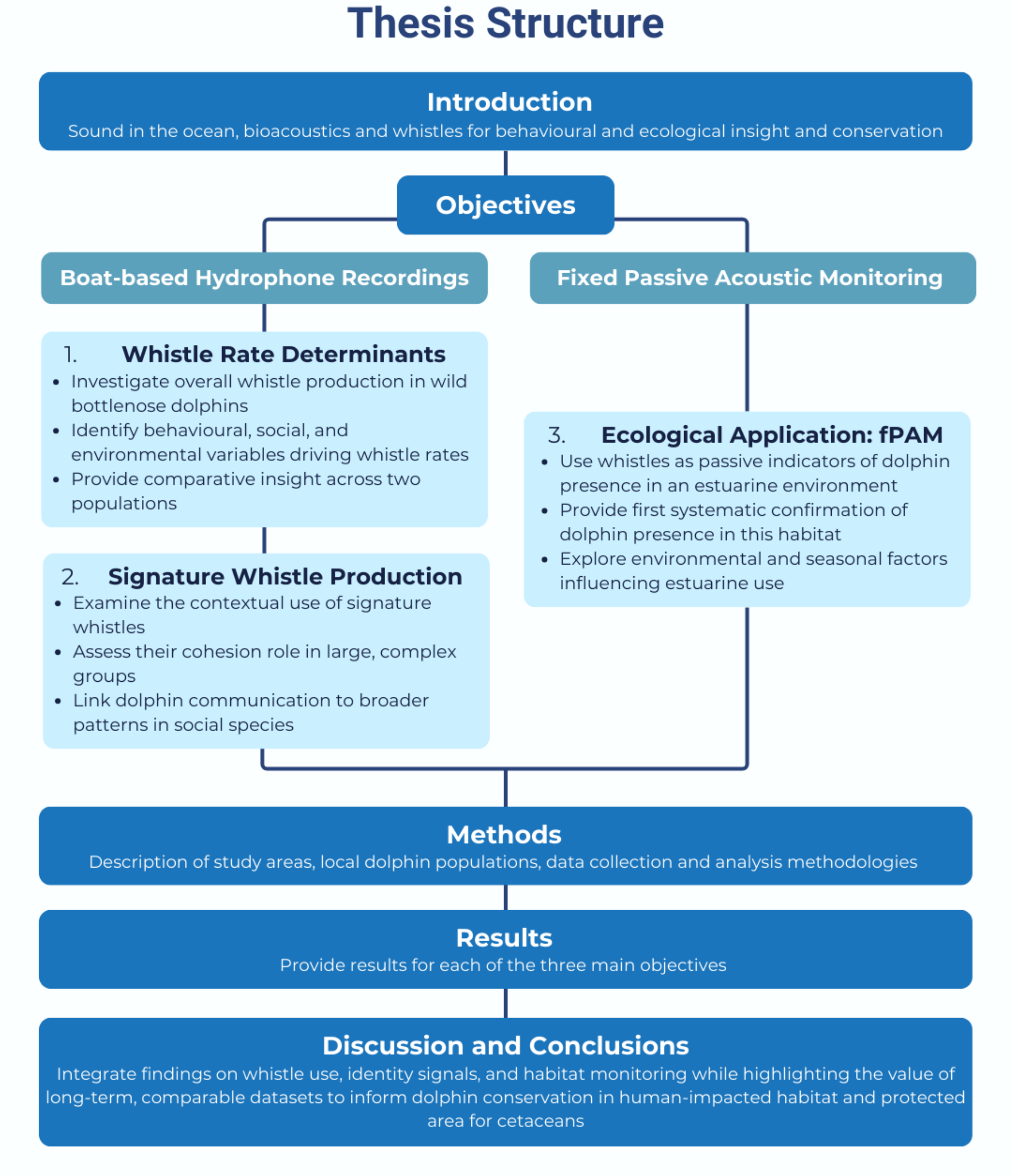
The thesis is structured in five main chapters, organised around the overarching objectives of the research (Figure 1.2). **Chapter 1** provides the general scientific background and conceptual framework, outlining the role of sound in the marine environment and introducing acoustic communication as a tool for investigating dolphin social, behavioural, and ecological dynamics. Additional and more detailed background context on animal communication, bioacoustics, and dolphin biology is provided in Appendix III. The more specific background and context for each objective are also outlined here in the following section (0).

Chapter 2 presents the materials and methods, describing the two study areas and the characteristics of the local dolphin populations. This chapter outlines the two main methodological frameworks used in the thesis: (1) Boat-based hydrophone recordings, which underpin Objectives 1 and 2, and (2) fixed Passive Acoustic Monitoring (PAM), which is applied to Objective 3. The chapter details data collection protocols, data organisation, spectrogram analysis, and statistical approaches associated with each framework and objective.

Chapter 3 presents the results organised by objective. Specifically, it reports the findings related to whistle rate determinants (Objective 1), the contextual production of signature whistles (Objective 2), and the ecological application of PAM to assess dolphin presence in an estuarine environment (Objective 3).

Chapter 4 integrates and discusses the results in relation to each objective and synthesises the findings across the thesis. This chapter highlights the main scientific contributions of the work, discusses their relevance for dolphin communication research and bioacoustics, explores implications for conservation and management, and identifies directions for future research.

Chapter 5 is comprised of general conclusions that summarise the key outcomes of the thesis and present an overarching conceptual framework linking the different objectives and approaches.



Thesis Structure

Introduction
Sound in the ocean, bioacoustics and whistles for behavioural and ecological insight and conservation

Objectives

Boat-based Hydrophone Recordings

Fixed Passive Acoustic Monitoring

1. **Whistle Rate Determinants**
- Investigate overall whistle production in wild bottlenose dolphins
- Identify behavioural, social, and environmental variables driving whistle rates
- Provide comparative insight across two populations

2. **Signature Whistle Production**
- Examine the contextual use of signature whistles
- Assess their cohesion role in large, complex groups
- Link dolphin communication to broader patterns in social species

3. **Ecological Application: fPAM**
- Use whistles as passive indicators of dolphin presence in an estuarine environment
- Provide first systematic confirmation of dolphin presence in this habitat
- Explore environmental and seasonal factors influencing estuarine use

Methods
Description of study areas, local dolphin populations, data collection and analysis methodologies

Results
Provide results for each of the three main objectives

Discussion and Conclusions
Integrate findings on whistle use, identity signals, and habitat monitoring while highlighting the value of long-term, comparable datasets to inform dolphin conservation in human-impacted habitat and protected area for cetaceans

Figure 1.2 Thesis Structure FlowchartThesis Objectives

1.4.1.1 Objective 1: Whistle Rate Determinants

This thesis objective corresponds to a scientific article published in the journal Bioacoustics *as:*

Mosca O, Methion S, Díaz López B. 2025. Whistle Rate Determinants in Wild Bottlenose dolphins: Behaviour, Location, and Group Size. *Bioacoustics*, 34(3), pp. 260–279 https://doi.org/10.1080/09524622.2025.2482918

The text has been adapted for inclusion in this thesis. Reuse rights and permissions for this publication are presented in Annex I.

Author Contribution: Data collection (partial), acoustic recording analysis, statistical analysis, writing of the original manuscript draft, and review and editing of the final version.

Objective-Specific Background and Aims

In highly social animals, vocal communication facilitates a variety of important functions across taxa (Schwartz and Freeberg, 2008). For example, sounds can be used to manipulate prey behaviours to facilitate capture (Janik, 2000). Other strategies include attracting other conspecifics to feed, through the use of food-specific calls, and facilitating cooperation during feeding (Brown, Brown and Shaffer, 1991; Acevedo-Gutiérrez and Stienessen, 2004; Mine *et al.*, 2022). Sounds are also important during reproductive strategies, such as mate attraction through the use of song in birds (Searcy and Yasukawa, 1996), advertisement calls in anurans (Bee, 2008; Toledo *et al.*, 2014), and high-frequency vocalisations in rodents (Zala *et al.*, 2020). After mating, males sometimes produce sounds while mate-guarding, to deter rivals (Tamura, 1995; King *et al.*, 2019). Competition between males can also be mediated through the use of acoustic signals, as is found in territorial male fish protecting their nests (Amorim *et al.*, 2006) or in male birds producing more costly signal to outperform their competitors (Price, Earnshaw and Webster, 2006). Vocalisations are also widely used as responses to predation threats through alarm calls (Hollén and Radford, 2009), which can vary based on the type of predation threat (Wheeler, 2010), as well as on the group composition of the listening conspecifics (Wilson-Henjum *et al.*, 2019). A predation threat can lead to fleeing behaviour, or cause a mobbing response to reduce the effectiveness of the predator, a signal type that can be understood across species boundaries (Dutour, Léna and Lengagne, 2017).

In aquatic environments, acoustic communication plays a particularly critical role due to the limitations of the other senses. Cetaceans are therefore well-suited as a model for examining underwater vocal communication, due to their complex social structures and diverse acoustic repertoire (Au and Hastings, 2008). Among them, the bottlenose dolphin has been extensively studied. This species lives in societies displaying fission–fusion dynamics (Connor *et al.*, 2000; Aureli *et al.*, 2008) and relies heavily on sound to mediate social interactions (Herzing, 2000; Janik, 2009; Díaz López, 2022; King, Connor and Montgomery, 2022).

Whistles are the most studied vocal signals in dolphins, and past research has identified a range of factors influencing whistle production. Group behaviour is one such example, with whistling rates often highest during social activity, possibly to maintain cohesion among more widely spaced individuals or to enhance communication during complex social interactions (Cook *et al.*, 2004; Quick and Janik, 2008; Díaz López and Bernal Shirai, 2010). Contrastingly, travelling behaviour is typically associated with lower whistle rates, as dolphins may maintain tighter group spacing and require less vocal coordination during displacement in one more defined direction (Cook *et al.*, 2004). The number of individuals within a group has also been shown to have a direct relationship with whistling activity, with larger groups resulting in a higher rate of whistle production (Jones and Sayigh, 2002; Cook *et al.*, 2004). However, this relationship may plateau in large groups when the number of acoustic signals could lead to masking within the group (Quick and Janik, 2008). Group composition, and more specifically the presence of dependent calves, has also been associated with changes in whistling rates (Hawkins and Gartside, 2010). Other variables such as seasonality (Tellechea, 2014), time of day (Oswald, Rankin and Barlow, 2008), and geographic location (Jones and Sayigh, 2002; Oswald, Rankin and Barlow, 2008; Luís *et al.*, 2021) have likewise been shown to influence whistle production in dolphins. It is important to note that the majority of studies on dolphin whistles are based on data collected in captivity, or during capture-release experiments, and datasets are often limited due to the logistical challenges of acoustic data collection in the wild. Varying methodologies, dolphin social structure and habitat between studies can also result in differences that should be interpreted with caution (Jones and Sayigh, 2002; La Manna *et al.*, 2019).

The first objective of this thesis is to investigate how multiple factors shape whistle production in bottlenose dolphins by analysing their individual and combined effects. Using a modelling framework, the influence of group size, group composition, behaviour, time of day, season, and location on whistle production was assessed. This provides a valuable opportunity to explore how social context and environmental conditions interact to influence vocal behaviour in a highly social marine mammal.

1.4.1.2 Objective 2: Signature Whistle Production

This thesis objective corresponds to a scientific article published in the journal Mammalian Biology *as:*

Mosca O, Methion S, Díaz López B. 2026. Calling out in the crowd: signature whistle production in bottlenose dolphins. *Mammalian Biology*. https://doi.org/10.1007/s42991-025-00556-1

The text has been adapted for inclusion in this thesis. Reuse rights and permissions for this publication are presented in Annex I.

Author Contribution: Data collection (partial), acoustic recording analysis, statistical analysis, writing of the original manuscript draft, and review and editing of the final version.

Objective-Specific Background and Aims

Signature vocalisations are individually distinctive signals that enable reliable conspecific recognition across a range of social and ecological contexts (Shapiro, 2010). Such signals are particularly important in species characterised by complex social organisation, variable group membership, or high local densities, where maintaining cohesion and coordinating interactions require accurate identification of specific individuals (Zhang, Zhao and Feng, 2017; Marconi *et al.*, 2020; Sun *et al.*, 2023). Under these conditions, vocal individuality provides a robust mechanism for social recognition when visual cues are limited, unreliable, or insufficient.

Across taxa, signature-like vocal signals fulfil several key social functions. They facilitate cohesion within spatially dispersed or dynamic groups by allowing individuals to identify one another over distance (Lehmann *et al.*, 2022). In reproductive contexts, individually distinctive vocalisations can mediate mate attraction and selection in acoustically complex environments (Zhang, Zhao and Feng, 2017; Marconi *et al.*, 2020). Vocal signatures also play a central role in maintaining stable social bonds, such as pair associations or parent–offspring contact, particularly in crowded or low-visibility settings where individuals must locate or recognise specific conspecifics (Insley, 1992; Torriani, Vannoni and McElligott, 2006; Briefer and McElligott, 2011; Levréro and Mathevon, 2012; Bowmaker-Falconer *et al.*, 2022; Sun *et al.*, 2023). Together, these functions highlight the adaptive value of vocal individuality as a flexible communication strategy for maintaining social structure, coordination, and cohesion in socially and environmentally challenging contexts.

As previously mentioned in Section 1.1, in marine systems, the functional importance of acoustic signals is further amplified by the physical properties of sound transmission underwater (Spiesberger and Metzger, 1991). A wide range of marine mammals have been shown to produce individually distinctive vocalisations, including bottlenose dolphins (*Tursiops truncatus*) (Caldwell, Caldwell and Tyack, 1990), common dolphins (*Delphinus delphis)* (Fearey *et al.*, 2019), rough-toothed dolphins (*Steno bredanensis*) (Ramos *et al.*, 2023), narwhals *(Monodon monoceros)* (Shapiro, 2006), elephant seals (*Mirounga angustirostris*) (Casey *et al.*, 2013) and manatees (*Trichechus inunguis)* (Sousa-Lima, Paglia and Da Fonseca, 2002).

Among marine mammals, bottlenose dolphins are particularly well-suited for investigating the use of individualised vocal signals due to their advanced cognitive abilities and highly dynamic social systems (Janik, 2009), making reliable individual recognition a key component of social organisation (Connor *et al.*, 2000; Aureli *et al.*, 2008). Within the whistle repertoire, signature whistles represent a distinct subset of stereotyped, frequency-modulated tonal signals that are individually unique and acquired through vocal learning early in life (Sayigh *et al.*, 1990; Tyack, 1997; Janik and Sayigh, 2013). Because dolphins generate sound using nasal structures rather than a larynx, they lack the anatomical constraints that produce stable voice cues in terrestrial mammals (Sayigh, Wells and Janik, 2017). As a result, the frequency modulation pattern of a signature whistle functions as an acoustic label, conveying individual identity and enabling dolphins to maintain contact, address specific conspecifics, and reinforce social bonds (Tyack and Sayigh, 1997; Janik and Sayigh, 2013; Sayigh *et al.*, 2022).

Research on signature whistles has a long history, with early studies showing that these calls are frequently produced during periods of separation, when individuals attempt to re-establish contact with their group (Caldwell and Caldwell, 1965; Caldwell, Caldwell and Tyack, 1990; Sayigh *et al.*, 2022). Despite substantial progress, much of the detailed knowledge on signature whistle production originates from studies of dolphins under human care or during temporary restraint, where individual identity and behavioural context can be tightly controlled (Caldwell and Caldwell, 1968; Smolker, Mann and Smuts, 1993; Janik and Sayigh, 2013; Sayigh *et al.*, 2022). In contrast, fewer studies have examined the contextual use of signature whistles in free-ranging populations, particularly across different ecological settings (Cook *et al.*, 2004; Terranova *et al.*, 2021; La Manna *et al.*, 2022).

Building on this gap, the second objective of this thesis is to investigate how social, behavioural, and ecological factors influence signature whistle production in wild bottlenose dolphins across two geographically distinct populations in the Mediterranean Sea (Sardinia) and the Atlantic Ocean (Galicia). Using long-term acoustic datasets, the probability of signature whistle occurrence was examined in relation to location, behavioural state, group size, and group composition. It was hypothesised that signature whistle production would vary systematically with social context, particularly group size (Kriesell *et al.*, 2014; La Manna *et al.*, 2022) and behaviour (Cook *et al.*, 2004), reflecting their role in maintaining cohesion and individual recognition within dynamic social systems.

1.4.1.3 Objective 3: Ecological Application: Dolphin Presence in an Estuary Using Fixed Passive Acoustic Monitoring

This thesis objective corresponds to a scientific article currently being prepared for submission.

Mosca O, Methion S, Padín X A, Martinez Fernández A, Gil Coto M, Díaz López B. Seasonal and Environmental Drivers of Bottlenose Dolphin (*Tursiops truncatus*) Presence in a Coastal Estuary using Fixed Passive Acoustic Monitoring

This study has been conducted as a collaboration between the BDRI and the STRAUSS Project managed by the CETMAR team (IIM - CSIC).

Author Contribution: Acoustic recording analysis, statistical analysis, writing of the original manuscript draft, review and editing of the final version.

Objective-Specific Background and Aims

Studying animal movement and habitat use is a cornerstone of ecological research, offering critical insights into species behaviour and informing conservation strategies (Krausman, 1999). For marine top predators such as cetaceans, habitat use is closely tied to prey distribution and availability (Irvine *et al.*, 1981; Redfern *et al.*, 2006; Díaz López and Methion, 2017). However, monitoring prey directly, in marine environments, presents logistical challenges, leading researchers to rely on environmental and anthropogenic variables as proxies to infer species movement and distribution patterns (Redfern *et al.*, 2006; Torres, Read and Halpin, 2008; Marini *et al.*, 2015; Giralt Paradell, Díaz López and Methion, 2019).

Odontocete cetaceans are found worldwide and have adapted to a variety of ecological niches, from deep oceanic waters to riverine systems, showcasing their evolutionary versatility (Hooker, 2009). Coastal populations, in particular, tend to form small social groups and inhabit highly dynamic environments influenced by variable bathymetry, tidal processes, upwelling events, human activities, and salinity gradients; factors that influence the distribution and availability of their prey and, as a result, their distribution and habitat use (Neumann, 2001; Mendes *et al.*, 2002; Fury and Harrison, 2011; Chabanne *et al.*, 2012; Dittmann *et al.*, 2016; Díaz López and Methion, 2017, 2024; Giralt Paradell, Díaz López and Methion, 2019; Methion and Díaz López, 2019; Carmen, Berrow and O'Brien, 2021; Bridge, Methion and Díaz López, 2023).

Among odontocetes, the bottlenose dolphin (*Tursiops* spp.) stands out as one of the most extensively studied species, renowned for its high degree of behavioural plasticity and adaptability across a variety of habitat types (Wells, Irvine and Scott, 1980; J Mann *et al.*, 2000). While primarily inhabiting the marine habitat, several populations have been documented using estuarine and riverine environments, such as those in Scotland (Wilson, Thompson and Hammond, 1997), Australia (Fury and Harrison, 2008), Portugal (dos Santos, Coniglione and Louro, 2007), northwestern Spain (Methion and Díaz López, 2018), and Ireland (Carmen, Berrow and O'Brien, 2021).

Estuarine environments are of significant ecological importance for bottlenose dolphins, serving as critical feeding grounds and habitats, as they often are nutrient-rich areas that support high densities of prey species (Ballance, 1992; Carmen, Berrow and O'Brien, 2021). Beyond the abundance of prey, these environments also provide conditions that shape social structures and ecological behaviours. Studies have shown that dolphins inhabiting estuarine areas are often socially distinct from those in adjacent marine habitats (Hohn *et al.*, 2022) and exhibit dietary differences, as demonstrated by isotope analyses (Cloyed *et al.*, 2021).

Several environmental variables have been linked to estuarine water habitat use in bottlenose dolphins, and they include seasonality and water temperature, which can indicate prey migration periods and changes in food availability (Wilson, Thompson and Hammond, 1997; Neumann, 2001; Dede *et al.*, 2013; Sprogis *et al.*, 2016). Seasonal dolphin movements have also been associated with mating and calf-rearing (Sprogis *et al.*, 2016), predator avoidance (Wells, Irvine and Scott, 1980), and seeking shelter from rough oceanographic conditions (Wilson, Thompson and Hammond, 1997). Additionally, tidal cycles (Fury and Harrison, 2008), seabed bathymetry (Hastie *et al.*, 2004), and wave power (Dittmann *et al.*, 2016) influence water flow and current velocity, which can aid in prey capture (Bailey *et al.*, 2010; Carmen, Berrow and O'Brien, 2021).

While estuaries are naturally important habitats for bottlenose dolphins, they are also crucial for human activities, leading to an increased exposure to various anthropogenic pressures. Activities such as aquaculture (Watson-Capps and Mann, 2005; Díaz López, 2006a; Díaz López and Methion, 2017), fisheries, agricultural runoff, and the resulting pollutants (Balmer *et al.*, 2012; Bridge, Methion and Díaz López, 2023), as well as general vessel traffic (Marley, Salgado Kent and Erbe, 2016) and high underwater noise (Marley *et al.*, 2017) can influence the distribution and habitat use of dolphins in estuarine environments. These anthropogenic pressures underscore the importance of studying estuarine habitats to better understand how dolphins navigate these challenges. Given the high variability of estuarine habitats and the behavioural plasticity of bottlenose dolphins, studies conducted on a case-by-case basis are important to identify the fine-scale movements and habitat use of each population and to develop tailored and effective conservation measures (Ingram and Rogan, 2002).

Passive Acoustic Monitoring (PAM) has emerged as an effective means of addressing this need (Merchant *et al.*, 2015; Erbs, Elwen and Gridley, 2017), and is widely used to study the distribution, density, and occurrence of cetaceans (Zimmer, 2011). Over the past decades, advancements in PAM equipment and methodology have expanded its applications, particularly for monitoring the effects of human activities on marine environments (Weilgart, 2007; André *et al.*, 2011). Fixed PAM systems, through moored autonomous recorders**,** enable continuous data collection over time, including in conditions where visual data collection is not feasible, such as at night, in poor weather conditions (Mann and Würsig, 2013; Ross *et al.*, 2023) and in areas with limited accessibility or data availability (Sousa-Lima *et al.*, 2013). Additionally, PAM is cost-effective for long-term studies and is suitable for collecting data across various spatial and temporal scales (Van Parijs *et al.*, 2009).

The Galician rías (NW Spain) are located within a complex and productive coastal system. Within this region, the Ría de Arousa stands out as the largest of the rías and supports a resident dolphin population that uses the area as a key feeding and calving ground (Methion and Díaz López, 2018). Bottlenose dolphins in Spanish waters are legally protected under several international and European frameworks (Convention on the Conservation of Migratory Species of Wild Animals (CMS), 1979; Council of Europe, 1979; Council of the European Communities, 1992; Marine Mammal Protected Areas Task Force, 2024), requiring the designation of Special Areas of Conservation (SACs) to safeguard their habitats. Within the Ría de Arousa, the estuarine area surrounding the Ulla River mouth includes the Cortegada archipelago, which is part of the Atlantic Islands National Park (Xunta de Galicia, 2025a) and lies in proximity to the Vilagarcía de Arousa harbour, a major port in the region. While dolphin presence, ecology, and behaviour have been well studied in the outer and central parts of the ría, particularly in relation to aquaculture (Díaz López and Methion, 2017; Methion and Díaz López, 2019; Bridge, Methion and Díaz López, 2023; Methion *et al.*, 2023), little is known about their use of the more enclosed, river-influenced estuarine zones. This inner area, shaped by freshwater inputs (Evans and Prego, 2003; Alvarez *et al.*, 2005), remains largely unexplored in terms of dolphin occurrence and habitat use.

Building on the behavioural insights explored in the previous research within this thesis, the third and final objective applies a more ecological perspective to investigating dolphin acoustic presence in a dynamic coastal environment. Using fixed PAM data in combination with oceanographic modelling and environmental variables, the aim is to assess whether bottlenose dolphins use the Ulla River mouth and to identify the temporal and environmental factors that might explain their acoustic presence in this estuarine zone. This integrative approach applies acoustic tools to ecological questions and contributes to a broader understanding of dolphin estuarine ecology in a previously understudied, human-impacted area that has remained difficult to access, with direct relevance for conservation planning.

CHAPTER 2: MATERIALS AND METHODS

This thesis combines different methodological approaches to investigate the vocal behaviour of bottlenose dolphins across two study areas: Sardinia (Mediterranean Sea) and Galicia (Atlantic Ocean).

Objectives 1 and 2 are based on acoustic monitoring through the use of a hydrophone deployed from a research vessel during systematic visual surveys of free-ranging bottlenose dolphins (Section 2.3). In all cases, the hydrophone was deployed in close proximity to the dolphins, allowing the acoustic recordings to be directly associated with detailed, visually-collected data on group size, composition, behaviour, and environmental context. This method was applied comparably across two study regions by the Bottlenose Dolphin Research Institute (BDRI - www.thebdri.com) as part of ongoing research programmes, for a cumulative period of 15 years: in Sardinia (Mediterranean Sea) from 2005 to 2013, and in Galicia (Atlantic Ocean) from 2014 to 2020. This consistency in data collection protocols across both regions allows for comparative analysis of whistle production and its drivers under different ecological and social conditions.

Objective 3 employs data collected with a fixed Passive Acoustic Monitoring (PAM) approach via a stationary hydrophone installed at the Ulla River estuary in the Ría de Arousa, Galicia, between 2017 and 2022 (Section 2.4). Unlike boat-based recordings, this approach provided continuous data collection independent of human presence, enabling the long-term monitoring of bottlenose dolphin acoustic presence in an area that is otherwise difficult to survey visually. The study developed from this objective was carried out in collaboration with the STRAUSS Project, jointly led by the following Spanish research groups: Centro Tecnológico do Mar (CETMAR), Instituto de Investigacións Mariñas (IIM), and the Consejo Superior de Investigaciones Científicas (CSIC). The members of the partner project supplied the acoustic recordings, along with a suite of environmental data and model outputs.

Personal Contributions

Objectives 1 and 2: I directly contributed in some occasions to the acoustic data collection in Galicia between 2018 and 2024, reviewed the acoustic data, creating spreadsheets with acoustic recording information and linking it to the visually collected data, conducting data random selection, spectrogram analysis, whistle counting and classification, and performing statistical modelling and manuscript writing under supervision from my supervisor and with feedback from coauthors.

Objective 3: I set up the PAMGuard environment with whistle detectors and classifiers and organised and processed all acoustic recordings, performing random quality checks. I then integrated the environmental variables provided by CETMAR and created the working dataset and carried out the statistical modelling and manuscript writing under supervision from my supervisor and with feedback from coauthors.

During this PhD, by working within the Bottlenose Dolphin Research Institute, I also had the opportunity to contribute to a number of other scientific activities beyond the scope of the present work, including collaborative projects, co-authored publications, the organisation of an international conference, and technical responsibilities at the institute. These experiences have greatly shaped my development as a scientist.

2.1 STUDY AREAS

This thesis research utilises a long-term dataset spanning nearly 15 years (Property of the BDRI), comprising data from two different marine habitats, as detailed here. The first part of the research period was conducted in the Mediterranean Sea, on the northeast coast of Sardinia, Italy (2.1.1). The latter part of this study was based on data from the Ría de Arousa, in the Galician region in northwestern Spain (2.1.2).

2.1.1 Mediterranean Sea (Sardinia, Italy)

The data analysed from the Mediterranean Sea were collected by the BDRI between 2005 and 2013. The study area is located along the north-eastern coast of Sardinia (Italy), particularly encompassing the Gulf of Aranci, the Gulf of Olbia, and the Gulf of Congianus (Figure 2.1).

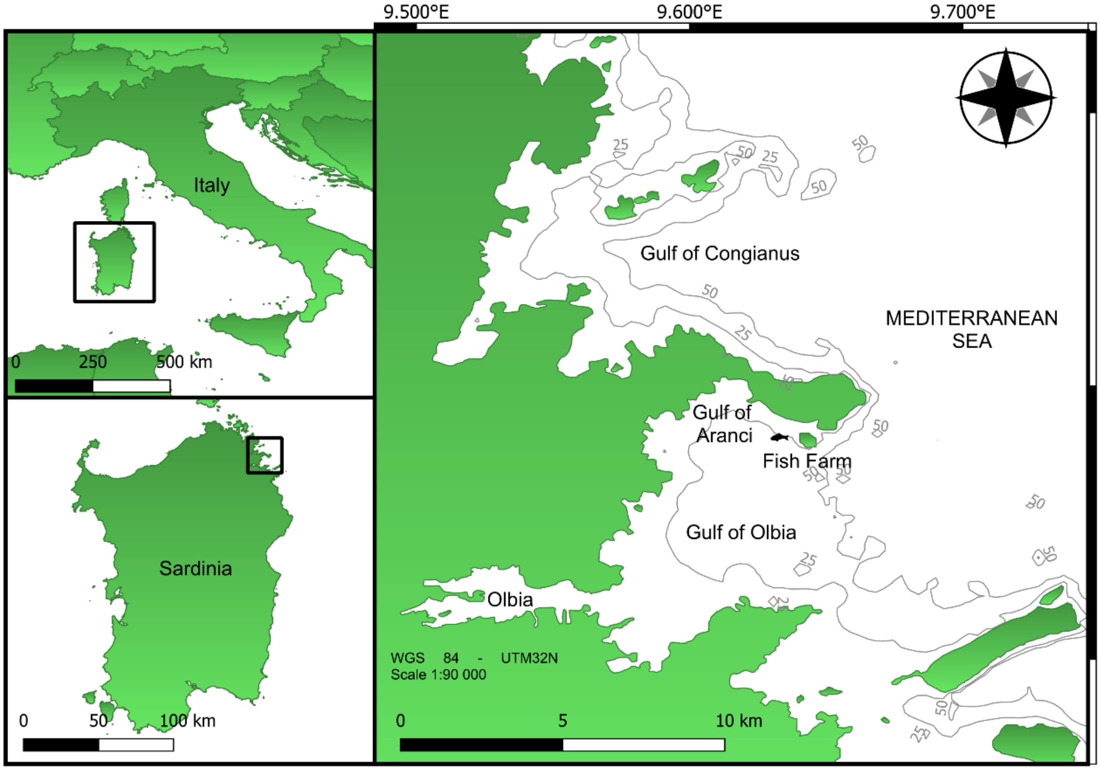


Figure 2.1 Map of the Study Area in Sardinia (Italy), Mediterranean Sea

This coastal region is located on the Tyrrhenian Sea, within the western Mediterranean. The Tyrrhenian Sea exhibits a quasi-permanent cyclonic circulation, with seasonal fluctuations in the flow of Modified Atlantic Water (MAW), which primarily enters via the Corsica Channel during summer, influencing water stratification and thermohaline properties (Artale *et al.*, 1994).

The full study area is about 750 km², reaching up to 20 km offshore with water depths of up to 200 m (Díaz López, 2019). It is characterised by intense anthropogenic use, including aquaculture (both fin-fish and shellfish farming), recreational and commercial fisheries, and high levels of tourism driven by five marinas and two major ferry ports (De Luca *et al.*, 2005; Díaz López and Bernal Shirai, 2008). The sea surface salinity within the study area typically exceeds 37 PSU, while water temperature ranges from 11°C in March to 26°C in August. Water clarity fluctuates between 11 and 22 m, and the seabed is mostly characterised by muddy sediments with patches of sand, and rocky substrates (Díaz López, Marini and Polo, 2005; Díaz López, 2006b; Díaz López and Bernal Shirai, 2008).

The study area is divided into three distinct zones (as described in Díaz López, 2019):

- **The Gulf of Olbia** (between 40.918° N, 9.503° E and 40.983° N, 9.654° E).

  This is the southernmost zone and faces the highest anthropogenic pressure, especially from aquaculture and fishing activities concentrated in the Olbia harbour and Aranci Bay (De Luca *et al.*, 2005; Díaz López, 2006b). The Port of Olbia is a major Mediterranean hub, serving around four million passengers annually and supporting robust commercial, industrial, and tourism activities. This results in high marine traffic, including ferries and recreational vessels, which represent the area's main marine anthropogenic pressure.

- **The Gulf of Congianus** (between 41.004° N, 9.509° E and 41.100° N, 9.657° E).

  This area includes the Mortorio archipelago and is part of the La Maddalena National Park. This zone represents a variety of ecologically significant Mediterranean habitats, with human activities largely restricted to seasonal tourism around the marinas of Marinella, Porto Rotondo, and Portisco (Díaz López, 2019).

- **The Open Waters region** (between 40.844° N, 9.657° E and 41.147° N, 9.889° E)

  This area extends up to 20 km offshore and includes the "Tavolara–Punta Coda Cavallo" marine protected area. It experiences the lowest marine traffic and is relatively undisturbed by human activities (Díaz López, 2019).

The presence of a marine fin-fish farm within the Gulf of Olbia section of the study area (Figure 2.1) is important to note, as many of the studies on the local bottlenose dolphin population were carried out within this structure (Díaz López, Marini and Polo, 2005; Díaz López and Bernal Shirai, 2008; Díaz López, 2012). The facility opened in 1995 and consists of 21 floating cages organised in three rows of seven cages, covering a total area of 2.4 ha (Díaz López and Bernal Shirai, 2007). Each cage is made of a nylon-mesh netting material and measures 22 m in diameter and 15 m in depth. This facility is located approximately 200 m offshore at depths of 18 to 26 m, and supports the production of 800–900 t of fish, including European sea bass (*Dicentrarchus labrax*), Gilthead sea bream (*Sparus aurata*), and corb (*Sciaena umbra*) (Díaz López and Bernal Shirai, 2007). The aquaculture infrastructure has been shown to significantly influence dolphin distribution and behaviour in the region, particularly in relation to foraging activities, as there is a high density of fish around the cages and dolphins have been observed to engage in both “predation” of wild fish aggregating around the structures and “depredation” of the farmed fish within the cages (Díaz López, 2006a) as described more in depth in section c.

2.1.2 Atlantic Ocean (Galicia, Spain)

The data collected in the Atlantic Ocean study area are from the Galician region in north-western Spain. The Galician coastline is located along the eastern boundary system of the North Atlantic Ocean and lies at the northern limit of the major upwelling system extending from north-west Africa (Santos *et al.*, 2011). This region is strongly influenced by seasonal upwelling events that mainly occur between April and October (deCastro *et al.*, 2008). These are driven by northerly winds, causing offshore movement of surface waters through Ekman transport, and resulting in the shoreward movement of cold, nutrient-rich Eastern North Atlantic Central Water (ENACW) (Herrera *et al.*, 2008) (Figure 2.2).

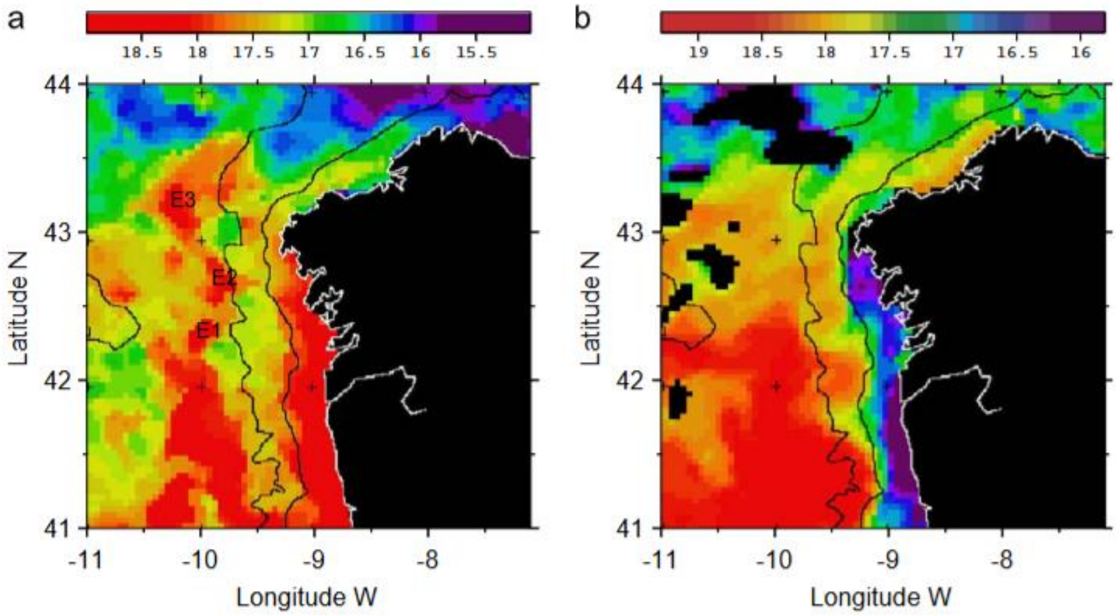


Figure 2.2 Sea Surface Temperature (SST) before (a) and during (b) an Upwelling event along the Galician Coast. Reproduced with permission from Torres and Barton, 2007. Copyright 2007, Elsevier

The upwelling and resulting cold, nutrient-rich water fertilises the euphotic zone, promoting high levels of primary productivity and making this coastline one of the most biologically productive in the world (Fraga, 1981; Alvarez *et al.*, 2005; Santos *et al.*, 2011). During the rest of the year, southerly winds cause downwelling conditions, leading to the movement of warmer, nutrient-depleted surface waters towards the coast (Torres *et al.*, 2003; Torres and Barton, 2007).

The southern Galician rías (called Rías Baixas) are a series of coastal inlets formed from ancient tectonic valleys that have been submerged by the sea (Prego, Barciela and Varela, 1999; Figueiras, Labarta and Fernández Reiriz, 2002; Méndez and Vilas, 2005), fed by rivers and opening to the Atlantic Ocean (Evans and Prego, 2003). The data for the studies within this thesis were collected in the Ría de Arousa, the largest and most productive of these rías. The Ría de Arousa is oriented northeast-southwest and has a V-shaped profile that widens from the mouth of the Ulla River to the Atlantic Ocean, approximately 25 km away (Prego, Barciela and Varela, 1999). It covers an area of approximately 240 km² (Prego, Barciela and Varela, 1999; Figueiras, Labarta and Fernández Reiriz, 2002), holds a volume of 4.5×10^9 m³, has an average depth of 19 m, and reaches a maximum depth of 70 m (Prego *et al.*, 2008; Ribeiro *et al.*, 2025). The ría exhibits a complex topography featuring several islands, including the barrier island of Sálvora, the internal island of Arousa giving the Ría its name, Cortegada island near the Ulla river, and La Toja near the peninsula of O Grove, along with smaller islets throughout the Ría (Otto, 1975) (Figure 2.3). The ría connects to the Atlantic Ocean through two entrances around the island of Sálvora. The southern entrance measures approximately 4.6 km in width and reaches a depth of 55 m, while the northern entrance is narrower and shallower (Alvarez *et al.*, 2005).

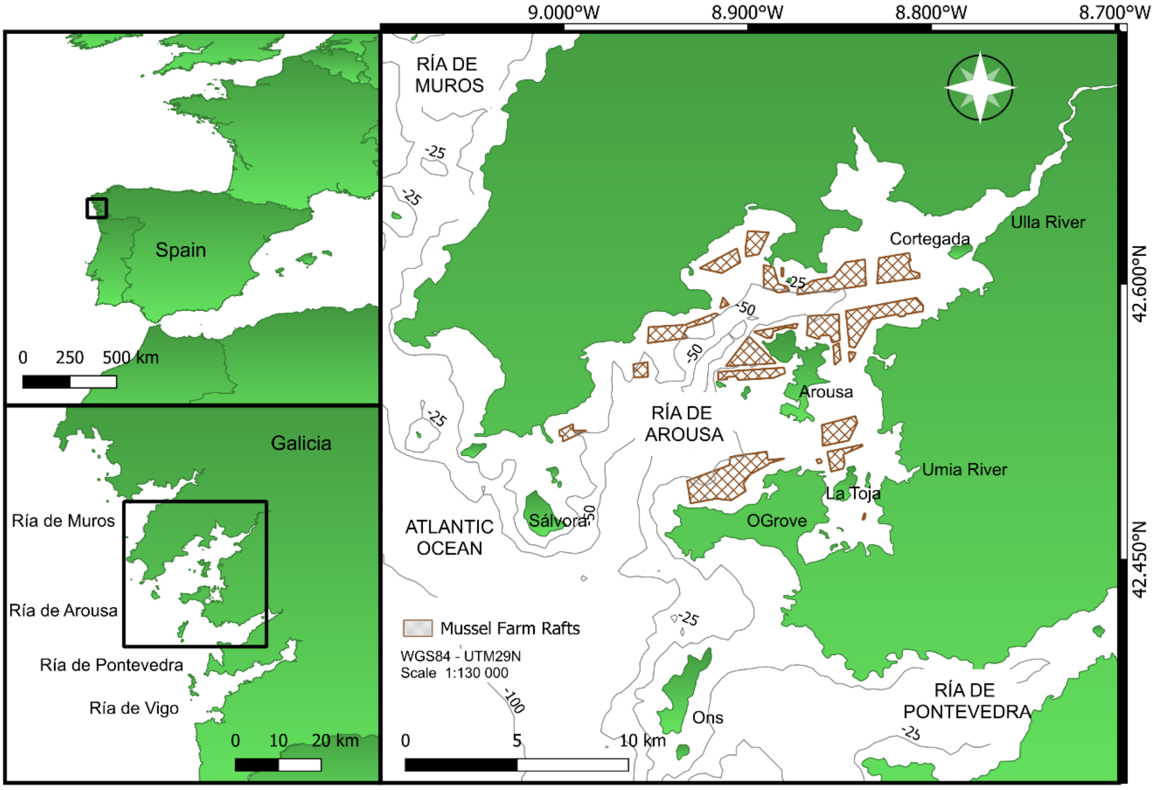


Figure 2.3 Map of the Study Area in Galicia (Spain), Atlantic Ocean

The hydrographic dynamics of the ría are driven by a combination of tidal forces, local and regional wind patterns, freshwater input, and thermal stratification (Otto, 1975; Alvarez *et al.*, 2005; deCastro *et al.*, 2008). The ría is characterised by a semidiurnal mesotidal regime, with tidal amplitudes ranging from 1.1 m during neap tides to 3.5 m during spring tides. Freshwater enters the system predominantly via the Ulla and Umia rivers, with the Ulla River contributing the larger share, particularly during the winter months (Alvarez *et al.*, 2005). The Ulla River is the ría's main tributary and has a drainage area of 2804 km² and an average discharge of 79 m³/s (Otero *et al.*, 2010), while the estuary itself spans approximately 7 km before merging with the Ría de Arousa (Alvarez *et al.*, 2005).

The Ría functions as a partially mixed estuary with positive residual circulation. Stratification is mainly caused by riverine discharge during winter and solar heating or coastal upwelling during summer (Alvarez *et al.*, 2005). Oceanographic processes here are divided into two distinct circulation cells corresponding to the inner and outer ría (Álvarez-Salgado *et al.*, 1996). The outer ría is influenced by oceanic processes through the two openings, north and south of the island of Sálvora, where water movement is rapid and affected by wind stress (Bermúdez *et al.*, 2013). In contrast, the inner ría is less affected by ocean water input and more affected by riverine discharge, leading to freshwater stratification in the winter (Bermúdez *et al.*, 2013; Ribeiro *et al.*, 2025). The middle zone acts as a boundary between these circulation cells, and is considered the most productive area, with more intense water dynamics (Álvarez-Salgado *et al.*, 1996). Given the range of interacting processes in the area, including high primary productivity from upwelling-driven blooms, inputs of suspended particulate matter (SPM) such as nutrients and sediments from river discharge and mixing (Prego *et al.*, 2008), as well as anthropogenic pollutants that may contribute to eutrophication (Bridge, Methion and Díaz López, 2023), these waters are considered optically complex (Spyrakos *et al.*, 2011). They are characterised by high turbidity, with Secchi depths (defining the euphotic zone) typically ranging between 2 and 12 m in the adjacent rías of Vigo and Pontevedra (Torres Palenzuela *et al.*, 2019).

Because of the seasonal upwelling events (Pardo *et al.*, 2011) leading to high primary productivity (Wooster, Bakun and McLain, 1976; Santos *et al.*, 2011) and marine biodiversity, the Galician rías have long supported substantial human activity, particularly aquaculture and fisheries (Prego, Barciela and Varela, 1999). Mussel farming, the most productive form of aquaculture in the region, began in the late 1940s and has since grown dramatically (Caballero Miguez, Garza Gil and Varela Lafuente, 2009; Labarta and Fernández-Reiriz, 2019). The primary farmed species is *Mytilus galloprovincialis*, which is farmed on suspended ropes attached to floating eucalyptus-wood rafts known as "bateas", which can be found throughout the rías (Fuentes *et al.*, 2000). The Ría de Arousa alone has around 2319 of these structures (Figure 2.4), almost 70% of the total mussel rafts in the region (Galicia Mussel Regulatory Council, 2025). Spain is currently the third-largest global producer of mussels after China and Chile, contributing nearly 10% of the world's output. Within Spain, the region of Galicia accounts for approximately 97% of national mussel production, making it a dominant force in European aquaculture (FAO, 2024).

Figure 2.4 Aerial view of the mussel farming rafts (bateas) in the Ría de Arousa. (Photo credit: Olga Mosca)

In addition to aquaculture, the region also supports a significant fishing industry. Galicia maintains the largest fishing fleet in Spain, with 4765 vessels operating across inshore and offshore zones (Ministerio de Agricultura, Pesca y Alimentación, 2025). These intensive human activities, particularly marine traffic, shellfish farming, and commercial fisheries, contribute to multiple pressures on the coastal environment, including habitat modification, underwater noise and pollution, overfishing, and bycatch risks for marine fauna (López *et al.*, 2003; Díaz López and Methion, 2017; Giralt Paradell *et al.*, 2021; Bridge, Methion and Díaz López, 2023).

2.2 DOLPHIN POPULATIONS

2.2.1 Mediterranean Sea (Sardinia, Italy)

Bottlenose dolphins in the Mediterranean Sea study area (Section 2.1.1) were mainly sighted (highest Sightings Per Unit Effort SPUE) in the Gulf of Olbia, particularly in the area of Aranci Bay (Díaz López, 2019). Abundance estimates based on photo-identification data indicate that the number of marked individuals ranged from 12 to 68, with an increasing trend observed between 2004 and 2013 (Díaz López, 2019). This trend could reflect either an actual population growth or an increased site fidelity of the individuals to the area. Out of 124 individuals identified during the study period, 35% were classified as females, 17% as males, and the remaining 48% could not be sexed. The mean group size was 4.06 individuals (± 0.14 SE), and 34% of the identified dolphins were recorded across multiple seasons and years, further supporting the idea of strong site fidelity in this population (Díaz López, 2019).

Dolphin behaviour, site fidelity and social structure in this study area appear to be linked to human activities and altered prey distribution (Díaz López, 2006b, 2012, 2019). In certain parts of the study area, such as offshore waters or the Gulf of Congianus, dolphins were predominantly observed travelling, while in Aranci Bay, in the Gulf of Olbia, dolphins were predominantly engaged in foraging behaviour (Díaz López, 2019). In this area, anthropogenic fishing activities, including trammel nets, gillnets, trawling operations, and the marine fin-fish farm (Díaz López, 2005, 2006b), have been linked to dolphin presence, and the increased feeding opportunities resulting from these anthropogenic activities have been shown to alter dolphin site fidelity (Díaz López, 2012).

Dolphins appear to exploit human fishing activities in several ways: by feeding on discarded fish from trammel fisheries (Díaz López, 2005, 2006b), by taking advantage of wild fish aggregating around the aquaculture infrastructure, and by actively depredating fish inside the nets (Díaz López, 2005, 2006b). While these more easily accessible food sources may provide energetic advantages, they may also carry ecological and social costs. The predictable availability of food near the fish farms has, in fact, been associated with changes in social structure, including a reduction in cooperative foraging and a decline in overall social cohesion among individuals (Díaz López and Bernal Shirai, 2008). Additionally, these interactions with fishing activities can result in negative outcomes for both dolphins and humans, through incidental entanglement (often affecting young individuals), potentially causing mortality, and equipment damage and economic losses for local fishers (Díaz López, 2005; Díaz López and Bernal Shirai, 2007). Mitigation strategies, such as acoustic harassment devices within the fish farm, have failed to prevent dolphins from approaching and damaging the nets (Díaz López and Mariño, 2011), highlighting the importance of considering such interactions in regional management plans (Díaz López and Bernal Shirai, 2008).

Historically, the Mediterranean subpopulation of bottlenose dolphins faced intense anthropogenic pressure, including deliberate culling, and was previously classified as "Vulnerable" (Bearzi, Fortuna and Reeves, 2009). Although population trends have improved in recent years, leading to the Mediterranean subpopulation of the bottlenose dolphin to be reclassified as "Least Concern" (Natoli *et al.*, 2021), the IUCN recommends continued monitoring, particularly in areas exposed to intense human activity such as aquaculture and fisheries (Natoli *et al.*, 2021).

Previous research in the Mediterranean study area has shown that bottlenose dolphin acoustic communication is linked to behaviour, social interactions and seasonality (Díaz López and Bernal Shirai, 2010; Díaz López, 2011, 2022). Vocal output increases with activity during social and foraging contexts, with whistles serving functions such as contact calls between mothers and calves (Díaz López and Bernal Shirai, 2010). Whistle contour shapes and spectral characteristics were also context-dependent, varying with behavioural state and displaying high intra-specific variability, reflecting their importance in complex social dynamics (Díaz López, 2011). Burst-pulsed sounds were associated with agonistic encounters and settling conflicts between individuals (Díaz López and Bernal Shirai, 2010), and their production varied based on season, sex composition of the dyad and social affiliation (Díaz López, 2022).

2.2.2 Atlantic Ocean (Galicia, Spain)

The Galician coastline is a very productive zone with a broad biodiversity of cetaceans, and bottlenose dolphins are the most frequently observed in coastal waters (López *et al.*, 2004; Pierce *et al.*, 2010). This species is linked to areas with a wider continental shelf and waters with higher productivity in the form of chlorophyll a concentration (Pierce *et al.*, 2010).Within this region, both coastal and offshore ecotypes are present, as supported by both genetic (Louis *et al.*, 2014) and isotope analysis (Fernández *et al.*, 2011). However, behavioural or ecological barriers appear to limit gene flow between the ecotypes (Fernández *et al.*, 2011).

Bottlenose dolphin diet in this region is dominated by fish (98%), with minor contributions from cephalopods (2%) (Santos *et al.*, 2007). Although there were at least 23 species of fish documented, the most frequently encountered are blue whiting (*Micromesistius poutassou*), European hake (*Merluccius merluccius*), grey mullet (*Mugil cephalus*), Atlantic horse mackerel (*Trachurus trachurus*), and conger eel (*Conger conger*). Additionally, at least 12 species of cephalopods made up dolphin diet, likely from the Ommastrephidae family (Santos *et al.*, 2007). It is important to note, however, that these data were obtained from stomach content analysis of stranded animals along the Galician coast (Santos *et al.*, 2007). Given the high survival and low mortality rates observed in the bottlenose dolphins regularly present in the Ría de Arousa (Methion and Díaz López, 2018), it is likely that the individuals sampled in the diet study originated from outside the rías, possibly from more offshore waters.

Bottlenose dolphins in the Ría de Arousa are observed year-round and display a high site fidelity. The estimated abundance is 56 to 144 individuals, with seasonal fluctuations likely influenced by prey availability (Methion and Díaz López, 2018). Of the 190 marked adult individuals, 30% were female, 21% were documented as male, and 49% were of unknown sex (Methion and Díaz López, 2018). Group sizes range from solitary individuals to aggregations of up to 64 dolphins, with a mean of 10.7 individuals (± 0.3 SE) (Methion *et al.*, 2023). Group size was correlated with both social and environmental factors; it tended to be larger when dependent calves were present, with elevated dissolved oxygen concentrations, moderate levels of chlorophyll-a (60 days prior), and a neutral North Atlantic Oscillation (NAO) index (Methion *et al.*, 2023).

In the Ría de Arousa, bottlenose dolphin foraging behaviour is strongly influenced by the presence of mussel rafts (bateas), which provide a rich and predictable feeding ground (Díaz López and Methion, 2017). Dolphins are observed foraging more frequently within mussel-farming areas compared to outside them, suggesting a preference for the waters around these structures, likely due to enhanced prey availability as the bateas act as fish-aggregating devices (FAD), providing dolphins with more easily available prey for opportunistic feeding (Díaz López and Methion, 2017; Methion and Díaz López, 2019). This foraging pattern also appears to shape social relationships within the population. Individuals that use similar foraging strategies, particularly those that forage frequently within the bateas, tend to exhibit closer social associations and occupy more central positions in the social network than those that forage outside (Methion and Díaz López, 2020).

Bottlenose dolphins in Galician waters are exposed to a variety of anthropogenic pressures due to the intensive human activity along the coast. While the interactions with the aquaculture industry may offer additional foraging opportunities, they also carry potential risks, such as habitat loss, entanglement in aquaculture gear, and disturbances by vessel traffic and farming operations (Methion and Díaz López, 2019). More broadly, bottlenose dolphins in Galicia face additional threats, including bycatch in gillnet and trawl fisheries (López *et al.*, 2003), and pollution from heavy metals and persistent organic pollutants like Polychlorinated Biphenyls (PCBs) (Méndez-Fernandez *et al.*, 2014, 2017; Bridge, Methion and Díaz López, 2023).

Bottlenose dolphins are protected under several national and international conservation frameworks. The Galician rías, as well as the western Iberian peninsula oceanic waters, have recently been included as Important Marine Mammal Areas (IMMA) by the Marine Mammal Protected Areas Task Force of the IUCN in 2024 (Marine Mammal Protected Areas Task Force, 2024). In the country of Spain, the species is listed as "Vulnerable" under the *Listado de Especies Silvestres en Régimen de Protección Especial* (Real Decreto 139/ 2011), and its interaction with human activities is further regulated by decrees such as Real Decreto 1727/2007, which governs boat traffic near cetaceans. At the European level, the species is included in Annexes II and IV of the EU Habitats Directive (92/43/EEC, 1992), requiring protection and the designation of Sites of Community Importance (SCI) and Special Areas of Conservation (SACs). Bottlenose dolphin conservation is also covered by multiple international agreements, including the Bern Convention (Council of Europe, 1979), the Bonn Convention (Convention on the Conservation of Migratory Species of Wild Animals (CMS), 1979), ACCOBAMS (Agreement on the Conservation of Cetaceans of the Black Sea, Mediterranean Sea and Contiguous Atlantic Area (ACCOBAMS), 1996) and ASCOBANS (Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas (ASCOBANS), 1992). Given the combination of anthropogenic threats and conservation requirements, continued research is essential to inform effective management strategies. Sustained monitoring will be critical to ensuring the long-term viability of the Galician bottlenose dolphin population.

2.3 BOAT-BASED HYDROPHONE RECORDINGS

The field data collection methodological approach employed to investigate Objectives 1 and 2 of this thesis follows standardised protocols developed by the Bottlenose Dolphin Research Institute (BDRI), ensuring consistency across all years and study sites. This methodological uniformity enables robust comparisons between the two geographically isolated dolphin populations despite differences in their geographic and ecological contexts, a challenge frequently mentioned as a limitation in comparing results between different populations. Data collection is structured into two main components: Visual data collection (Section 2.3.1.1), which included information on dolphin group size and composition, behavioural states, and individual identification through photo-identification techniques; and Acoustic data collection (Section 2.3.1.2), which was carried out with an omnidirectional hydrophone deployed from the research vessel whenever environmental and logistical conditions allowed.

2.3.1 Data Collection

2.3.1.1 Visual Data Collection

Following established protocols (Díaz López and Bernal Shirai, 2010; Methion and Díaz López, 2019) data were collected year-round from motorised research vessels during daylight hours under favourable environmental conditions, specifically when the Douglas sea state was ≤ 3, and visibility was not compromised by fog or precipitation. Research vessels maintained a constant cruising speed of 6 kn, while a minimum of three trained observers were searching for dolphins by scanning 360° around the vessel using the naked eye and 10×50 binoculars.

A group of dolphins was defined as one or more individuals within a 100 m radius exhibiting cohesive behaviour, and as soon as a group was sighted, the vessel ceased its search and slowly approached the group to minimise disturbance (Methion and Díaz López, 2018). Behavioural data were then collected from the group, and observations were terminated when the group was lost, its composition changed, or the weather conditions deteriorated (Díaz López, 2006a, 2011; Methion and Díaz López, 2019). From each group, a number of variables were collected, including Date, Time (UTC), GPS position (UTM), group size and composition, individual dolphin IDs through photographic identification and behaviour of the group every five minutes (Methion and Díaz López, 2019).

Group size was initially estimated in the field and later confirmed or corrected based on photographic evidence (Díaz López and Bernal Shirai, 2008). Bottlenose dolphins encountered during field surveys were classified into three age classes based on morphological and behavioural criteria observed in the field and verified through photographic documentation (Mann *et al.*, 2000; Díaz López, 2006b) (Figure 2.5). Adults were identified as individuals measuring between 2.5 and 3.5 m, with darker skin colouration and typically more prominent rake marks and skin lesions, consistent with their larger size and accumulated social interactions. Newborns were recognised by their close association with the presumed mother, typically swimming in the "infant position" (echelon position) beneath her abdomen with uncoordinated surfacing behaviour. These calves were less than 1.5 m in length, often showing visible foetal folds or lines, and were born within the same calendar year. Immature dolphins were identified by their consistent proximity to the mother, swimming just behind or beside her, but not in the infant position, and exhibited lighter skin pigmentation with fewer rake marks. They were generally about two-thirds the length of an adult (Díaz López, 2006b). For the purposes of this thesis, both newborn and immature dolphins were collectively classified as “dependent calves”, representing all individuals still reliant on maternal care.

Figure 2.5 Photographs showing adult dolphins swimming with a newborn individual (a) and an immature individual (b). Both these categories were considered "dependent calves". Reproduced with author permission from Methion, 2019.

Sex determination of bottlenose dolphins was conducted through direct field observations and confirmed with photographic evidence of the genital region when possible (following Díaz López, 2012) (Figure 2.6). Males were identified by the presence of an erection or a noticeable gap greater than 2.5 cm between the genital and anal slits. Females were recognised either by the visible presence of mammary slits with no discernible gap between the genital and anal slits, or through repeated observations of a closely associated newborn swimming in the infant position, indicating maternal care. These identification methods provided a reliable basis for classifying individuals by sex during encounters (Díaz López, 2012).

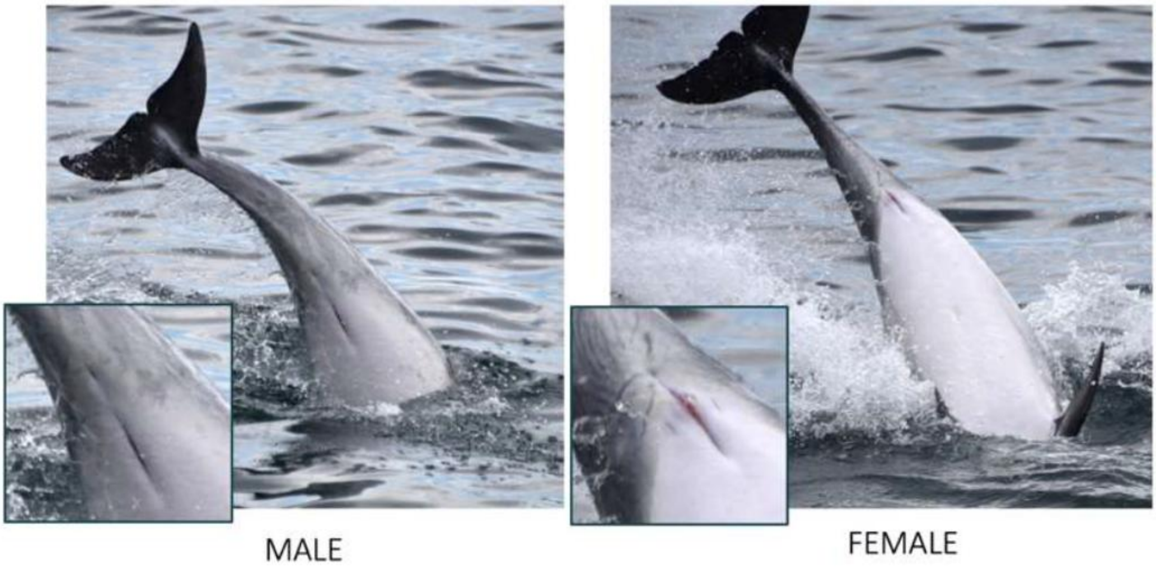


Figure 2.6 Photographs illustrating bottlenose dolphin genital area for sex categorisation. Reproduced with author permission from Methion, 2019

Group behaviour was recorded using a group-follow protocol, based on five-minute sampling (Methion and Díaz López, 2019). The predominant behavioural state was defined as the activity performed by at least 50% of individuals for more than half the sampling period (Methion and Díaz López, 2019). Four broad behavioural states were classified: foraging, resting, socialising, and travelling (Table 2.1). These were inferred from a combination of parameters, including dive patterns, swim direction and speed, inter-individual distance, and direct contact among dolphins (Díaz López, 2006a). To minimise observer bias, behavioural assessments were performed by a single experienced researcher throughout the data collection period.

Table 2.1 Description of the behavioural states of bottlenose dolphins assessed for each group every 5 minutes. Reproduced with permission from Methion and Díaz López, 2019. Copyright 2019, John Wiley and Sons.

Behaviour	Description
Foraging	Solitary or aggregation of bottlenose dolphins swimming in different directions within the same area. Dolphins usually remain in the same area, engaging in carousel and cross-swimming behaviours. In larger groups, the group may be split into two or more subgroups spread over a large area (≥100 m), or individuals may be completely dispersed. **Surface-feeding**: Includes fast surfacing (chasing prey close to the surface), feeding rushes towards the surface or obstacles (e.g., rocks, shellfish platforms), catching prey, fish kicking or tossing, and ventral swimming. **Deep diving**: Characterised by a sequence of regular dives followed by steep dives (tail-stock or flukes-up dives), and then long dives (>60 seconds) (Díaz López et al., 2008).
Resting	Solitary or aggregation of bottlenose dolphins surfacing at a slow and constant speed (<2 knots). The group is tight (<1 body length, ~3 meters). Surfacing often involves synchronous diving behaviour between two or more individuals and floating at the surface. Most ventilations are regular, and dives are short (<60 seconds), with no steep dives observed. When this behavioural state ends, there is a drastic behavioural shift involving significant changes in speed, direction, dive interval, and behavioural events.
Socialising	Aggregation of bottlenose dolphins interacting at the surface and underwater with one or several other dolphins. Can include synchronous dives, body contact, biting, rolling, charging, chasing, somersaults, mating, genital inspections, tail slaps, leaps, bows, and breaches. Individuals change position in the group and swimming direction varies. The group can be split into small subgroups spread over a large area. The dive interval is short (<60 seconds).
Travelling	Solitary or aggregation of bottlenose dolphins regularly surfacing (constant dive intervals <60 seconds) at a constant speed (>2 kt) and with one goal direction. If there are several individuals in the group, the group is generally cohesive and the inter-individual distance is usually less than 3 body lengths (approximately 9 metres).

Photographic identification was carried out using DSLR cameras with 35–300 mm telephoto zoom lenses, capturing both sides of the dorsal fin of each dolphin present, regardless of age class, sex, or marking distinctiveness (Díaz López, 2012). These images were used to assess individual identity, confirm group size, and infer sex and age class when possible, following protocols established by Díaz López (2012).

2.3.1.2 Acoustic Data Collection

Acoustic data collection by the BDRI throughout both long-term studies was conducted non-invasively, meaning that there was no physical contact with the animals being recorded. Acoustic recordings were taken when sea conditions were favourable (< 1 on the Douglas sea force scale), and if the focal group of bottlenose dolphins was clearly identifiable and no other cetaceans were present within the surrounding area, in order to ensure that no other animals than the focus group were recorded (Díaz López and Bernal Shirai, 2010; Díaz López, 2011). Once a group was detected and approached for visual monitoring, recordings started only after a habituation period of at least 20 min after the beginning of the behavioural observations (Díaz López and Bernal Shirai, 2010; Díaz López, 2011). This precaution ensured that the dolphins had acclimated to the presence of the research vessel, and that behavioural and acoustic data were not artefacts of disturbance (Díaz López and Bernal Shirai, 2010; Díaz López, 2011). Throughout both long-term studies, dolphins were habituated to high vessel activity, and the acoustic recordings did not appear to cause any stress or changes in behaviour (Díaz López, 2011, 2022).

During data collection, the engine of the research vessel was turned off to reduce ambient noise and avoid behavioural disturbance, and the boat was allowed to drift at a distance of 10 to 50 m from the focal group (Díaz López and Bernal Shirai, 2010; Díaz López, 2011). An omnidirectional hydrophone, deployed to a depth of 7 to 9 m, was connected to a professional-grade two-channel mobile digital recorder (Díaz López and Bernal Shirai, 2010; Díaz López, 2011). From 2005 to 2009, recordings were made at a 44 kHz sampling rate (16-bit), resulting in a Nyquist frequency of 22 kHz, which is considered sufficient for capturing the majority of bottlenose dolphin whistle frequencies (Herzing, 2000; Janik, 2009; Díaz López, 2011), as the analysis entailed counting the individual whistles rather than collecting detailed spectrographic measurements of the full contour. From 2009 onwards, the sampling frequency was 96 kHz. Acoustic recordings were monitored in real-time via headphones for quality assurance.

One of the main limitations of collecting recordings with a hydrophone is that sounds cannot be attributed to specific individuals. This challenge is in addition to the fact that dolphins lack voice cues (Sayigh, Wells and Janik, 2017) and often produce no reliable external indicators of sound production, although bubble streams can sometimes accompany whistles (Fripp, 2006; Janik, 2009). Furthermore, underwater visibility from the research vessel was limited, and the data were collected without handling or interacting with the animals, which also made the assignment of sounds to individuals not possible. For these reasons, a focal group approach was adopted as the sampling unit (Boisseau, 2005; Morisaka *et al.*, 2005; Quick and Janik, 2008; Díaz López and Bernal Shirai, 2010; Díaz López, 2011), with sounds attributed to the group as a whole rather than to specific dolphins. The high amplitude of the sounds within the recordings, together with the fact that no other groups were present within the visual field, ensured that the sounds analysed originated from the focal dolphins closest to the boat (Díaz López and Bernal Shirai, 2010; Díaz López, 2011). Group composition was carefully monitored throughout, and recordings were stopped if the composition changed or if the animals could no longer be reliably followed (Díaz López and Bernal Shirai, 2010; Díaz López, 2011).

2.3.2 Data Organisation

All acoustic recordings collected over the 15-year period were reviewed and matched with the corresponding visual data, ensuring that information on behaviour, environment, and group composition could be integrated with acoustic output. Because the number and duration of recordings varied between sightings (due to sighting duration and the manual start–stop operation of the recorder), all recordings from the same sighting were first pooled. Only sightings with at least three minutes of analysable, high-quality audio were retained. Quality was assessed manually, with recordings included only if whistles were clearly audible and visible in spectrograms, with a signal-to-noise ratio above 20 dB and no masking from boat engines, wave slap, or other anthropogenic noise (Morrison, DeLong and Wilcox, 2020). The consistently high amplitude of recorded whistles, coupled with the close proximity of the animals to the hydrophone, further confirmed the focus group as the source of the recorded sounds (Díaz López, 2011). Sightings with fewer than three minutes of suitable data (66 in total) were excluded. To remove potential bias from recording length and to minimise autocorrelation, three one-minute samples were then randomly selected from each retained sighting using a random number generator (Haahr, 2019). With an average recording duration of ~12 min per sighting, most selected minutes were non-contiguous, further reducing the risk of temporal dependence; only ~12% of sightings had three to five minutes of usable data, where contiguous samples were unavoidable. This process resulted in a standardised dataset of 1119 one-minute samples from 373 dolphin sightings, which was then used for spectrogram analysis.

2.3.3 Spectrogram Analysis

All 1119 randomly selected one-minute samples were visualised as spectrograms using SPECTROGRAM © 6.2.3 software on a PC platform. A 4096-point Hamming window, a 10 s display frame, and a dynamic range of –90 dB were applied consistently across all analyses. Spectrograms were displayed in the 1–22 kHz range, ensuring comparability between study sites and types of equipment. This frequency range was deemed suitable for the detection and counting of whistles, rather than for detailed acoustic parameter measurements (Herzing, 2000; Janik, 2009; Díaz López, 2011).

2.3.3.1 Whistle Rate Determination (Objective 1)

Each spectrogram was inspected manually, with whistles verified both visually and aurally through headphone playback, ensuring robust classification. Whistles were defined as continuous tonal sounds that could be clearly distinguished in both visual and auditory inspections. Two whistles were considered independent if separated by more than 300 ms on the spectrogram (Díaz López, 2011), a slightly more conservative threshold than the 250 ms used in other studies (Esch, Sayigh and Wells, 2009; Janik *et al.*, 2012), to avoid overestimating whistle counts. Overlapping whistles were counted as separate signals.

For each sample, the total number of whistles per minute was documented. In this thesis section, the term “Whistle Rate” refers to the number of whistles detected in each one-minute sample of the focal group (Boisseau, 2005; Morisaka *et al.*, 2005; Quick and Janik, 2008; Díaz López, 2011, 2022). This measure is considered a reliable proxy for whistle production rate, given the close proximity of the animals during recordings, the consistently high signal-to-noise ratio, and the absence of other visible dolphin groups in the area (Díaz López, 2011). All whistle counts data were recorded in a structured database to facilitate subsequent statistical analyses and cross-referencing with behavioural and environmental parameters.

2.3.3.2 Signature Whistle Identification (Objective 2)

To determine the presence of signature whistles in each analysed sample, the SIGnature IDentification (SIGID) method developed by Janik and colleagues (2012) was applied. According to this method, a whistle was classified as a signature whistle when at least 75% of whistles with the same frequency modulation pattern were produced within bouts displaying inter-whistle intervals of 1–10 s (Figure 2.7). A binary value ("present" = 1) was assigned to a sample if such a bout consisted of at least four repeated whistle units matching this criterion.

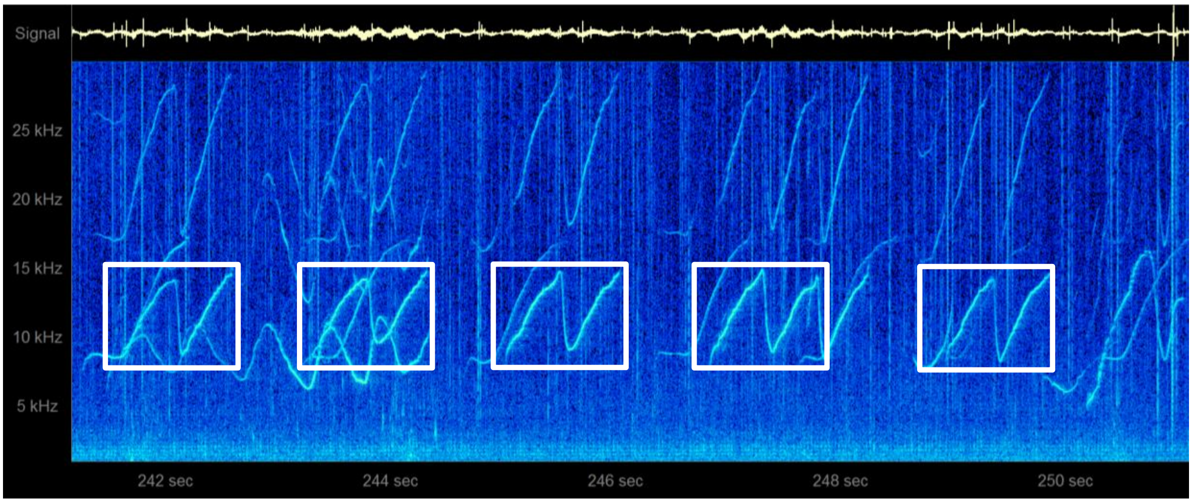


Figure 2.7 Spectrogram showing bottlenose dolphin signature whistles displayed using SPECTROGRAM © version 6.2.3. FFT= 4096, display window duration=10 s. This image was generated from an acoustic recording collected by the Bottlenose Dolphin Research Institute (BDRI) and processed by the author for this thesis

Due to the highly conservative nature of the SIGID approach, the likelihood of false positives was minimal, making this a robust and reliable method for identifying signature vocalisations (Janik *et al.*, 2012). To ensure the correct classification of this variable, each randomly selected acoustic sample was further inspected at least 10 s before and 10 s after the limits of the selected minute whenever possible, allowing for the detection of whistles that may have been part of a contiguous signature whistle sequence straddling the sample boundary.

2.3.4 Statistical Analysis

2.3.4.1 Whistle Rate Determinants

All statistical analyses were performed using R software (R Core Team, 2017). To examine the effects of the explanatory variables on dolphin Whistle Rate (used as the response variable), a Generalised Linear Mixed Model (GLMM) framework was used. GLMMs are an extension of generalised linear models (GLMs) by allowing for both fixed and random effects, and can accommodate a range of data distributions (McCullagh and Nelder, 1989). Nine explanatory variables (Table 2.2) were included in the analysis: Location, Season, Time of day (each day, hours of daylight were equally divided into thirds to represent proportional parts of the day as daylight varies throughout the year), Group behaviour, Total group size, Number of adults, Number of dependent calves, Presence of dependent calves, and a Group ID code.

Table 2.2 List of explanatory variables used in statistical analysis including variable type and categorical levels where applicable.

Variable		Variable Type	Levels
1	Location	Categorical	Galicia Sardinia
2	Season	Categorical	Winter: January-March Spring: April-June Summer: July-September Autumn: October-December
3	Time of Day	Categorical	Morning Afternoon Evening
4	Group Behaviour	Categorical	Feed Social Travel Rest
5	Total Group Size	Numerical	Positive Integer Number
6	Number of Adults	Numerical	Positive Integer Number
7	Number of Dependent Calves	Numerical	Positive Integer Number
8	Presence of Dependent Calves	Binary	Presence/Absence
9	Group ID Code	Numerical	Positive Integer Number

The Group ID code represented a unique identifier for each group composition based on individual photo-identification. Group ID was included as a random effect to account for repeated measures from the same dolphin group. This variable was available for 321 out of the 373 groups. Of these 321 groups, 270 corresponded to unique compositions, indicating that repeated group configurations accounted for only 16% of the dataset. The remaining 52 groups, corresponding to 156 samples (as each dolphin group had three randomly-selected one-minute acoustic samples), lacked a complete set of explanatory variables and were therefore excluded, since GLMMs require complete cases for all predictors.

Before fitting models, all continuous variables were tested for collinearity using a Spearman correlation test. Variable pairs with a correlation coefficient above $\rho = 0.7$ were considered to be highly correlated and, therefore, were not included in the same model covariate set (Schober, Boer and Schwarte, 2018). Additionally, an initial general linear model (GLM) including all variables was run, and the Variance Inflation Factor (VIF) was calculated using the ‘car’ package (Fox and Weisberg, 2019). A threshold of VIF > 3 was used to flag multicollinearity (Dormann *et al.*, 2012), and variables exceeding this threshold were excluded from being included together in the same model. In this dataset, the strongest correlation was found between ‘Total group size’ and ‘Number of adults’ (Spearman $\rho = 0.94$, $p < 0.01$). Because of this, only one of these variables could be used in the final models. “Total Group size” (hereafter referred to simply as Group Size) was selected for further analysis, as this metric is commonly used in similar studies, especially when precise group composition is difficult to assess (Quick and Janik, 2008; Díaz López and Bernal Shirai, 2010; Hernandez, Solangi and Kuczaj, 2010).

Once collinearity was addressed, an initial GLMM was constructed including all non-colinear variables and a set of interaction terms. These interactions were: Location × Behaviour, Location × Group Size, and Behaviour × Group Size. The model was run using the 'glmmTMB' package (Brooks *et al.*, 2017). Given that the response variable (Whistle Rate) was a zero-inflated count variable, a negative binomial distribution with linear parameterisation ('nbinom1') was selected, following recommendations for this type of data (Hardin and Hilbe, 2007). Model selection was carried out through a combination of forward and backward stepwise procedures based on the Akaike Information Criterion (AIC). The model with the lowest AIC value was chosen as the final model. Model fit and residual patterns were examined using the 'DHARMa' package and the 'simulateResiduals' function (Hartig, 2016) to assess any violations of model assumptions. To interpret the effect of each predictor, the incident rate ratio (IRR) was calculated for each level of the variables in the final model. The IRR is particularly useful when working with count data in a GLMM framework, as it expresses the change in the expected value of the response variable (in this case, Whistle Rate) for a one-unit increase in the predictor, while holding all other predictors constant (Hilbe, 2011). For example, an IRR of 2 for a given variable would indicate that the Whistle Rate doubles when moving from one level of the variable to the next. Finally, model outputs and predictions were visualised using the 'sjPlot' package (Lüdecke, 2023).

2.3.4.2 Signature Whistle Production

The analysis focused on modelling the presence/absence of signature whistles within individual acoustic samples as the response variable. To evaluate how social, behavioural and ecological factors influenced this response, Generalised Linear Mixed Models (GLMMs) were implemented in R (R Core Team, 2017). This modelling framework was selected because it is well suited for binary response variables and allows the simultaneous inclusion of fixed and random effects (McCullagh and Nelder 1989).

Initially, a set of nine explanatory variables was considered: Location (Galicia or Sardinia), Season (Winter (January-March), Spring (April-June), Summer (July-September) and Autumn (October-December)), Moment of the Day (Morning, Afternoon and Evening, representing equal proportions of daylight time), group behaviour (hereafter "Behaviour"), Group Size, Number of adults, Number of dependent calves, Presence of dependent calves (binary), and Group ID code (a numeric identifier assigned to each sighting with a distinct combination of individuals). The latter was included as a random effect.

Prior to model construction, Shapiro–Wilk tests were conducted to assess the distribution of continuous predictors (Group Size, Number of adults, and Number of dependent calves). Pairwise correlations among these variables revealed a strong association ($\rho > 0.7$, Schober, Boer and Schwarte, 2018) between Group size and Number of adults ($\rho = 0.94$). To avoid redundancy while retaining the most biologically informative variable, Number of adults was excluded from subsequent analyses in favour of Group size. To further assess multicollinearity among predictors, an initial General Linear Model (GLM) was fitted using the reduced covariate set. Variance Inflation Factors (VIFs) were then calculated using the car package (Fox and Weisberg, 2019), applying a conservative threshold of VIF > 3. None of the remaining predictors exceeded this threshold, resulting in a final set of eight explanatory variables: Location, Season, Moment of the Day, Behaviour, Group size, Number of dependent calves, Presence of dependent calves, and Group ID code.

Following these collinearity checks, a binomial GLMM was fitted using the "glmmTMB" package (Brooks *et al.*, 2017), incorporating all previously-selected fixed and random effect terms, and a set of biologically relevant interaction terms. The interactions tested were Location × Behaviour, Location × Group size, and Behaviour × Group size, allowing assessment of whether the effect of one predictor depended on the level of another (McCullagh and Nelder, 1989). Model selection was conducted using the dredge function from the "MuMIn" package (Barton, 2009), which generated a candidate model set comprising all combinations of predictors and interaction terms. Models were ranked according to Akaike Information Criterion (AIC), and the model with the lowest AIC was retained for further evaluation. Model adequacy was assessed through residual diagnostics using the "DHARMa" package (Hartig, 2016). Simulated residuals were examined using quantile–quantile plots and residuals-versus-predicted plots, and the absence of systematic patterns was taken as evidence of appropriate model fit. Effects of explanatory variables were interpreted using log-odds estimates derived from the fitted model. In the context of binomial GLMMs, log-odds represent the natural logarithm of the odds of signature whistle occurrence relative to non-occurrence (Hilbe, 2009). Model coefficients therefore describe the expected change in log-odds associated with a one-unit increase in a predictor, assuming other variables remain constant. For instance, a coefficient of 0.69 corresponds approximately to a doubling of the odds of occurrence ($e^{0.69} \approx 2$).

To facilitate interpretation of behavioural effects, the final model was reparameterised, setting Travel as the reference category instead of Feed, which is the default reference level due to alphabetical ordering. This adjustment enabled direct estimation of additional pairwise behavioural contrasts, including comparisons between Social and Travel behaviours, along with their associated log-odds.

Finally, to further explore significant interaction effects, post hoc analyses were performed by fitting separate GLMMs for relevant predictor combinations. When continuous predictors produced non-linear response patterns, pairwise comparisons of estimated trends were conducted using the "emmeans" package (Lenth and Piaskowski, 2017). Model explanatory power was quantified using marginal and conditional R^2 values calculated with the "performance" package (Lüdecke *et al.*, 2021). Graphical representations of model outputs were generated using the "sjplot" package (Lüdecke, 2023).

2.4 FIXED PASSIVE ACOUSTIC MONITORING

The second data collection methodological approach used in this thesis is fixed Passive Acoustic Monitoring PAM. While PAM broadly refers to any technique that records underwater sounds without emitting signals (as sonar does), in this thesis, fixed PAM specifically refers to continuous, unsupervised recordings made by an autonomous, moored platform. Unlike boat-based hydrophone recordings, this approach operates independently of dolphin presence and without concurrent visual observations. This methodology does not provide direct evidence of the physical presence of dolphins, but only their acoustic presence, and offers temporal consistency across day and night and under a wide range of environmental conditions. Unlike boat-based hydrophone surveys, which require suitable weather, visibility, and field effort, fixed PAM generates continuous datasets that allow questions of a more ecological nature to be addressed, particularly in areas that are otherwise difficult to monitor with vessels.

2.4.1 Acoustic Data Collection and Explanatory Variable Extraction

Data were collected between August 23rd, 2017 and February 4th, 2022, at a fixed oceanographic monitoring station on the north side of Cortegada Island (42.62682ºN, -8.78233ºW), within the Ría de Arousa estuary in northwestern Spain (Xunta de Galicia, 2025c) (Figure 2.8). This platform was designed to monitor underwater acoustic activity and associated environmental variables. It is equipped with a hydrophone and a Conductivity-Temperature-Depth (CTD) unit, which enables in situ recording of acoustic signals and water column properties.

This monitoring platform is part of a network along the Galician coast, under the management of the Centro Tecnológico do Mar (CETMAR). The acoustic and environmental data were collected as part of the STRAUSS project, through which the Bottlenose Dolphin Research Institute (BDRI) collaborated by analysing the acoustic recordings to determine dolphin presence.

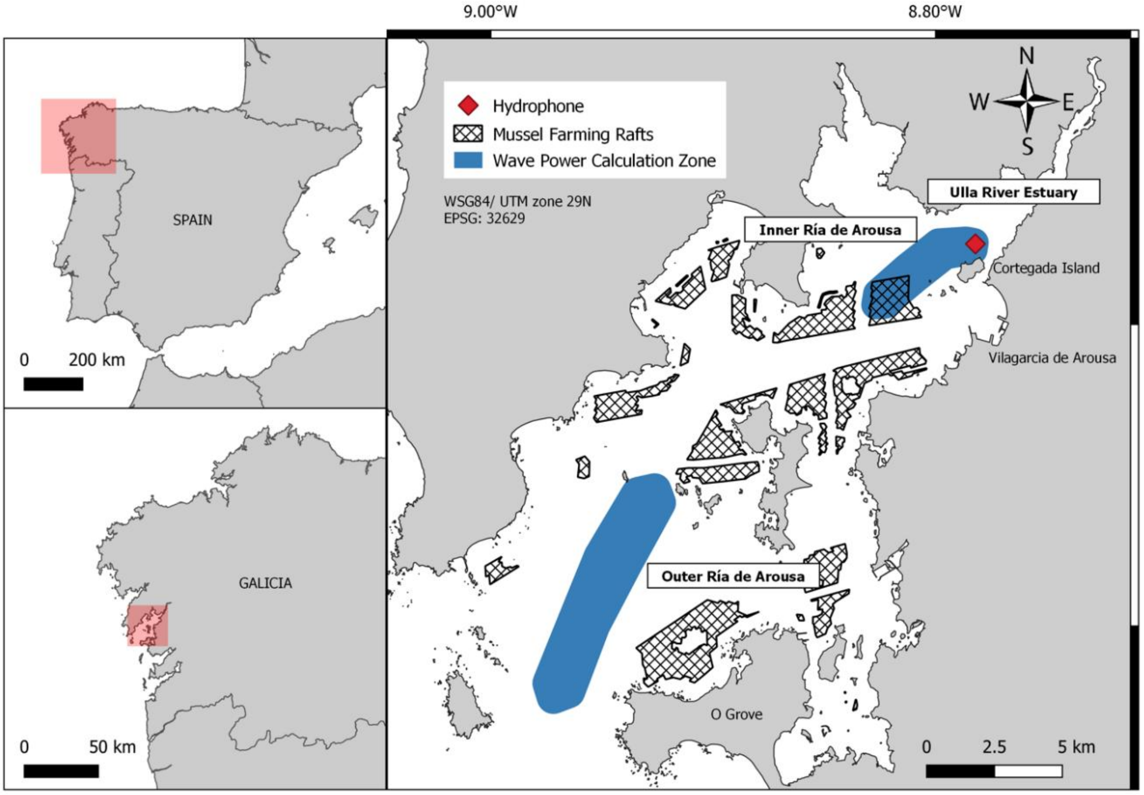


Figure 2.8 Map of study area, hydrophone location and wave power calculation areas

The hydrophone used was an Ocean Sonics icListen HF ALTA, with a recording bandwidth of 10 Hz to 200 kHz, sampling frequency of 196 kHz, Nyquist frequency of 98 kHz, sensitivity of -173 dB re V/µPa, and a peak SPL of 180 dB re µPa (Ocean Sonics, 2025). The CTD sensor deployed was a Sea-Bird SBE 37-SI MicroCAT, a moored instrument capable of high-accuracy measurements of temperature and salinity, commonly used in long-term oceanographic monitoring programs (Sea-Bird Scientific, 2025). In addition to these direct measurements, a suite of additional oceanographic and environmental variables was obtained from public datasets, numerical models, and satellite observations. The full set of variable types is described below. With the exception of the assignment of the “Season” variable, all of the following variables were collected or calculated by the CETMAR team.

1. **Acoustic Data**
   The hydrophone was configured to record one-minute audio segments every three minutes. Each file was automatically named with the corresponding date and timestamp, enabling clear interpretation of the acoustic analysis output file. Due to the remote nature of the platform and logistical constraints (battery replacement and change of data storage equipment), particularly those caused by technical malfunctions and restricted field access during the COVID-19 pandemic, there were periods of data interruption. These gaps are reflected in Figure 3.13. For the purposes of this study,

acoustic data were processed at an hourly resolution. Each hour was assigned a binary value for dolphin whistle presence: “1” if at least one whistle was detected during that hour, and “0” otherwise.

2. **Day/Night Classification**
   Each hourly data point was categorised as either "day" or "night" based on whether the majority of the hour coincided with the sun being above or below the horizon at the hydrophone location. This was achieved by using a custom macro that calculates the solar zenith angle, which represents the angle between the sun and the vertical direction at a given time and location. A threshold of 90 degrees was used to distinguish between daylight (sun above the horizon) and nighttime (sun below the horizon). The solar zenith angle was computed using latitude, longitude, and UTC time for each data point, following the methods described in Duffett-Smith (1988). Calculations were implemented in a spreadsheet with a Visual Basic macro used to automate the process.

3. **Season**
   Seasons were assigned to each hourly sample unit based on the calendar month:
   - Winter: January–March
   - Spring: April–June
   - Summer: July–September
   - Autumn: October–December

4. **Temperature (°C) and Salinity (psu)**
   Temperature and salinity data were collected at both the sea surface and at depth (approximately 3 to 4 m deep) using the CTD sensor installed on the fixed acoustic monitoring platform. Measurements were recorded every 10 minutes throughout the study period. Each data point was assigned a quality control value: “1” for accurate values, “4” for probable errors, and “9” for definite errors. Prior to analysis, all CTD data were screened to retain only those measurements with a quality score of 1, ensuring the reliability of the hourly averaged values. This filtering process introduced gaps in the time series where insufficient valid data were available for a given hour. These discontinuities are reflected in Figure 3.13.

5. **Wave Power (W/m)**
   Wave power was computed using the Simulating Waves Nearshore (SWAN) model (Meteo Galicia, 2025) at both inner and outer ría locations. The hourly values were averaged across four positions in each zone (Figure 2.8). Power was calculated using the formula:

$$P_w = E \cdot C_g, \quad \text{where} \quad E = \frac{1}{8}\rho g H^2$$

- ρ: water density (kg/m³)
- g: gravitational acceleration (9.81 m/s²)

- H: significant wave height
- C_g: group velocity of the wave

6. **Wave Height (m)**
   Wave height was retrieved from the SWAN model data provided by MeteoGalicia. Hourly data were extracted from the Thematic Real-time Environmental Distributed Data Services (THREDDS) Data Server using historical SWAN simulations (Meteo Galicia, 2025).

7. **Current Velocity (m/s)**
   Hourly current velocity values at the river mouth were extracted from the Regional Ocean Modelling System (ROMS) (Meteo Galicia, 2025). Current direction was defined along the axis from the mussel platform near Cortegada Island toward the river mouth, with positive values indicating flow into the river and negative values indicating flow toward the outer ría. Current velocity was used as a proxy for tidal flow, under the assumption that variations in current speed and direction at this location are primarily driven by the tidal cycle.

8. **Ulla River Discharge (m^3/s)**
   The daily average continental discharge from the Ulla River was obtained using the Soil and Water Assessment Tool (SWAT) outputs provided by MeteoGalicia (Meteo Galicia, 2025).

9. **Chlorophyll-a Concentration (mg/m^3)**
   Daily chlorophyll-a values were sourced from the Copernicus “Atlantic Ocean Colour” dataset. Data were collected for the hydrophone location on the sample day, as well as 3, 7, 15, and 30 days prior. Differences in concentration between each of these intervals and the sample date were calculated. Average values for the sample date were also obtained for the outer ría.

10. **Upwelling Index (UI) ($m^3/s/km$)**
    The upwelling index at geographical coordinates 42°N, 10°W, which represents the region of interest (Gonzalez-Nuevo, Gago and Cabanas, 2014), was obtained for the period 2017–2022 from the Instituto Español de Oceanografía (IEO-CSIC, 2025). This index is calculated following Lavín *et al.* (1991) and is based on six-hourly geostrophic winds derived from the Navy Operational Global Atmospheric Prediction System (NOGAPS), maintained by the Fleet Numerical Meteorology and Oceanography Center (FNMOC).
    Daily UI values were collected for the hydrophone location for the sample day, and at 3, 7, 15, and 30-day lags. Instances where UI exceeded 500 were recorded and summarised across each lag interval.

11. **Fish Landing Data (Kg)**
    Daily landings of European eel (*Anguilla anguilla*) and lamprey (*Petromyzon marinus*) were obtained from the Galician fisheries database (Xunta de Galicia, 2025b) for the Carril harbour, closest to the acoustic platform. Available data were averaged weekly and applied to all hourly points within that week.

2.4.2 Acoustic Data Processing and Whistle Detection

To assess the presence of dolphin vocalisations, acoustic data files were systematically processed using the PAMGuard software suite (Gillespie *et al.*, 2009). Specifically, the "Whistle and Moan" detector (Webber *et al.*, 2022) was employed in conjunction with the ROCCA (Real-time Odontocete Call Classification Algorithm) random forest classifier (Oswald *et al.*, 2011), configured with parameters optimised for odontocete species in the Northeast Atlantic (PAMGuard, 2025). Acoustic files were batch-processed at 64x real-time speed using a PC equipped with adequate memory and a video card suitable for high-throughput acoustic analysis.

Acoustic files were processed in batches typically comprising eight to 12 days of recordings, depending on available processing time. After each batch was analysed, the resulting detection output file (exported in .csv format with one row per detection, including filename and timestamp) was manually reviewed to generate an hourly dolphin whistle presence/absence dataset. Each hour within the study period was assigned a value of “1” (whistles detected), “0” (no detections), or left empty if no recording was available. Whistles were chosen as the focal signal type as a proxy for dolphin presence over echolocation clicks due to their broader propagation patterns. While clicks are emitted in highly directional, narrow beams (Au, Floyd and Haun, 1978; Branstetter and Mercado, 2007; Branstetter *et al.*, 2012) that may be masked by marine anthropogenic noise, such as vessel traffic (Dey *et al.*, 2019), whistles possess lower fundamental frequencies with harmonic structures that radiate more omnidirectionally (Branstetter *et al.*, 2012; Jones *et al.*, 2019). This property increases the likelihood of detection regardless of the dolphin’s orientation relative to the hydrophone, and whistles have been used in previous PAM studies to indicate dolphin spatio-temporal habitat use patterns (Gregorietti *et al.*, 2021). Additionally, the availability of full audio recordings allowed for the possibility of manual cross-verification of whistle detection events.

To ensure detection accuracy and minimise false positives, systematic quality checks were implemented for each batch. All isolated detections (defined as single, non-clustered detections not associated with a sequence of nearby detections) were manually verified using Raven PRO Version 1.6.5 (K. Lisa Yang Center for Conservation Bioacoustics at the Cornell Lab of Ornithology, 2024), by visually inspecting the spectrogram at the reported time. Additionally, 15 random detections per batch were selected using a random number generator (Haahr, 2019) based on the range of row numbers in the detection file. These were also manually validated with Raven Pro 1.6.5 Software. Across thousands of verification instances, no false positives were identified.

Although the Whistle and Moan detector and ROCCA also provide measurements of whistle parameters and species classification (Oswald *et al.*, 2011; PAMGuard, 2025), these outputs were not used for analysis. It was noted that the automatic contour windows often did not align well with the whistle contour, rendering the additional measurements and species assignment inaccurate. While ROCCA can perform more reliably when detections are manually adjusted, the volume of data in this project made individual correction of detections infeasible. Therefore, the system was used strictly as a robust detection tool, rather than for parameter extraction. Given ongoing long-term cetacean monitoring in the study area by the BDRI within the waters of the Ría de Arousa (Methion and Díaz López, 2018), all detected whistles were attributed to *Tursiops truncatus.*

The acoustic presence data were compiled into a dataset in which each sample was associated with the corresponding environmental and temporal variables, providing the basis for subsequent statistical analyses.

2.4.3 Data Organisation

To improve model performance, the hourly data were grouped into three-hour time blocks, which helped by increasing the percentage of whistle-positive samples while still preserving enough detail to explore general patterns in the data. Within each three-hour block, continuous environmental variables (e.g., temperature, salinity, and current speed) were averaged to provide a representative value for the entire period. For wave power, both the mean and the maximum value observed within each block were calculated to capture variability and peak energy events. Each block was classified as day or night based on whether the majority of the period occurred during daylight hours. Seasonal classification, which was based on calendar month, remained unaffected by the aggregation.

A wide range of variables were included in the dataset, encompassing physical, chemical, biological, and temporal elements. These included water column properties (temperature and salinity at both surface and bottom), oceanographic dynamics (current speed, river discharge, and wave power), chlorophyll-a concentrations and their changes over time, fish landing proxies for two target species, and upwelling indices with multiple temporal lags and threshold-based metrics. All variables used, along with their respective subtypes and units, are summarised in the table below (Table 2.3).

Table 2.3 Initial Model Explanatory Variable Set. Variables are grouped by category and include physical, oceanographic, biological, and temporal predictors used to model dolphin acoustic presence

Variable Group	Variable Name	Unit/Type
Light	Day/Night	Categorical
Season	Season	Categorical
Salinity	Sea Surface Salinity	psu
	Bottom Salinity	psu
Temperature	Sea Surface Temperature	°C
	Bottom Temperature	°C
Ocean Dynamics	Current Velocity	m/s
River Discharge	Ulla River Discharge	m^3/s
Wave Power	Wave Power Inner Ría (Average)	kW/m
	Wave Power Inner Ría (Max)	kW/m
	Wave Power Outer Ría (Average)	kW/m
	Wave Power Outer Ría (Max)	kW/m
Upwelling Index (UI)	UI (Same Day)	$m^3/s/km$
	UI (3 Days Prior)	$m^3/s/km$
	UI (7 Days Prior)	$m^3/s/km$
	UI (15 Days Prior)	$m^3/s/km$
	UI (30 Days Prior)	$m^3/s/km$
	UI >500 (3 Days Prior)	$m^3/s/km$
	UI >500 (7 Days Prior)	$m^3/s/km$
	UI >500 (15 Days Prior)	$m^3/s/km$
	UI >500 (30 Days Prior)	$m^3/s/km$
Chlorophyll-a	Chlorophyll-a Inner Ría	mg/m^3
	Chlorophyll-a Outer Ría	mg/m^3
	Chl-a Inner (3 Days Prior)	mg/m^3
	Chl-a Inner (7 Days Prior)	mg/m^3
	Chl-a Inner (15 Days Prior)	mg/m^3
	Chl-a Inner (30 Days Prior)	mg/m^3
	Chl-a Difference (3 Days Prior)	mg/m^3
	Chl-a Difference (7 Days Prior)	mg/m^3
	Chl-a Difference (15 Days Prior)	mg/m^3
	Chl-a Difference (30 Days Prior)	mg/m^3
Eel	Eel Landings	kg
Lamprey	Lamprey Landings	kg

2.4.4 Statistical Analysis

To standardise variable scales and facilitate meaningful comparisons across predictors, all continuous variables were z-score transformed before analysis. This transformation involved subtracting the mean and dividing by the standard deviation (SD) of each variable, resulting in standardised scores with a mean of 0 and a standard deviation of 1 (McKim, 2022). Z-score standardisation was important in this context because the continuous variables included in the models exhibited widely different value ranges and measurement units. Rescaling to a common standard improves model interpretability, especially in generalised additive models (GAMs), where smooth terms can be difficult to compare when variables are on different scales (Al-Faiz, Ibrahim and Hadi, 2019). This approach also reduces data skewness, mitigates the influence of scale-dependent variance, and preserves intrinsic relationships among variables, thereby maintaining the integrity of the dataset for statistical modelling (Nkikabahizi, Cheruiyot and Kibe, 2022).

All statistical analyses were carried out using R software (R Core Team, 2017). Variables were tested for normality, and none followed a Gaussian distribution. Generalised Additive Models (GAMs) were selected as the main analytical tool because they are non-parametric extensions of generalised linear models (GLMs) and are well-suited for capturing the complex, non-linear relationships that often occur between environmental and biological variables in ecological datasets (Hastie and Tibshirani, 1987; Wood, 2017).

Variables were grouped into functional blocks based on ecological relevance (Table 2.3), and prior to model fitting, cross-correlation analysis of continuous variables indicated that strong correlations (> 0.7, Schober, Boer and Schwarte, 2018) occurred only among variables of the same type (e.g., among upwelling index-related variables). To address this, only one variable from each variable group was included in any candidate model set moving forward.

Bottlenose dolphin acoustic presence–absence was modelled using a binomial GAM with a logistic link function, using the "mgcv" package (Wood, 2011). Before running each GAM, a General Linear Model (GLM) was fitted using the same set of predictors to assess collinearity. Variance Inflation Factors (VIFs) were calculated using the "car" package (Fox and Weisberg, 2019), and only variable combinations with all VIFs < 3 were retained for further analysis (Dormann *et al.*, 2012). Model selection followed a multi-model inference approach (following Díaz López and Methion, 2018). A global model was constructed with one representative variable from each functional group, and all simplified versions of this model were generated using the dredge function in the "MuMIn" package (Barton, 2011). Models were compared using AICc, and those within ΔAICc < 2 of the top model were retained for model averaging. Akaike weights were used to assess relative model support, and the summed weights across the model set provided a measure of relative variable importance (Burnham and Anderson, 2002; Grueber et al., 2011). Final inferences were drawn from the averaged top models, allowing robust estimation of predictor effects while accounting for uncertainty in model selection.

CHAPTER 3: RESULTS

This chapter presents the results obtained in relation to the three main objectives of the thesis. First, results related to the determinants of whistle production in bottlenose dolphins are presented (Section 3.1). This is followed by the results concerning the contextual use of signature whistles (Section 3.2). Finally, results from the application of fixed passive acoustic monitoring are outlined, focusing on patterns of dolphin acoustic presence in an estuarine environment (Section 3.3).

3.1 WHISTLE RATE DETERMINANTS

A total of 464 dolphin group sightings were recorded across Sardinia and Galicia over a 15-year period. After applying the random selection procedure, the dataset used for statistical analysis was reduced to 373 group sightings across 273 unique sampling days (Table 3.1). The original dataset included 11,345 min of recordings (approximately 189 h), while the random selection retained 1119 min (approximately 19 h). Sardinia contributed more recordings than Galicia overall, which reflects both a longer period of data collection and a greater number of sampling days. The average duration of individual recordings was higher in the random selection compared to the full dataset, as only sightings above a certain duration threshold were included, which effectively excluded many shorter samples.

Table 3.1 Summary of dataset characteristics (Full and Random selection): comparison by location. Reproduced with permission from Mosca, Methion and Díaz López, 2025, Copyright 2025, Informa UK Limited, trading as Taylor & Francis Group

		Original (Full) Dataset	Random Selection
Years	**Sardinia**	9	9
	Galicia	6	6
	Total	15	15
Days	**Sardinia**	279	199
	Galicia	95	74
	Total	374	273
Number # of Sightings	**Sardinia**	344	284
	Galicia	120	89
	Total	464	373
Total Duration of recordings (Minutes)	**Sardinia**	9494.3	852
	Galicia	1850.9	267
	Total	11345.2	1119
Number # of Recordings	**Sardinia**	1537	506
	Galicia	400	189
	Total	1937	695
Average Duration of Recordings (Minutes)	**Sardinia**	6.69 ± 0.28	11.83 ± 0.79
	Galicia	4.63 ± 0.30	14.53 ± 2.26
	Total	6.23 ± 0.23	12.14 ± 0.74

A visual representation of the distribution of the randomly selected acoustic samples with respect to year, season, Time of Day and Behaviour is provided in the following figures (Figure 3.1 to Figure 3.4).

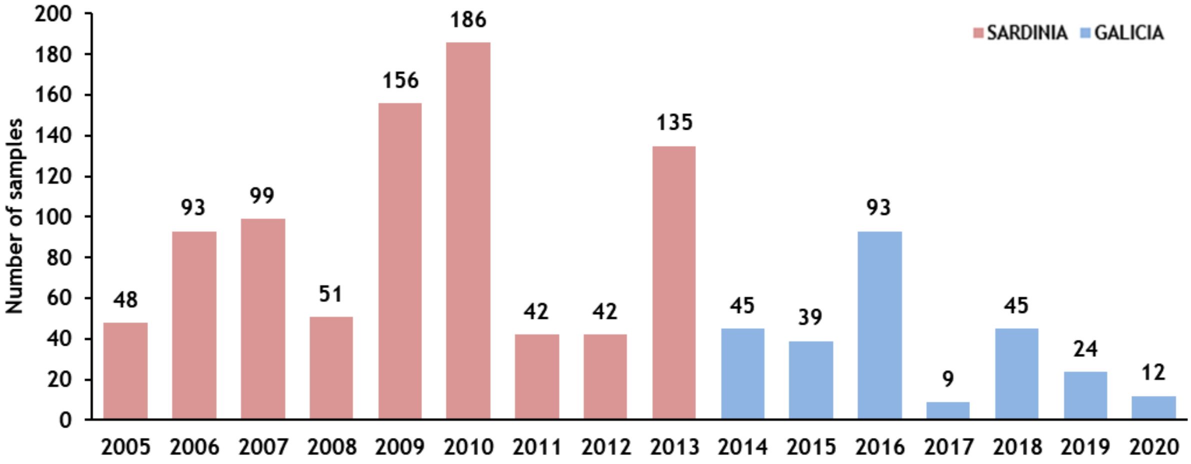


Figure 3.1 Yearly distribution of analysed acoustic samples (minutes). Red = samples collected in Sardinia, Blue = samples collected in Galicia

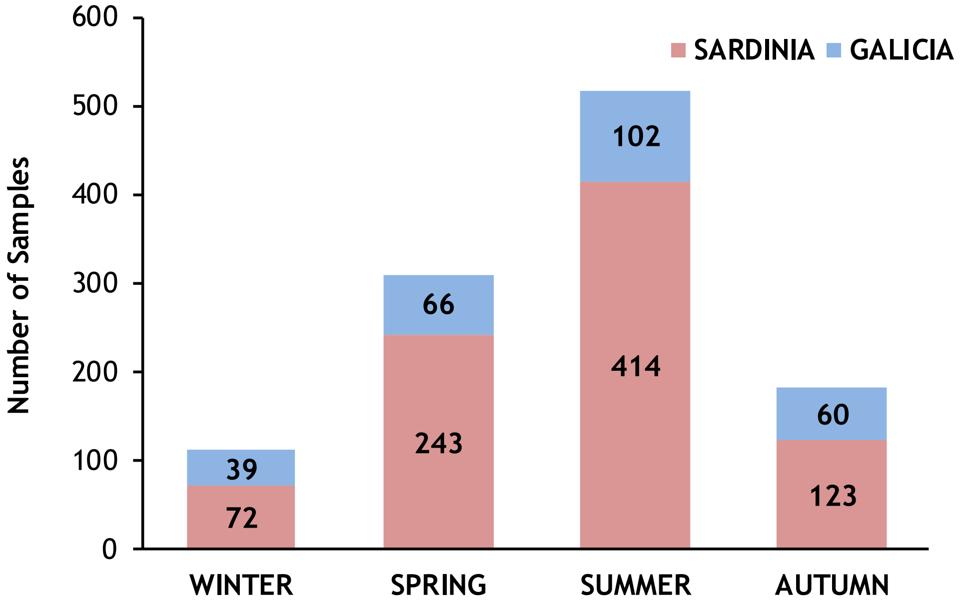


Figure 3.2 Distribution of analysed acoustic samples (minutes) with respect to seasons. Winter = January, February, March; Spring = April, May, June; Summer = July, August, September; Autumn = October, November, December. Red = samples collected in Sardinia, Blue= samples collected in Galicia

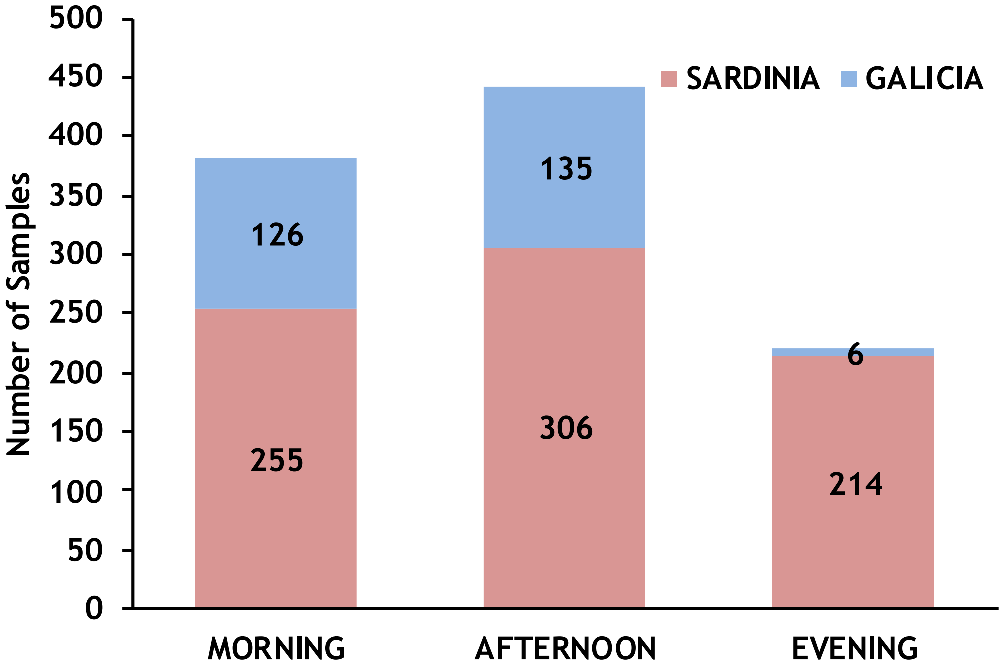


Figure 3.3 Distribution of analysed acoustic samples (minutes) with respect to time of day. Morning, afternoon and evening are equal thirds of the day between sunrise and sunset, and night samples were collected between sunset and sunrise. Red = samples collected in Sardinia, Blue = samples collected in Galicia

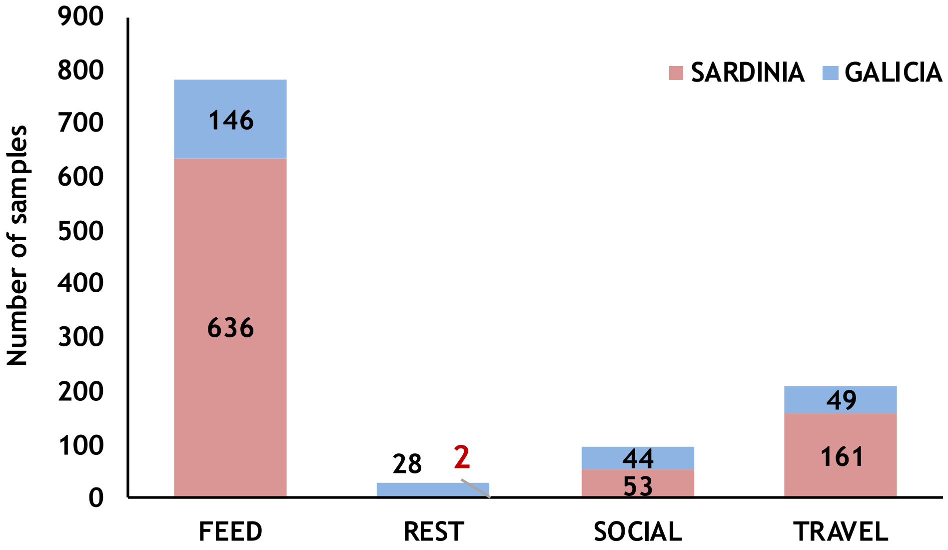


Figure 3.4 Distribution of analysed acoustic samples (minutes) with respect to group behaviour. Red = samples collected in Sardinia, Blue = samples collected in Galicia

Whistles were detected in 441 out of the 1119 acoustic samples analysed, representing approximately 39% of the dataset. The overall Whistle Rate across all samples was 3.05 ± 0.23 (SE) whistles per minute, with values ranging from 0 to 74 whistles per minute and a median of 0. Whistle rate averages by behavioural category and study site are presented in Table 3.2. In both Sardinia and Galicia, whistle rates were higher during social and feeding contexts, while no whistles were recorded during resting events.

Out of the 321 dolphin groups for which individual identification was available, 270 were made up of unique group compositions. This indicates that 84% of the identified groups were formed by different combinations of individuals, highlighting the high degree of variability in group structure within the dataset.

Table 3.2 Whistle Rate (#whistles/minute) by behaviour and study area. Values given are mean ± standard error (SE). Reproduced from Mosca, Methion and Díaz López, 2025

	Social	Feed	Travel	Rest	Overall
Sardinia	4.08 ± 1.03	1.90 ± 0.18	1.96 ± 0.43	0	2.04 ± 0.17
Galicia	10 ± 1.94	5.77 ± 0.78	2.94 ± 0.81	0	6.23 ± 0.77

The final GLMM model had the lowest AIC score among all tested model combinations (AIC = 3164.6), with a Δ AIC of 11.5 compared to the initial full model. The fixed effect variables present in the final model subset included: Location, Behaviour, and Group Size, along with two interaction terms: Location × Group Size and Behaviour × Group Size Table 3.3. Group ID Code was included as a random effect to account for repeated measures. No significant patterns were observed in the model residuals (Figure A-IV. 1 and Figure A-IV. 2 in Annex IV).

Table 3.3 Best GLMM model (negative binomial distribution) of Whistle Rate. Reproduced with permission from Mosca, Methion and Díaz López, 2025, Copyright 2025, Informa UK Limited, trading as Taylor & Francis Group

AIC	BIC	logLik	deviance	df.resid
3164.6	3223	-1570.3	3140.6	948

Random Effects:

Conditional Model:

Groups	**Name**	**Variance**	**Std.Dev.**
id	(Intercept)	0.5032	0.7093

Number of obs: 960, groups: id, 225

	Estimate	Std. Error	z value	Pr(>|z|)	
(Intercept)	1.05E+00	2.34E-01	4.471	7.78E-06	***
Sardinia v Galicia	-1.69E+00	2.77E-01	-6.124	9.11E-10	***
Rest v Feed	-9.22E+00	1.38E+04	-0.001	0.99947	
Social v Feed	6.99E-01	3.42E-01	2.044	0.04095	*
Travel v Feed	-6.37E-01	2.42E-01	-2.629	0.00856	**
Group Size	2.01E-02	8.64E-03	2.325	0.02006	*
Sardinia*Group Size v Galicia*Group Size	2.00E-01	2.35E-02	8.5	< 0.001	***
Rest*Group Size v Feed*Group Size	-2.84E+00	6.45E+03	0	0.99965	
Social*Group Size v Feed*Group Size	-5.97E-02	3.27E-02	-1.825	0.068	.
Travel*Group Size v Feed*Group Size	1.57E-02	1.63E-02	0.96	0.33691	

Significance codes: ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05

Abbreviations: **AIC** = Akaike Information Criterion; **BIC** = Bayesian Information Criterion; **logLik** = Log-likelihood of the fitted model; **df.resid** = Residual degrees of freedom; **Std.Dev.** = Standard deviation of the random effect; **Std. Error** = Standard error of the fixed-effect estimate; **z value** = Standardised test statistic; **Pr(>|z|)** = Probability (p-value) of observing a test statistic equal to or more extreme than the given z-value under the null hypothesis.

The incidence rate ratio (IRR) of each variable level of the final GLMM is shown in Figure 3.5. The strongest effect observed in the model was for the variable Location, with Sardinia showing an IRR of 0.18 ($p < 0.001$), indicating that, on average, the Whistle Rate in Sardinia was only 18% of that recorded in Galicia. This suggests that whistle occurrence was over five times higher in Galicia compared to Sardinia. The final model identified Location ($p < 0.001$), Behaviour ($p < 0.001$), Group Size ($p < 0.01$), and the interaction term Location × Group Size ($p < 0.05$) as having a significant effect on Whistle Rate (Figure 3.5 and Table 3.3 Best GLMM model (negative binomial distribution) of Whistle Rate.).

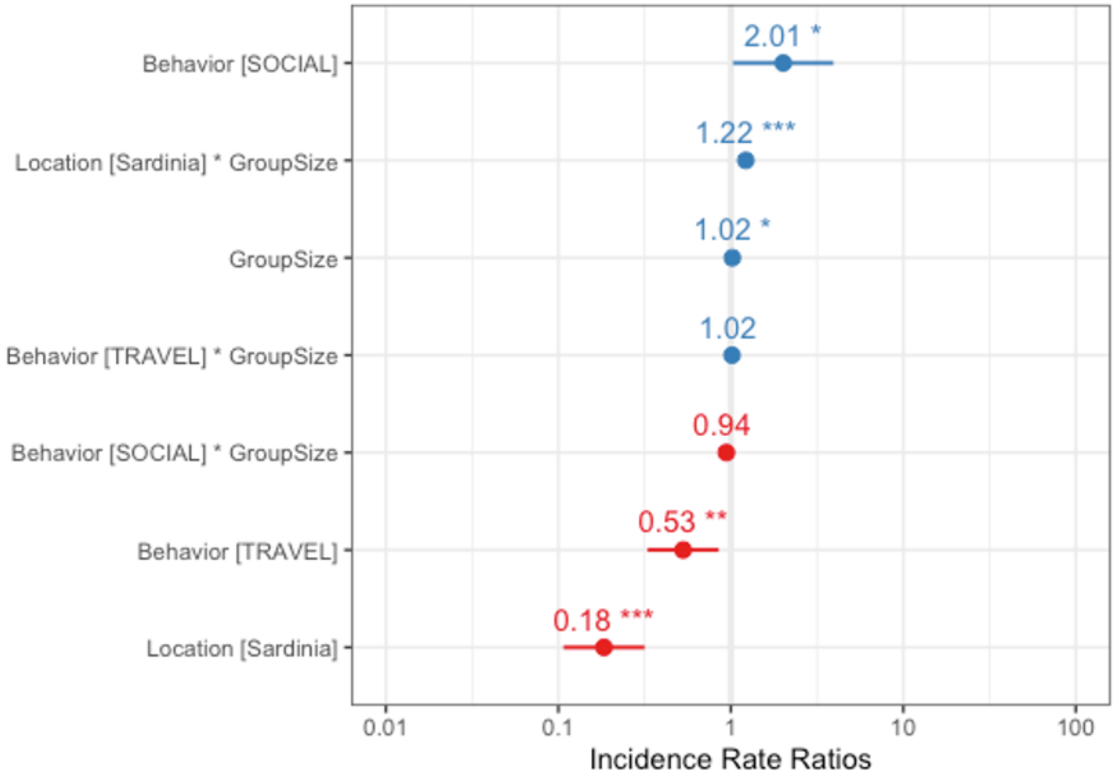


Figure 3.5 Incidence rate ratios (IRR) of the final GLMM model. Significance codes: '*' P < 0.001, '**' P < 0.01, '*' P < 0.05. Blue indicates an IRR value above 1 (positive), and Red indicates an IRR value of less than 1 (negative), indicating whether the level of the variable displayed has a positive or negative effect (respectively) on the response variable when compared to the reference level of each variable. Reproduced with permission from Mosca, Methion and Díaz López, 2025, Copyright 2025, Informa UK Limited, trading as Taylor & Francis Group**

To visualise the effects of the significant predictors in the final model, a set of prediction plots was generated using the sjPlot package (Lüdecke, 2023). These figures illustrate the relationship between each significant variable and the predicted Whistle Rate. Predicted Whistle Rate was found to differ significantly between the two study locations, with higher values observed in Galicia compared to Sardinia ($p < 0.001$) (Figure 3.6).

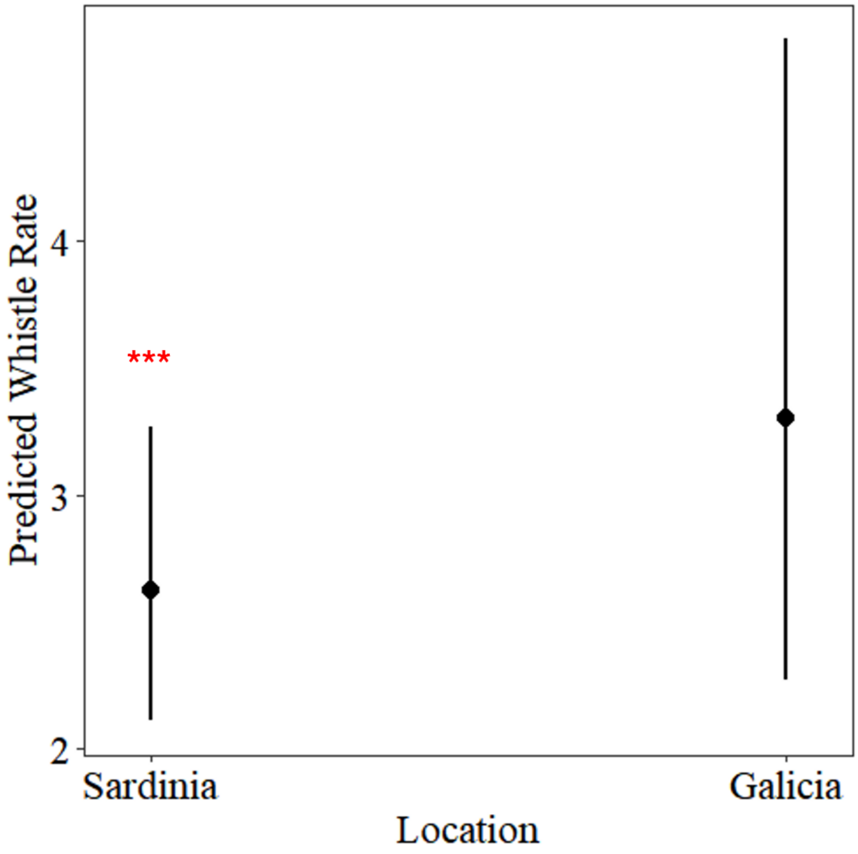


Figure 3.6 GLMM Model prediction for the significant term 'Location'. Significance codes: ***p < 0.001 Reproduced with permission from Mosca, Methion and Díaz López, 2025, Copyright 2025, Informa UK Limited, trading as Taylor & Francis Group

When examining the effect of behavioural state, Whistle Rate was highest during social interactions, followed by feeding and travelling. Statistical comparisons showed that social behaviour was associated with significantly higher rates than both feeding ($p < 0.05$) and travelling ($p < 0.01$), while travelling also resulted in significantly lower Whistle Rates than feeding ($p < 0.01$). No whistles were recorded during resting behaviour. These patterns are illustrated in the behaviour-specific predictions (Figure 3.7).

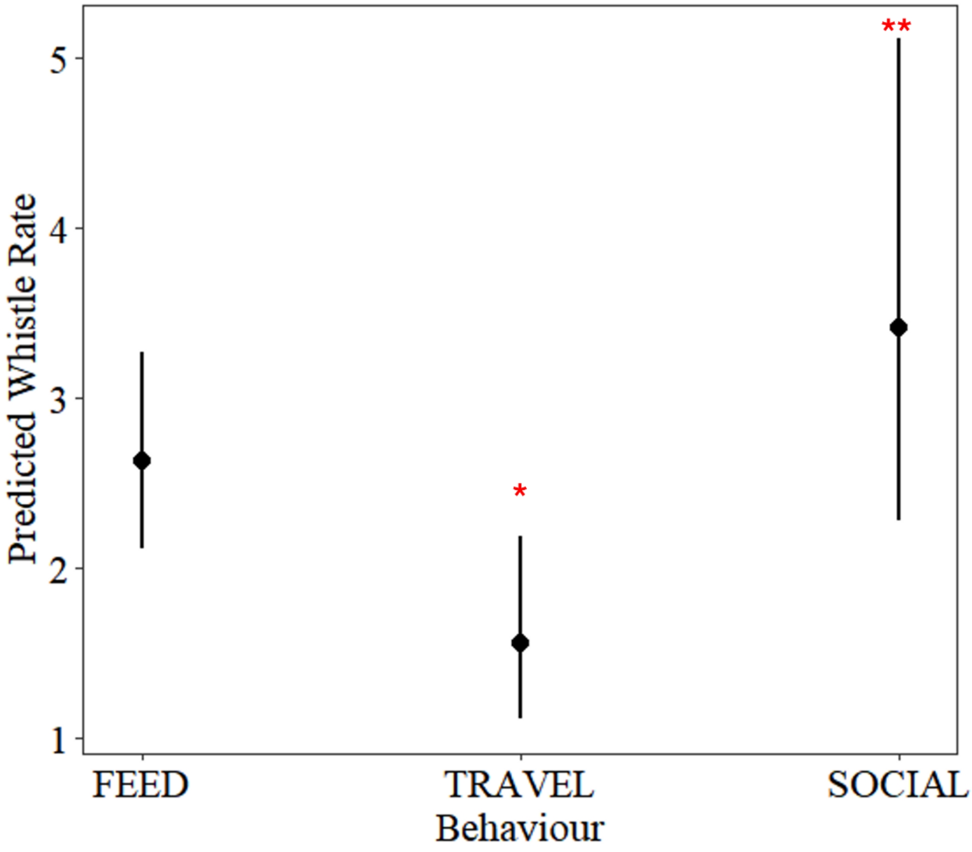


Figure 3.7 GLMM Model prediction for the significant term 'Behaviour'. Significance codes: *p < 0.05, **p < 0.01. Reproduced with permission from Mosca, Methion and Díaz López, 2025, Copyright 2025, Informa UK Limited, trading as Taylor & Francis Group

Whistle Rate increased with Group Size, and this effect was statistically significant across the dataset ($p < 0.05$) (Figure 3.5, Table 3.3). The interaction between Location and Group Size was also significant ($p < 0.001$), suggesting that the influence of group size on whistle production varied between Sardinia and Galicia. To better illustrate this relationship, the interaction term is presented in the prediction plots, which show that Whistle Rate rose with increasing group size in both regions, but more steeply in Sardinia (Figure 3.8). Each plot displays predicted values up to the maximum group size observed in that specific location (20 in Sardinia and 60 in Galicia), in order to avoid over-extrapolation beyond the available data. Extending the x-axis to a shared maximum across locations would have resulted in disproportionately large and uncertain predictions for Sardinia, as reflected by increasingly wide confidence intervals at larger group sizes.

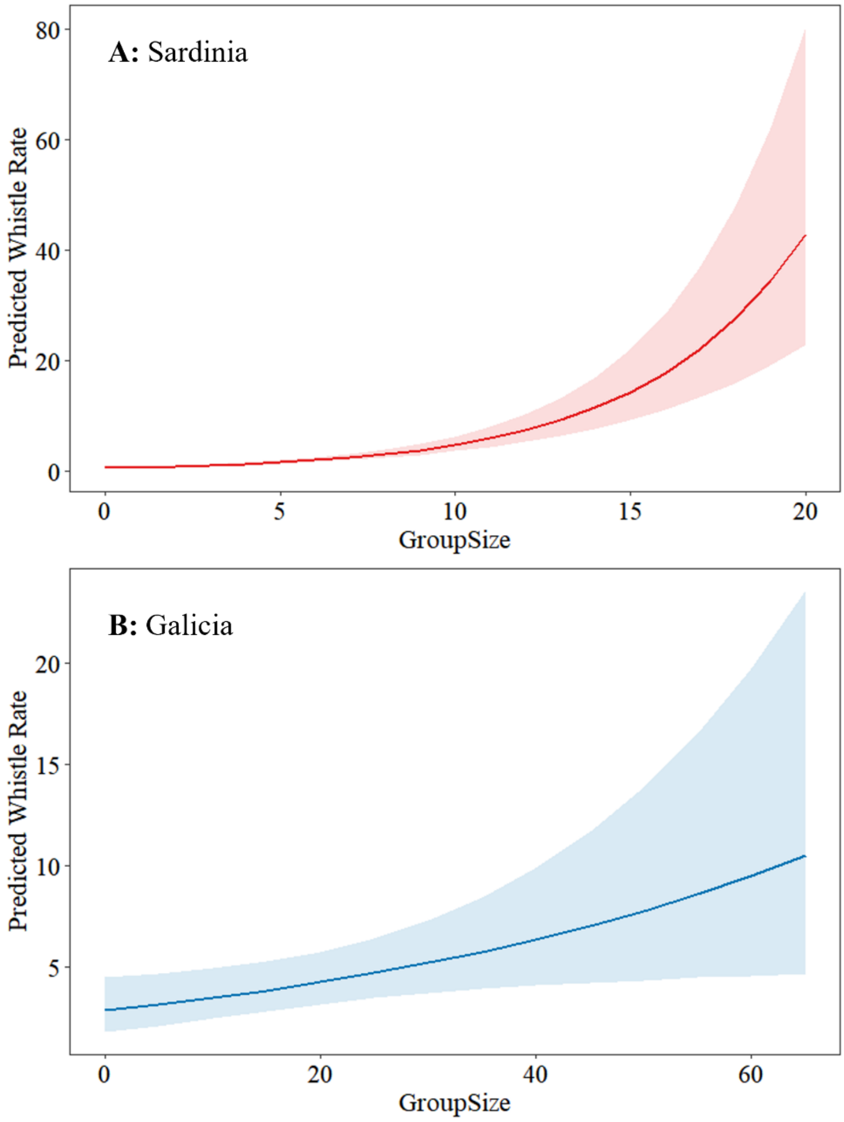


Figure 3.8 GLMM Model prediction for the significant terms 'group size' and 'Location × Group size'. A (top) is the predicted increase of whistle rate with group size in Sardinia. B (bottom) is the predicted increase of whistle rate with group size in Galicia. Reproduced with permission from Mosca, Methion and Díaz López, 2025, Copyright 2025, Informa UK Limited, trading as Taylor & Francis Group

3.2 SIGNATURE WHISTLE PRODUCTION

Signature whistles were detected in 108 of the 1119 acoustic samples analysed, corresponding to 9.65% of the total dataset. The relative occurrence of signature whistles across the two study locations is illustrated in Figure 3.9.

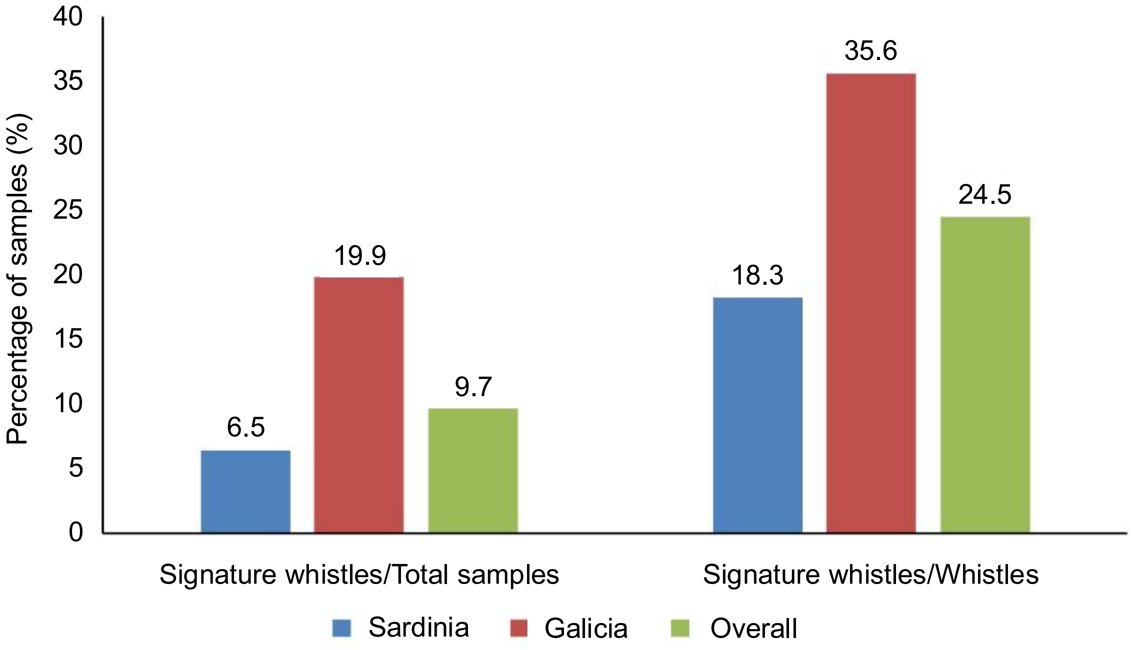


Figure 3.9 Signature Whistle presence in the analysed recording samples. Left: Percentage of overall samples with signature whistles (over the total number of samples analysed). Right: Percentage of whistle samples with signature whistle presence (over samples with presence of whistles). Reproduced with permission from Mosca, Methion and Díaz López, 2026, Copyright 2026 Springer Nature

The resulting GLMM model (best fitting, final model after selection process) had a lower AIC value than the initial model, with a Δ AIC of 8.3, indicating an improved fit (Table 3.4). This model retained the following explanatory variables: Location, Behaviour, Group size, and the interaction term: Location × Group size. Diagnostic checks based on residual simulations did not reveal any systematic deviations or violations of model assumptions (Figure A-IV. 3 and Figure A-IV. 4 in Annex IV). Results from this model showed that the probability of detecting signature whistles was significantly influenced by Location ($p = 0.001$), Group size ($p = 0.028$), and the interaction term Location × Group size ($p < 0.001$) (Table 3.4).

Table 3.4. Summary of the best-fitting (most parsimonious) binomial Generalised Linear Mixed Model (GLMM) assessing the effects of location, behaviour, and group size (and their interaction) on the probability of signature whistle presence. The model includes Group ID as a random intercept to account for repeated observations of the same group. Family = binomial (logit link). Reproduced with permission from Supplementary materials: Mosca, Methion and Díaz López, 2026, Copyright 2026 Springer Nature

AIC	BIC	logLik	deviance	df.resid	
512.8	551.7	-248.4	496.8	952	
Random effects:					
Conditional model:					
Groups	**Name**	**Variance**	**Std.Dev.**		
id	(Intercept)	2.121	1.456		
Number of obs: 960, groups: id, 225					
Conditional model					
	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**	
(Intercept)	-2.540	0.575	-4.418	9.98E-06	***
Sardinia vs. Galicia	-2.214	0.691	-3.206	0.001	**
Rest vs. Feed	-19.409	5647.270	-0.003	0.997	
Social vs. Feed	0.564	0.481	1.171	0.241	
Travel vs. Feed	-0.712	0.425	-1.677	0.094	.
Group Size	0.0441	0.020	2.200	0.0278	*
Sardinia*GS vs. Galicia*GS	0.208	0.061	3.413	0.001	***

Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Abbreviations: **AIC** = Akaike Information Criterion; **BIC** = Bayesian Information Criterion; **logLik** = Log-likelihood of the fitted model; **df.resid** = Residual degrees of freedom; **Std.Dev.** = Standard deviation of the random effect; **Std. Error** = Standard error of the fixed-effect estimate; **z value** = Standardised test statistic; **Pr(>|z|)** = Probability (p-value) of observing a test statistic equal to or more extreme than the given z-value under the null hypothesis.

The variable “Behaviour” was retained in the final model, and further examination using a reparameterised version to allow for pairwise comparisons among behavioural categories revealed a significant difference between Social and Travel behaviours ($p = 0.025$; Table 3.5). Specifically, signature whistles were more likely to be present during social interactions than during travelling.

Table 3.5 Summary of the reparametrised binomial GLMM, identical to the model in Table 3.4, but using “Travel” as the reference level for the categorical variable Behaviour (instead of the default alphabetical level “Feed”). This reparameterisation was used to enable pairwise comparison between Social and Travel behavioural states (shaded blue). Family = binomial (logit link). Reproduced with permission from Supplementary materials: Mosca, Methion and Díaz López, 2026, Copyright 2026 Springer Nature

AIC	BIC	logLik	deviance	df.resid	
512.8	551.7	-248.4	496.8	952	
Random effects:					
Conditional model:					
Groups	**Name**	**Variance**	**Std.Dev.**		
id	(Intercept)	2.121	1.456		
Number of obs: 960, groups: id, 225					
Conditional model					
	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**	
(Intercept)	-3.25242	0.65085	-4.997	5.82E-07	***
Sardinia vs Galicia	-2.21392	0.69063	-3.206	0.001348	**
Feed vs Tavel	0.7121	0.42457	1.677	0.093502	.
Rest vs Travel	-19.2348	7391.544	-0.003	0.997924	
Social vs Travel	1.27565	0.56817	2.245	0.024755	*
Group size	0.04411	0.02005	2.2	0.027798	*
Location*Group size Sardinia vs Galicia	0.20753	0.0608	3.413	0.000642	***
Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1					

Abbreviations: **AIC** = Akaike Information Criterion; **BIC** = Bayesian Information Criterion; **logLik** = Log-likelihood of the fitted model; **df.resid** = Residual degrees of freedom; **Std.Dev.** = Standard deviation of the random effect; **Std. Error** = Standard error of the fixed-effect estimate; **z value** = Standardised test statistic; **Pr(>|z|)** = Probability (p-value) of observing a test statistic equal to or more extreme than the given z-value under the null hypothesis.

Effect size estimates expressed as log-odds ratios are presented in Figure 3.10. The contrast between Sardinia and Galicia yielded a log-odds estimate of −2.214, corresponding to an odds ratio of approximately 0.11 ($e^{-2.214} \approx 0.11$). This indicates that the odds of signature whistle occurrence in Sardinia were about 89% lower than in Galicia, or conversely, that signature whistles were approximately nine times more likely to be detected in Galicia. Group size had a positive effect on signature whistle presence, with a log-odds estimate of 0.0441, equivalent to an odds ratio of 1.045 ($e^{0.0441} \approx 1.045$), indicating an increase of approximately 4.5% in the odds of signature whistle presence with each additional individual in the group.

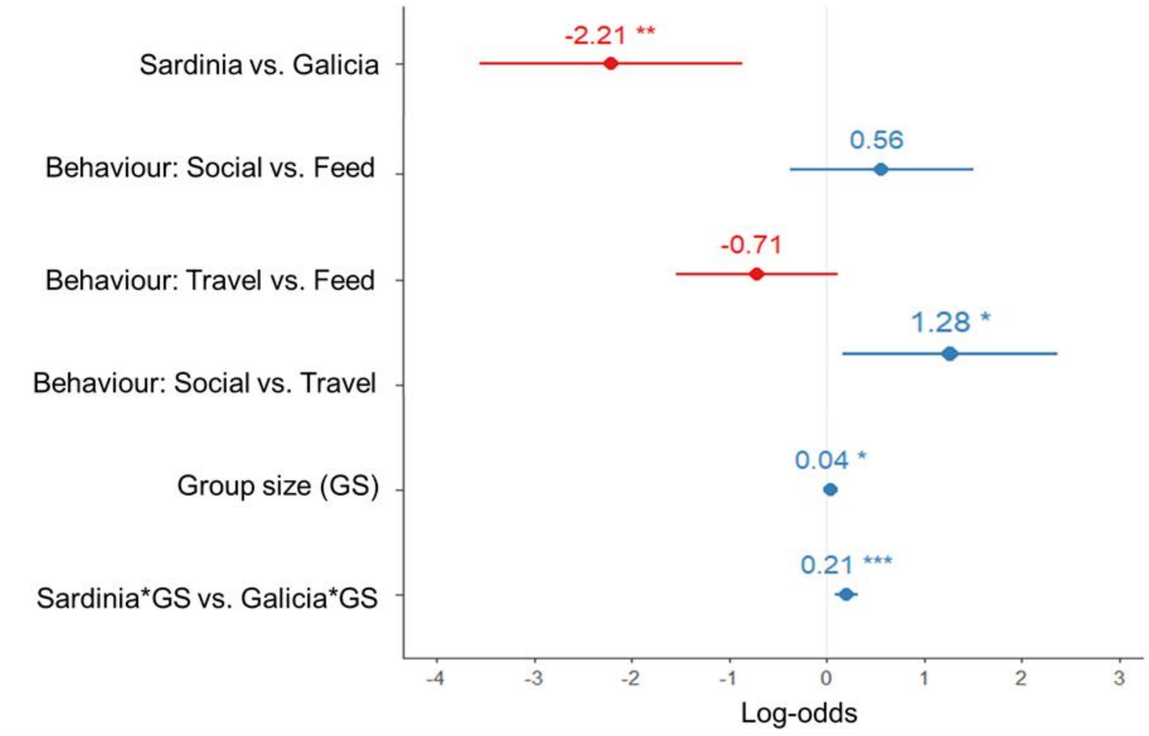


Figure 3.10 Log Odds for the Final GLMM Model. GS (Group Size). Blue indicates positive values, and Red indicates negative values, reflecting the change in log-odds of signature whistle presence for a one-unit increase in each predictor variable, holding all other variables constant. Significance codes : '*' P < 0.001, '**' P < 0.01, '*' P < 0.05. Reproduced with permission from Mosca, Methion and Díaz López, 2026, Copyright 2026 Springer Nature**

The interaction between Location and Group size was also significant (log-odds = 0.208; $p < 0.001$), corresponding to an odds ratio of 1.23 ($e^{0.208} \approx 1.23$). This interaction indicates that the effect of increasing group size on the probability of signature whistle presence was stronger in Sardinia than in Galicia, with each additional dolphin in Sardinia increasing the odds by a further 23% relative to Galicia. Predicted probabilities derived from this interaction illustrate that, although signature whistle presence increased with group size in both locations, the rate of increase was steeper in Sardinia (Figure 3.11). To further examine this pattern, separate GLMMs were fitted for each study area using Group size as the sole predictor. Comparison of the resulting slopes confirmed a significantly stronger relationship between group size and signature whistle presence in Sardinia compared to Galicia ($z = -3.41$, $p < 0.001$). This difference was also reflected in the variance explained by the models, with marginal and conditional R^2 values of 0.148 and 0.578 for Galicia, and 0.091 and 0.527 for Sardinia, respectively.

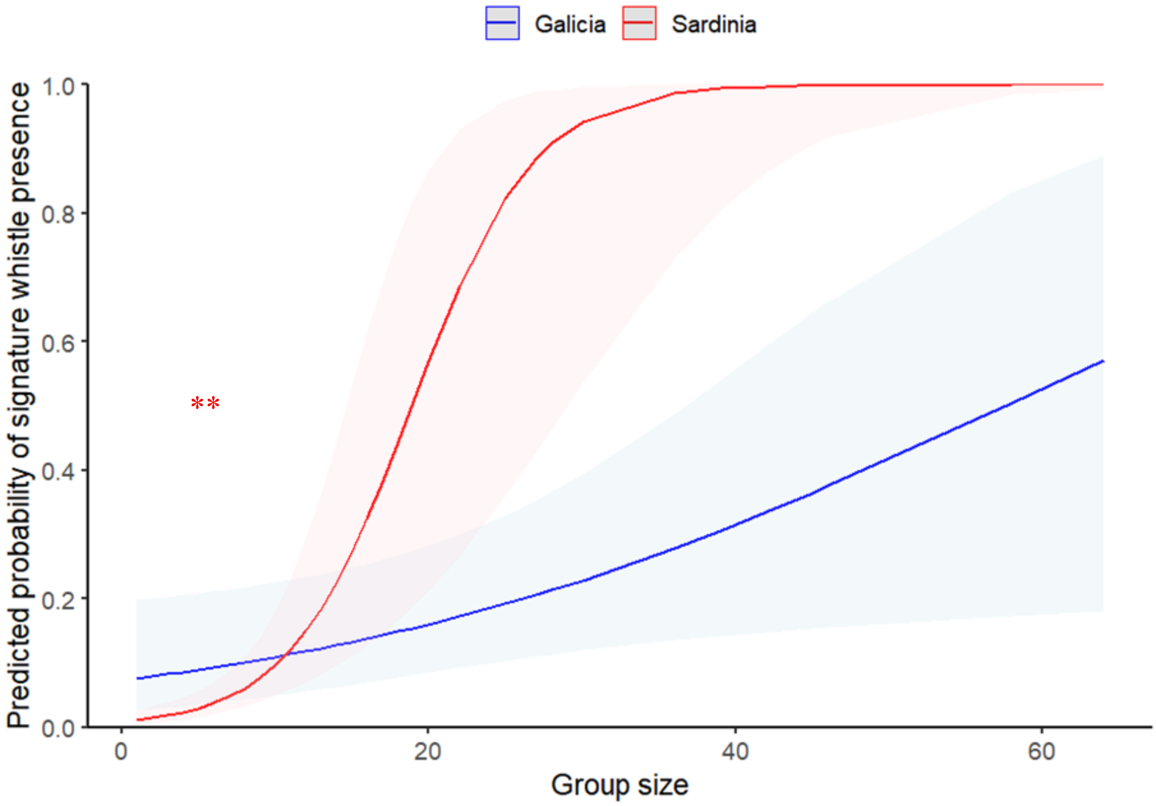


Figure 3.11 Predicted probability of signature whistle presence in relation to group size for the two study locations, illustrating the "Location × Group size" interaction term from the final (best-fitting) binomial Generalised Linear Mixed Model (GLMM). The red line represents Sardinia and the blue line represents Galicia, with shaded areas indicating 95% confidence intervals

3.3 ECOLOGICAL APPLICATION: FPAM

In total, there were 22,242 h of available acoustic data (over 330,000 acoustic files) collected between 28/07/2017 and 04/02/2022. Of those, 1237 h had dolphin whistle detections, representing 5.56% of the dataset. Whistle detections during daylight hours comprised 5.87% of the samples, and 5.24% of the detections occurred at night. Dolphin acoustic presence varied seasonally from 2.81% of samples in Autumn (October-December), to 7.52% of samples in Spring (April-June) (Figure 3.12).

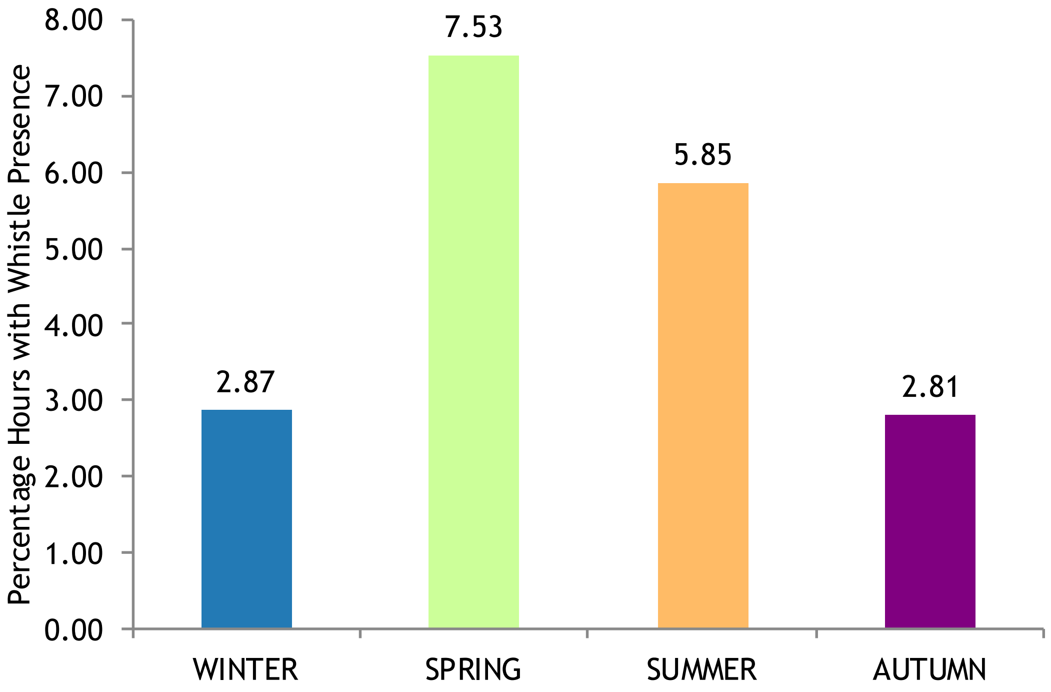


Figure 3.12 Proportion of hourly samples containing dolphin whistles, grouped by season

Representative variables from each variable group were plotted across time (Figure 3.13). These plots highlight the seasonal dynamics of the study area and identify temporal gaps in the dataset.

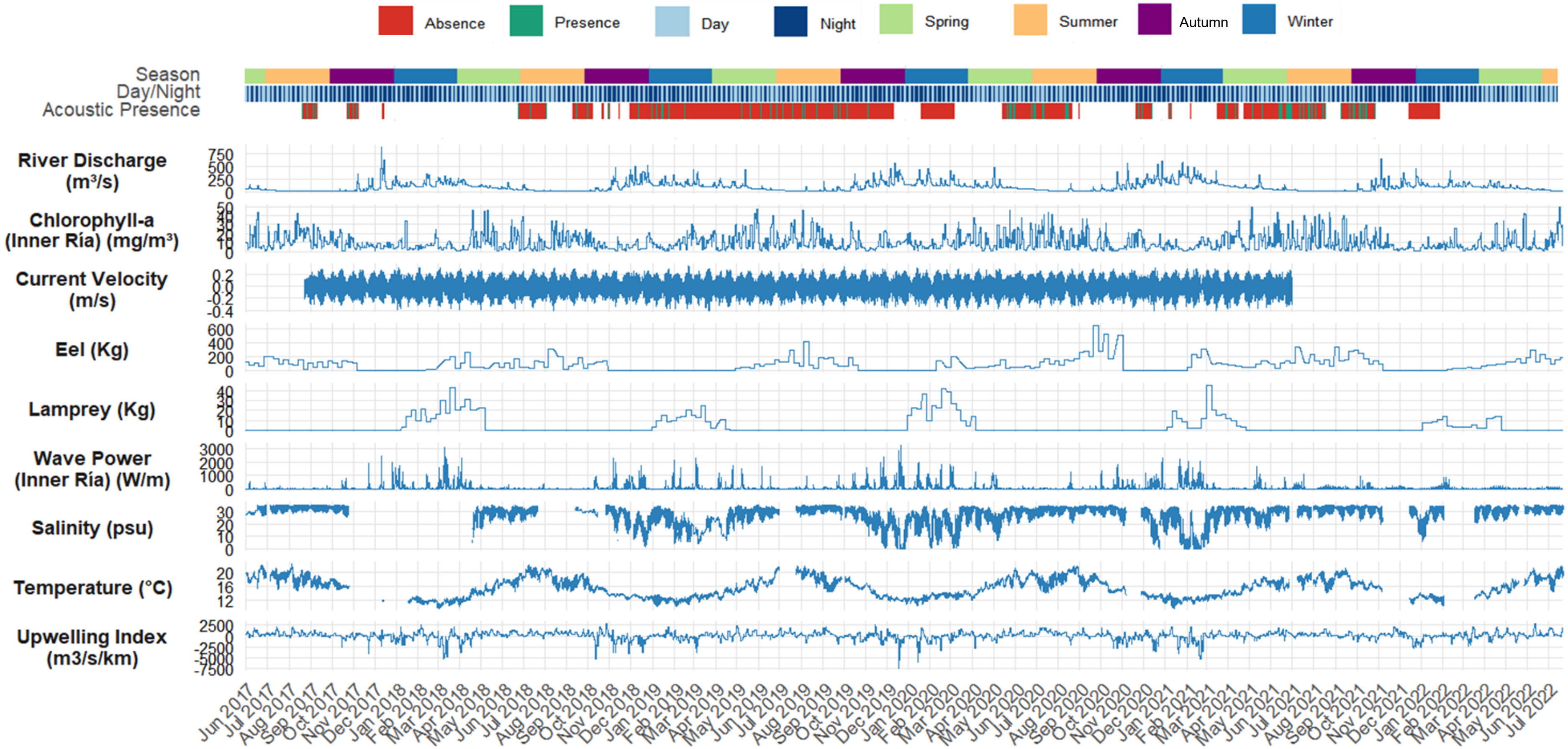


Figure 3.13 Temporal distribution of explanatory variables across the study period. Representative variables from each group are plotted to show seasonal variability and data gaps

After aggregating the dataset into three-hour sampling blocks, 7424 samples were available for modelling, with 1013 blocks (13.6%) containing at least one dolphin whistle detection. A total of 4207 candidate models were tested using a dredge approach. Based on AICc scores, the top 10 models are shown in Table 3.6.

The top-ranked GAM model (Model 1988) included the following predictors: Season, Sea Surface Salinity, Bottom Temperature, Wave Power Inner Ría (Max), Upwelling Index >500 (15 Days Prior), Chlorophyll-a Concentration Inner (30 Days Prior), Eel landings, and Lamprey landings. This model had an AIC of 3447.2, an AICc of 3467.8, and explained 7.67% of the deviance (Table 3.6).

The second-ranked model (Model 2037) included the same predictors as Model 1988, as well as Current Velocity and River Discharge, with an AIC of 3439.9, an AICc 3468.4, and explained 8.33% of the deviance.

Since both models were within ΔAICc < 2, they were averaged for final inference.

Table 3.6 Top 10 models from the model dredge selection procedure, showing the explanatory variables included and sorted by ΔAICc. Models shaded in green indicate those with ΔAICc < 2 that were subsequently averaged

Rank	Model	Day	Season	SSS	BT	WP	UI_500_15	Chl_30	C	RD	Eel	Lamprey	AIC	Dev. Explained	AICc	Δi	wi
1	**1988**		✓	✓	✓	✓	✓	✓	✓		✓	✓	**3447.2**	**0.0767**	**3467.77**	**0.00**	**0.4558**
2	**2037**		✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	**3439.9**	**0.0833**	**3468.37**	**0.60**	**0.3381**
3	2047	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	3441.5	0.0834	3469.93	2.16	0.1547
4	1985		✓	✓	✓	✓	✓	✓	✓	✓		✓	3443.1	0.0814	3474.04	6.27	0.0198
5	1981			✓	✓	✓	✓	✓	✓	✓	✓	✓	3437.9	0.0823	3475.55	7.78	0.0093
6	2039	✓	✓	✓	✓	✓	✓	✓	✓	✓		✓	3444.6	0.0815	3475.65	7.88	0.0089
7	2036	✓		✓	✓	✓	✓	✓	✓	✓	✓	✓	3439.6	0.0824	3476.18	8.41	0.0068
8	1817			✓	✓	✓	✓	✓	✓	✓		✓	3437.5	0.0854	3476.97	9.20	0.0046
9	1984	✓		✓	✓	✓	✓	✓	✓	✓		✓	3439.2	0.0855	3478.67	10.90	0.0020
10	1816			✓	✓	✓	✓	✓	✓	✓	✓		3447.0	0.0777	3485.22	17.45	0.00007

Abbreviations: **SSS:** Sea Surface Salinity, **BT:** Bottom Temperature, **WP:** Wave Power Inner Ría (Max), **UI_500_15:** Upwelling Index >500 (15 Days Prior), **Chl_30:** Chlorophyll-a concentration Inner (30 Days Prior), **C:** Current Speed, **RD:** River Discharge. **AIC:** Akaike Information Criterion, **Dev. Explained:** Deviance Explained**, AICc**= Akaike Information Criterion corrected for small sample size, **Δi**= difference in AICc between each model and the first-ranked model, **wi**= Akaike weight providing the relative support of each model compared to the others.

Across the averaged model set, most variables were retained consistently, with relative variable importance (RVI) = 1 for Bottom Temperature, Wave Power Inner Ría (Max), Upwelling Index >500 (15 Days Prior), Chlorophyll-a Concentration Inner (30 Days Prior), and Lamprey landings, indicating their contribution to dolphin acoustic presence in both top averaged models. The Eel landings variable had lower support (RVI = 0.43), as it was only included in one of the top two models (Table 3.7).

Significant predictors of dolphin acoustic presence included Season (Summer vs. Autumn), Bottom Temperature, Wave Power Inner Ría (Max), Upwelling Index >500 (15 Days Prior), Chlorophyll-a Concentration Inner (30 Days Prior), Eel, and Lamprey, with Lamprey landings showing a significant effect across all degrees of freedom (Table 3.7). In contrast, Sea Surface Salinity, Current Speed, and River Discharge did not show significant effects (Table 3.7). The Day/Night variable was not included in either of the top two models, indicating it is not an important predictor of dolphin acoustic presence in this dataset.

Table 3.7 Coefficients of the averaged Generalised Additive Models (GAMs) showing the effects of explanatory variables on bottlenose dolphin acoustic presence. Superscripts represent smooth splines for each degree of freedom

Term	Estimate	Std. Error	Adjusted SE	z value	Pr(>z)		RVI
(Intercept)	-2.09	0.16	0.16	12.74	<2e-16	***	
Spring	0.14	0.20	0.20	0.69	0.49		
Summer	-0.60	0.24	0.24	2.53	0.01	*	1
Winter	-0.09	0.36	0.36	0.25	0.81		
SSS^1	-0.01	0.07	0.07	0.18	0.86		1
SSS^2	0.07	0.15	0.15	0.46	0.65		
SSS^3	-0.22	0.30	0.30	0.73	0.46		
SSS^4	0.06	0.11	0.11	0.58	0.56		
BT ^{1}	0.56	0.22	0.22	2.53	0.01	*	1
BT ^{2}	-0.46	0.40	0.40	1.17	0.24		
BT ^{3}	-0.94	0.65	0.65	1.44	0.15		
BT ^{4}	-0.25	0.23	0.23	1.11	0.27		
WP ^{1}	0.00	0.00	0.00	0.01	1.00		1
WP ^{2}	0.00	0.01	0.01	0.00	1.00		
WP ^{3}	0.00	0.02	0.02	0.00	1.00		
WP ^{4}	-0.34	0.09	0.09	3.64	0.00	***	
UI_500_15^1	-0.26	0.09	0.09	2.73	0.01	**	1
UI_500_15^2	-0.31	0.37	0.37	0.82	0.41		
UI_500_15^3	0.71	0.69	0.69	1.03	0.31		
UI_500_15^4	0.05	0.17	0.17	0.29	0.77		
Chl_30^1	-0.01	0.22	0.22	0.06	0.96		1
Chl_30^2	1.09	0.40	0.40	2.70	0.01	**	
Chl_30^3	-1.81	0.72	0.72	2.52	0.01	*	
Chl_30^4	0.16	0.22	0.22	0.72	0.47		
C^1	-0.18	0.18	0.18	1.01	0.32		0.43
C^2	0.26	0.27	0.27	0.97	0.33		
C^3	0.68	0.48	0.48	1.43	0.15		
C^4	0.20	0.17	0.17	1.16	0.25		
Eel^1	-0.01	0.03	0.03	0.25	0.80		1
Eel^2	-0.01	0.05	0.05	0.26	0.79		
Eel^3	0.06	0.15	0.15	0.37	0.71		
Eel^4	0.13	0.06	0.06	2.06	0.04	*	
Lamprey^1	1.69	0.76	0.76	2.21	0.03	*	1
Lamprey^2	-9.79	3.41	3.41	2.87	0.00	**	
Lamprey^3	-10.38	3.86	3.86	2.69	0.01	**	
Lamprey^4	1.16	0.51	0.52	2.26	0.02	*	
RD^1	-0.23	0.35	0.35	0.65	0.52		1
RD^2	0.85	1.24	1.24	0.69	0.49		
RD^3	2.11	2.99	3.00	0.71	0.48		
RD^4	-0.29	0.46	0.46	0.64	0.52		

Abbreviations: **SSS**: Sea Surface Salinity, **BT**: Bottom Temperature, **WP**: Wave Power Inner Ría (Max), **UI_500_15**: Upwelling Index >500 (15 Days Prior), **Chl_30**: Chlorophyll-a concentration Inner (30 Days Prior),

C: Current Speed, **RD**: River Discharge. **Std. Error**: Standard error of the estimated coefficient, **Adjusted SE**: Standard error adjusted for model averaging, **z value**: Test statistic calculated as the ratio of the estimate to its standard error, **Pr(>z)**: Probability value associated with the z statistic (significance level), **RVI**: Relative Variable Importance, calculated as the sum of Akaike weights across all models in which the variable appears.

Partial effects of each continuous predictor are plotted in Figure 3.14. These smooth terms illustrate the non-linear relationships between dolphin acoustic presence and the covariates included in the averaged model.

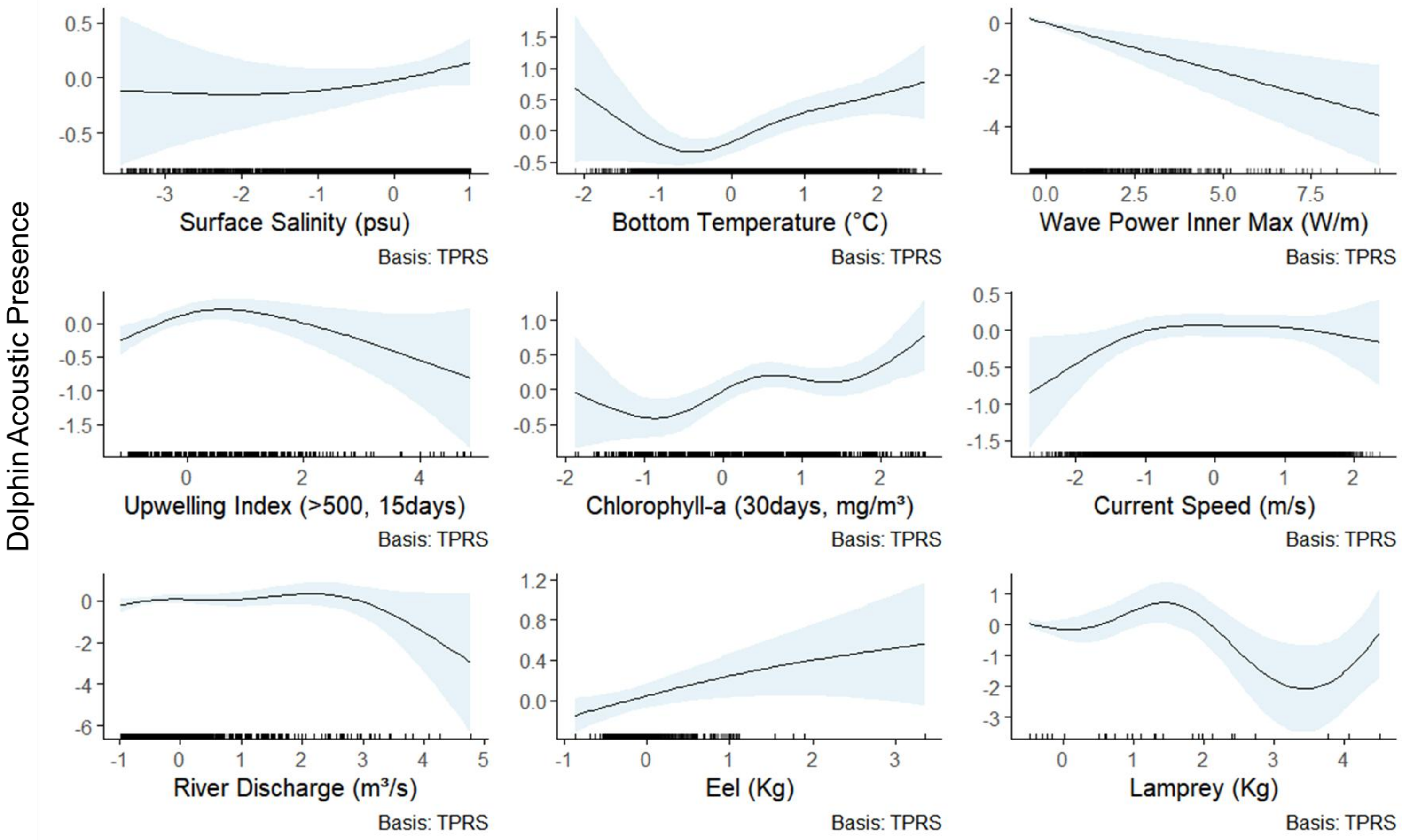


Figure 3.14 Averaged predictions of dolphin whistle presence for each smooth term present in the final GAM model, with 95% confidence intervals (CI)

CHAPTER 4:
GENERAL DISCUSSION

This chapter elaborates on the main thesis findings. It first discusses the results of each objective in turn, before integrating them to highlight the overall relevance of the thesis and its key contributions to behavioural ecology, bioacoustics, and ecological applications. It then considers the implications of these findings for conservation and management and outlines future research avenues that build on both the results and the unique long-term datasets presented here.

4.1 DISCUSSION BY OBJECTIVE

4.1.1 Whistle Rate Determinants

The first objective of this thesis was to investigate the combination of factors that influence whistle production in a highly social and vocally active marine top predator. The use of a generalised linear mixed model (GLMM) approach highlighted how variables such as group size, location, and behaviour work in combination to shape whistle rates, underlining the complex interplay between social structure and environmental context.

Group size emerged as a key predictor of Whistle Rate, and as expected, larger groups of dolphins produced more whistles. On a basic level, this finding is intuitive, as the presence of more individuals in a group would naturally increase the number of animals that could be vocalising at any one time. This pattern is consistent with previous research on the same study species (Jones and Sayigh, 2002; Cook *et al.*, 2004), reinforcing the idea that acoustic output generally scales with group size in bottlenose dolphins. However, beyond this straightforward explanation, whistles also serve important social functions in group cohesion. Bottlenose dolphins use these calls to help maintain group structure and cohesion (Janik and Slater, 1998), not just during reunions, but potentially throughout everyday interactions within established groups. For example, in groups that include dependent calves, whistles may help mothers and calves maintain close contact (Díaz López and Bernal Shirai, 2010). This concept finds parallels in other social species as well. In goats, for example, specific individuals have been observed using calls that prompt the group to stay together (O'Bryan *et al.*, 2019). In this light, the increase in whistle production in larger groups could reflect the higher coordination demands among members. Conversely, smaller groups may rely less on vocal cues since physical proximity and coordination are more easily maintained without the need for continuous acoustic signalling (Cook *et al.*, 2004).

Understanding why group sizes vary in the first place requires examining the ecological and social context of each population. Group size in bottlenose dolphins is influenced by both environmental conditions and social dynamics, which vary depending on the location (Connor *et al.*, 2000). The two populations examined in this research offer a clear example of such variation. Average group sizes in Galicia (10.7 ± SE 0.3; Methion *et al.*, 2023) are larger than those recorded in Sardinia (3.51 ± SE 0.1; Díaz López, 2012, 2019). These differences can be linked to habitat conditions: the oligotrophic waters around Sardinia are less nutrient-rich and support patchy prey distributions, which may limit group sizes (Lochet and Leveau, 1990). In contrast, the Galician rías benefit from freshwater inflow and seasonal coastal upwelling events (Gonzalez-Nuevo, Gago and Cabanas, 2014; Giralt Paradell *et al.*, 2020), creating an environment with higher prey availability (Methion and Díaz López, 2019). This productivity allows dolphins to form and maintain larger groups, potentially encouraging cooperative strategies such as coordinated hunting or reduced individual foraging effort (Gowans, Würsig and Karczmarski, 2007). Recent research conducted in the Galicia study area confirms that dolphin group sizes are shaped by a combination of environmental and social drivers, from chlorophyll-a concentration and dissolved oxygen levels to the presence of dependent calves (Methion *et al.*, 2023). Such environmental differences between the two sites not only influence group size but likely contribute to the differences in Whistle Rate observed across locations.

Larger groups in Galicia, made possible by richer prey fields, exhibited higher Whistle Rates. Furthermore, water quality could play a role in communication strategies. Nutrient-rich waters may also be more turbid, potentially making visual cues less effective and increasing reliance on acoustic signals (Zelick, Mann and Popper, 1999). Although turbidity was not directly measured in this study, its potential role in shaping communication warrants further exploration.

The interaction between location and group size further illustrates how context modifies communication patterns. The model showed that the relationship between Whistle Rate and group size was steeper in Sardinia than in Galicia. This finding is reminiscent of findings from previous studies (Jones and Sayigh, 2002; Quick and Janik, 2008) that noted that whistle production increases with group size up to a point, after which it begins to plateau. Such patterns are thought to reflect strategies to avoid acoustic interference, or "signal masking," which occurs when a signal fails to reach a receiver because it is overlapped by other sounds (Krause, 1993). Masking can be caused by other animals, environmental noise, or anthropogenic sources, and individuals must keep their signals within available temporal and frequency niches to communicate effectively. Dolphins may address this by increasing repetition rates or reducing signal complexity, for example, by simplifying modulation patterns to prioritise essential information, or by reducing the overall number of whistles (Krause, 1993; Branstetter and Sills, 2022). In Galicia, where average group sizes, on average, exceed 10 individuals, dolphins may regularly employ such masking-reduction strategies, leading to the more gradual increase in whistle production observed in the model. In Sardinia, by contrast, groups are generally smaller, and these strategies may be less frequently needed, resulting in a sharper rise in whistle rate as group size increases. This pattern reinforces the idea that social structure, shaped by ecological conditions, influences both the use and modulation of acoustic signals within dolphin populations.

Beyond group size and location, this analysis also highlights that Whistle Rate varied significantly depending on group behaviour. This is consistent with findings in other cetacean research (Cook *et al.*, 2004; Quick and Janik, 2008; Díaz López and Bernal Shirai, 2010; Hawkins and Gartside, 2010), and with communication patterns observed in a wide range of other taxa (Rendall, Cheney and Seyfarth, 2000; Amorim *et al.*, 2006; Lehmann *et al.*, 2022). Within the data processed in this thesis, whistles were most frequent during social interactions, followed by feeding, travelling, and no whistles were recorded during resting behaviour. These patterns align with the idea that acoustic communication is influenced by behavioural context, especially levels of social engagement and emotional arousal. Resting behaviour, being low in activity and interaction, is generally associated with minimal need for vocal communication, a pattern also seen in other species like gorillas, where vocal output increases as groups transition out of rest periods (Harcourt and Stewart, 1994). While travelling, dolphins tend to maintain a consistent direction and tight group formation, likely using visual or tactile cues for coordination. Whistles in this context may serve a more basic coordination role, which could explain the relatively low vocal output observed (Cook *et al.*, 2004; Quick and Janik, 2008; Hawkins and Gartside, 2010). Feeding, on the other hand, involves increased excitement and may include cooperative behaviours or food-associated calls (Acevedo-Gutiérrez and Stienessen, 2004). These calls could help dolphins coordinate their foraging efforts, similar to how other cooperative hunters or food-calling species communicate (Brown, Brown and Shaffer, 1991). Social behaviour encompasses a wide range of interactions, from affiliative contact to competition, mating, and aggression, and it showed the highest levels of whistle production within this study. This is in line with research in other taxa where vocalisations mediate complex social behaviours, such as dominance (e.g. in bats: Gadziola *et al.*, 2012), reproductive signalling (e.g. in fish: Schärer *et al.*, 2012), and courtship (e.g. in mice: Marconi *et al.*, 2020). The strong association between social interaction and increased vocal output is a recurring theme across many species (May-Collado, Agnarsson and Wartzok, 2007; Leighton and Birmingham, 2021), and bottlenose dolphins are no exception.

Interestingly, the temporal variable "season" did not emerge as a significant predictor of Whistle Rate in the final model. This outcome is consistent with recent findings from the same Sardinian population, where no seasonal differences were observed in whistle exchange between dolphin dyads. However, that study did report clear seasonal variation in the use of other vocalisations, particularly burst-pulsed sounds, which were strongly associated with the mating season and dyad composition (Díaz López, 2022). These results suggest that while whistle production may remain relatively stable across seasons, other vocal signal types are more sensitive to seasonal social dynamics. Nonetheless, seasonality may still influence whistle use in more indirect ways. For instance, shifts in behaviour such as increased socialising or feeding, both of which were associated with higher Whistle Rates in this study, can follow seasonal patterns. Reproductive cycles, such as calving periods, are also seasonal and known to affect vocal behaviour in mother–calf pairs (Smolker, Mann and Smuts, 1993; Fripp and Tyack, 2008; Smith *et al.*, 2016). In addition, environmental changes that occur throughout the year, such as fluctuations in prey availability or energetic demands, may impact activity levels and thereby influence acoustic output (Gillooly and Ophir, 2010; McCluskey, Bejder and Loneragan, 2016). Previous studies have found seasonal variation in whistle production linked to such factors. For example, Hernandez and colleagues (2010) reported changes in whistle use corresponding to seasonal shifts in behaviour, while Tellechea (2014) identified associations of whistle-use seasonality with sea surface temperature. These findings suggest that although season, when defined in broad calendar terms, may not directly predict Whistle Rate, the ecological and social changes that occur seasonally can still shape vocal behaviour in more complex ways.

Looking ahead, future studies could build on this foundation by incorporating more individual-level variables, including sex, age, identity, social network position, and personality (Díaz López, 2020). Such detailed investigations may uncover more about the rich communicative landscape of this highly vocal species.

4.1.2 Signature Whistle Production

The second objective of this work was to build upon the previous knowledge acquired and delve into the contextual use of dolphin individually-specific signature whistles, providing new insights into how social, behavioural, and ecological factors shape their production in wild populations. This analysis shows that the probability of signature whistle production varies with group size, behaviour, and habitat context. The results of this analysis show that the occurrence of signature whistles varies across social and ecological contexts as a function of group size, behaviour, and location. In particular, the relationship between group size and the probability of detecting signature whistles differed between the two study areas, indicating that local environmental and social conditions influence how dolphins deploy individually distinctive vocal signals to maintain cohesion. In addition, signature whistles were more frequently detected during social interactions than during travelling, underscoring their role in communication and coordination during periods of heightened social engagement.

The binomial GLMM results demonstrate that signature whistle presence is shaped by interacting social and ecological factors rather than by single predictors only. The most parsimonious model retained group size, location, and their interaction as significant effects, indicating that the influence of increasing group size on signature whistle production differs between study areas. Predicted probability curves revealed a positive association between group size and signature whistle occurrence in both regions, although this increase was steeper in Sardinia than in Galicia, with the two curves converging at approximately ten individuals. This pattern suggests that dolphins adjust their use of identity signals in response to the ecological characteristics of their habitat, consistent with the Acoustic Adaptation Hypothesis, which proposes that communication strategies evolve in relation to local environmental constraints (Ey and Fischer, 2009; La Manna *et al.*, 2022). The contrast between the productive, dynamic coastal systems of Galicia (Figueiras, Labarta and Fernández Reiriz, 2002) and the comparatively oligotrophic Mediterranean environment of Sardinia (Lochet and Leveau, 1990) provides a plausible ecological framework for these differences in social organisation and communication demands.

As previously described, the populations in the two study areas differ markedly in their typical group sizes, which likely contributes to the observed patterns of signature whistle occurrence. In Galicia, where larger aggregations are common (Methion and Díaz López, 2018; Methion *et al.*, 2023), a greater overall proportion of acoustic samples contained signature whistles. In Sardinia, where large groups are less frequent (Díaz López 2012; 2019), the sharper increase in signature whistle probability with group size may reflect the stronger relative impact of adding individuals to otherwise small social units. In contrast, the more gradual increase observed in Galicia suggests that dolphins in consistently large groups may modulate their vocal output to maintain communication efficiency and reduce the risk of signal overlap. Together, these results indicate that while signature whistle production increases with group size in both populations, the underlying dynamics differ according to local grouping patterns and communication constraints.

The association between group size and signature whistle production can be interpreted through complementary social and spatial perspectives. From a social-structural viewpoint, research in Sardinia has shown that anthropogenic disturbance can reduce social cohesion, leading to less stable and less interconnected groups (Díaz López and Bernal Shirai, 2008; Díaz López, 2019). Under such conditions, the reduced need for maintaining contact with multiple social partners may partly explain the lower overall probability of signature whistle emission. In contrast, the larger and more socially complex groups characteristic of the Galician population (Methion and Díaz López, 2020) are likely to place greater demands on individual recognition and coordination, favouring increased use of individually distinctive vocalisations.

From a spatial and sensory perspective, individuals in smaller groups are more likely to remain in close proximity, potentially reducing reliance on long-range acoustic signals and allowing greater use of alternative recognition cues, including cross-modal signals such as gustatory identification (Watwood *et al.*, 2005; Bruck, Walmsley and Janik, 2022). In larger aggregations, by contrast, acoustic signals may become increasingly important for maintaining cohesion among dispersed group members. Studies of free-ranging bottlenose dolphins have similarly reported higher rates of signature whistle use as group size increases (Cook *et al.*, 2004), supporting the idea that these calls function as contact signals in socially demanding contexts.

Taken together, these findings suggest that elevated signature whistle production in larger groups reflects an increased requirement for maintaining social cohesion. Previous research on both wild and captive dolphins has linked signature whistle use to separation, reunion, and meeting events (Janik and Slater, 1998; Quick and Janik, 2012). In the present study, acoustic data were collected from stable groups without observed fission or fusion events, yet the probability of signature whistle occurrence still rose with group size. This pattern implies that cohesion-related signalling may also be important within stable social units, particularly during socially interactive behaviours. Indeed, behavioural context emerged as a key driver of signature whistle production, with higher probabilities during social interactions than during travelling. Social behaviours encompass a wide range of affiliative and competitive interactions, which likely increase both the need for individual recognition and the frequency of vocal exchanges (Cook *et al.*, 2004). The stereotyped and individually distinctive nature of signature whistles (Sayigh *et al.*, 2022) makes them particularly well suited for facilitating recognition and coordination in such complex group settings. Comparable reliance on individually distinctive vocal signals has been documented across taxa living in socially dense environments (Insley, 1992; Bowmaker-Falconer *et al.*, 2022; Sun *et al.*, 2023), reinforcing the broader relevance of this communication strategy.

Methodological considerations are important when interpreting these results. Signature whistles are often produced in repetitive bouts and may not always be acoustically distinct from non-signature whistles, complicating classification without detailed analytical approaches (Janik and Sayigh, 2013a). This analysis employed the SIGID method (Janik *et al.*, 2012), which is known for its conservative classification criteria and low false-positive rates, although it may exclude a substantial proportion of true signature whistles (Janik *et al.*, 2012; Luís, Couchinho and dos Santos, 2015). The conservative nature of this method, however, is also a strength, as it ensures a robust dataset of confirmed signature whistles, strengthening confidence in the modelled relationships. Furthermore, to avoid inflation of response variables due to repetitive whistle loops, signature whistle counts were deliberately excluded from the analysis, as repeated elements of the same signature whistle could otherwise be treated as independent observations (Jones and Sayigh, 2002), potentially introducing bias to the analysis.

The association between signature whistle occurrence and group size and behaviour has potential applications for passive acoustic monitoring. Because signature whistles encode individual identity, their detection could provide a conservative minimum estimate of the number of dolphins present in an area, even in the absence of visual observations (Fandel, Silva and Bailey, 2024). Developing approaches that use the number of unique signature whistles as a proxy for group size could enhance monitoring efforts in regions where visual surveys are logistically constrained, offering valuable insights under poor weather conditions or during periods when direct observation is not feasible.

4.1.3 Ecological Application: fPAM

The third and final objective of this thesis was to utilise fixed Passive Acoustic Monitoring, and in particular whistle presence, as a way to provide more ecological-based knowledge on dolphins' use of habitat within an urbanised estuary. This analysis represents the first attempt at describing bottlenose dolphin presence within the Ulla estuarine habitat in the Ría de Arousa (Galicia, NW Spain). Dolphin acoustic presence in the Ulla River estuary was indeed confirmed and occurred year-round across the six-year dataset. Additionally, results indicate seasonal variation in acoustic presence, most likely reflecting shifts in prey availability. Although several temporal, environmental, and biological variables were retained in the final model, these covariates are themselves seasonally variable. This suggests that the observed patterns of dolphin presence might not be driven by these factors directly, but rather by the cyclic environmental changes that shape prey availability in the estuary.

Seasonal variation in habitat use has been documented in a number of bottlenose dolphin (*Tursiops* spp.) populations inhabiting estuarine or semi-enclosed systems (Wilson, Thompson and Hammond, 1997; Neumann, 2001; Fury and Harrison, 2011). Within this analysis, season was also a significant predictor, with Autumn showing significantly lower acoustic presence compared to Summer, and acoustic presence peaked in spring and summer periods between the months of April and September. Water temperature emerged as another significant covariate within the final averaged model. Because water temperature follows a seasonal cycle, it is likely to influence dolphin distribution indirectly (Neumann, 2001). In some estuarine systems, very high water temperatures (>28°C) have been shown to directly affect dolphin distribution through adverse effects in the form of thermoregulatory stress (Fury and Harrison, 2011). However, water temperatures in the present study area did not exceed 22°C, making a direct physiological effect unlikely. River discharge also influenced dolphin acoustic presence, which is consistent with findings in Indo-Pacific humpback dolphins, where seasonal rainfall affecting river output caused shifts in dolphin distribution toward more seaward areas during the wet season (Lin, Akamatsu and Chou, 2015). Primary productivity, here represented by chlorophyll-a concentrations, is often linked to dolphin occurrence, as it reflects temperature-driven seasonal changes in prey abundance, affecting dolphin distribution patterns (Zepeda-Borja *et al.*, 2022). Oceanographic variables, such as the upwelling index and wave power, also reflect broad seasonal fluctuations in the study area, rather than directly affecting local dynamics within the estuary itself. The inner ría, where the estuary is located, is highly sheltered and largely unaffected by oceanic processes (Álvarez-Salgado *et al.*, 1996), so upwelling events calculated outside the ría are unlikely to strongly affect conditions within the river mouth. Likewise, the inversely proportional relationship between wave power and dolphin acoustic presence observed in the smooths plot likely reflects the naturally lower wave power observed in spring and summer, when weather conditions are calmer. The relationship between wave power and dolphin presence, however, could be further investigated, as other studies on cetaceans have found a link between swell and dolphin distribution, potentially through altered hydrodynamic mechanisms and prey distribution (Dittmann *et al.*, 2016). When drawing a comparison between methodological approaches carried out in this thesis, and thinking of the relationship between season and whistle production rather than animal distribution, the results from the analysis from Objective 1 indicate that whistle production is not driven by seasons, a result that is also found among dolphin dyads in the Mediterranean study population (Díaz López, 2022). In these studies, the concurrent visual observation allowed for a number of other variables to be considered, such as the group size and behaviour of the dolphins, which are indeed found to be drivers of whistle production (Quick and Janik, 2008; Díaz López and Bernal Shirai, 2010; Mosca, Methion and Díaz López, 2025). By contrast, the fixed PAM approach used in this analysis only recorded acoustic output, meaning that associated group size and behavioural context could not be assessed directly. The previous acoustic knowledge on the local population through behavioural acoustic studies, therefore, provides crucial information for interpreting the results within this final thesis section. In this light, seasonal variation of whistles reported in the estuary through fixed PAM, is likely linked to the behaviour and number of individuals present, factors which themselves vary with seasonal changes in prey availability (Neumann, 2001; Gillooly and Ophir, 2010; McCluskey, Bejder and Loneragan, 2016; Methion *et al.*, 2023), leading to higher levels of activity during feeding and socialising and collaborative strategies requiring communication (Silber, 1986; Acevedo-Gutiérrez and Stienessen, 2004; Díaz López and Bernal Shirai, 2010).

It is an established concept within the study of cetacean habitat modelling that prey availability is the main driver of dolphin distribution (Irvine *et al.*, 1981; Fury and Harrison, 2011). Estuarine habitats often function as important foraging grounds for bottlenose dolphins because their bathymetric features, tidal regimes, and freshwater inputs can concentrate prey (Carmen, Berrow and O'Brien, 2021). The Ría de Arousa is a well-known important foraging area for this species (Methion and Díaz López, 2019), both due to its rich and productive waters driven by seasonal upwelling (Torres and Barton, 2007; Giralt Paradell *et al.*, 2020; Methion *et al.*, 2023), and the high concentration of prey around the widespread aquaculture rafts within the area (Díaz López and Methion, 2017; Methion and Díaz López, 2019). While previous studies on bottlenose dolphin diet in Galician waters provide some information on likely prey species (Santos *et al.*, 2007), these studies are based on stranded individuals (Fernández *et al.*, 2011; Louis *et al.*, 2014) that likely foraged on the continental shelf, outside the rías. These studies are therefore unlikely to accurately represent the diets of estuary-dwelling individuals, as estuarine and offshore populations have been shown to differ in dietary composition and isotopic signatures due to differences in prey base (Olin *et al.*, 2011).

The seasonal variation in estuarine water use by dolphins displayed in this third objective may reflect the opportunistic exploitation of diadromous fish species (fish that migrate between freshwater and marine environments during different phases of their life cycle). Several such species, including the sea lamprey (*Petromyzon marinus*), and European eel (*Anguilla anguilla*) migrate through the Ulla River (Caballero Miguez, Garza Gil and Varela Lafuente, 2009; Silva *et al.*, 2013; Gradín *et al.*, 2014). Within the final averaged GAM model of this study, both lamprey and eel variables showed a significant effect on dolphin acoustic presence. The lamprey is known to migrate seaward between October and May, peaking in March, often remaining near the estuary before moving offshore (Silva *et al.*, 2013). The eel has two downstream movement peaks with silver eels (adult) primarily moving downstream in the Autumn (October), and the yellow eels (juveniles) moving downstream in summer (June/July) (Gradín *et al.*, 2014). Lamprey is indeed present in the Ulla river estuary zone, as indicated by local fisheries landings data and reports, and has been reported as a major prey item for bottlenose dolphins in other areas of the world (Romero *et al.*, 2014). Additionally, there are anecdotal reports of eel depredation and gear damage in local fisheries by dolphins (Voz de Galicia, 2025). Given bottlenose dolphin behavioural plasticity and opportunistic feeding habits (Leatherwood and Reeves, 2012; Reynolds, Wells and Eide, 2013), local exploitation of these seasonally available diadromous prey resources is therefore plausible. This study included two species of diadromous fish; however, it is also possible that other non-commercial species within the Ulla estuary are preyed upon by dolphins, such as the sea trout (*Salmo trutta L.*), whose migration has been documented to occur between April and July (Caballero Miguez, Garza Gil and Varela Lafuente, 2009).

While fish landings data inherently represent only the commercially-caught portion of the population and do not provide absolute prey abundance estimates, they can still be used as proxies for fish availability (Fury and Harrison, 2011; Leitão *et al.*, 2022). Together, these lines of evidence point to prey distribution as a key driver of dolphin estuarine use. To confirm the presence and role of diadromous species in dolphin diets, future diet studies of estuary-dwelling individuals through stable isotope or fatty acid analyses (Fernández *et al.*, 2011; Quérouil *et al.*, 2013) would help determine whether lamprey, trout, or eel indeed form part of the prey base in this habitat. To ensure meaningful results, such studies should rely on live biopsy sampling of individuals physically observed within the estuarine area of interest. Simply sampling dolphins within the ría or surrounding coastal waters might not accurately reflect values from individuals feeding within the rivers, as recent research has shown isotopic (dietary) differences even between social groups within the same population (Genov, Vighi and Hammond, 2025). Additionally, behavioural studies indicate that certain foraging strategies might be employed preferentially by certain individuals or subgroups within the broader social network (Methion and Díaz López, 2019). Detailed and targeted future diet studies could therefore further clarify niche differentiation between dolphins exploiting estuarine versus offshore resources, improving our understanding of foraging ecology in Galician waters and strengthening the conservation relevance of these findings.

Foraging activity has been closely linked to increased acoustic production in dolphins, with certain vocal signals functioning as food calls to attract conspecifics (Acevedo-Gutiérrez and Stienessen, 2004; King and Janik, 2015), and even to modify prey behaviour (Janik, 2000). Whistles in particular have been associated with high-activity behaviours such as feeding in both the population in Sardinia (Díaz López and Bernal Shirai, 2010; Díaz López, 2011), and in Galicia (Mosca, Methion and Díaz López, 2025) as outlined in Objective 1 of this thesis. The notion that dolphins may seasonally take advantage of a higher availability of prey species within the estuary is therefore supported by the increase in whistle detections, a sound type that has been associated with foraging activities, further reinforcing the importance of employing complementary methodological approaches to acoustic studies, as was possible to do within this thesis.

This third analysis is based on a robust dataset collected over multiple years, seasons, and environmental conditions, providing a strong basis for investigating dolphin use of the Ulla estuary. Fixed PAM offers valuable insight into river use and complements previous behavioural and acoustic studies in the broader study area. Although fixed PAM is a strong tool, there are also a number of limitations to be aware of (Ross *et al.*, 2023). In this study, while the hydrophone platform was located directly in front of the Ulla estuary behind

Cortegada Island, the nature of underwater sound propagation, sound wave reflection, and refraction may have resulted in some sounds from surrounding areas being recorded. In the area adjacent to the estuary are mussel rafts (bateas), which are known fish-aggregating structures, and dolphins have been reported to exhibit foraging behaviours around them (Díaz López and Methion, 2017; Methion and Díaz López, 2019). This would therefore result in some of the acoustic activity of dolphins outside the estuary proper being included in this analysis. Although this may be the case, the waters surrounding the estuary within the ría may still be affected by the same seasonally variable processes as the waters within the river mouth proper. Additionally, as with all passive acoustic studies with no visual observations, detections only occur when dolphins are vocalising, effectively missing the times when animals might be present but not producing sounds (Mellinger *et al.*, 2007; Zimmer, 2011; Ross *et al.*, 2023). While this is a noteworthy limitation, results from the analysis within Objective 1 (Mosca, Methion and Díaz López, 2025), as well as other previous studies (Jones and Sayigh, 2002; Acevedo-Gutiérrez and Stienessen, 2004; Díaz López and Bernal Shirai, 2010) linked dolphin whistles to behaviour, with high rates during higher-activity contexts such as feeding and socialising, and absence mainly during resting. Unless animals were in the area resting or were solitary non-whistling individuals, whistle detections are therefore likely a reasonable proxy for dolphin presence.

Ecological questions are inherently broad and famously difficult to answer, as habitat use in marine top predators is shaped by an intricate interplay of processes operating across multiple spatial and temporal scales and influenced by environmental variability, prey dynamics and stochastic events (Block *et al.*, 2011; Fortuna *et al.*, 2024). The top GAM models in this analysis explained between 7 and 9% of the deviance, which might appear to be low, but is within expectations for ecological models (Møller and Jennions, 2002; Peek *et al.*, 2003). Low explained variance is common in ecology because no single, or even limited set of variables can capture the full complexity of animal–environment relationships, and ecological models often operate with incomplete knowledge of all relevant processes, with many factors contributing to unexplained variability (Møller and Jennions, 2002; Peek *et al.*, 2003). Even though many of the covariates used in this model serve as proxies for broader processes such as prey distribution, a substantial proportion of the variation in dolphin presence is likely driven by factors outside the scope of environmental monitoring. These include social relationships, group dynamics, composition and behaviour, which have been shown to shape movement patterns and habitat use (Mann *et al.*, 2000; Gowans, Würsig and Karczmarski, 2007; La Manna *et al.*, 2023; Methion *et al.*, 2023), as well as individual-level traits or personality that may influence individual habitat use and foraging decisions (Díaz López, 2020). Additional factors not included in the model, such as terrestrial runoff, agricultural activity, pollutant loads, bathymetric complexity, and tidal category, may also influence dolphin distribution by affecting prey availability (Mendes *et al.*, 2002; Hastie *et al.*, 2004; Fury and Harrison, 2011; Carmen, Berrow and O'Brien, 2021; Bridge, Methion and Díaz López, 2023). Recognising the multifactorial nature of dolphin ecology is therefore critical when interpreting model performance.

4.2 INTEGRATIVE DISCUSSION

4.2.1 Thesis Relevance

This thesis sets out to examine how bottlenose dolphins use sound across social and ecological contexts, with emphasis on overall whistle production rate, the contextual use of signature whistles, and the application of whistle presence as a tool for assessing dolphin habitat use in a previously unexplored estuarine environment. The research was based on extensive datasets collected over nearly 20 years by the Bottlenose Dolphin Research Institute (BDRI) in two distinct regions and employed complementary methodological approaches: boat-based hydrophone recordings and fixed Passive Acoustic Monitoring (PAM). Together, these approaches contributed original knowledge on how bottlenose dolphin acoustic communication is shaped by behavioural, social, and ecological factors, confirmed for the first time the acoustic presence of bottlenose dolphins in the Ulla estuary, and provided baseline data for future ecological and conservation assessments.

One of the major strengths of this work lies in the amount and diversity of data available across nearly two decades in wild populations, an uncommon scenario in cetacean bioacoustics (Sayigh, 2013). Boat-based acoustic recordings paired with visual observations are typically limited in duration and behavioural scope due to weather, logistics, and availability of field teams (Jolliffe *et al.*, 2025). In contrast, the multi-year datasets analysed here, particularly those spanning more than 15 years, introduced substantial biological and environmental variability rarely present in shorter studies. This variability enabled conservative random subsampling to minimise temporal autocorrelation and recording-length bias, strengthening the robustness of the statistical analyses (Colegrave and Ruxton, 2018; Gratton and Mundry, 2019).

While both the Sardinian and Galician bottlenose dolphin populations have been the focus of long-term ecological monitoring (Díaz López, 2006a, 2019; Díaz López and Bernal Shirai, 2008; Methion and Díaz López, 2018, 2019; Methion *et al.*, 2023), this thesis provides the first dedicated analysis of dolphin acoustic behaviour in Galicia and the first documentation of acoustic presence in the Ulla estuary, a region well studied in terms of oceanography (Álvarez-Salgado *et al.*, 1996; Bermúdez *et al.*, 2013), water chemistry (Prego *et al.*, 2008), and diadromous fish biology (Saura *et al.*, 2006; Caballero, Cobo and González, 2007; Gradín *et al.*, 2014; Saavedra-Nieves *et al.*, 2020), yet previously unexamined from a cetacean acoustic perspective.

The comparative value of this work is further enhanced by the fact that the datasets used in Objectives 1 and 2 were collected in two geographically and ecologically distinct areas using an identical sampling protocol. This consistency is rarely found in cross-population acoustic studies, where differences in equipment, recording settings, observer effort, or behavioural categorisation often limit interpretability (Jones and Sayigh, 2002). Here, methodological equivalence allowed reliable comparisons between two wild populations exposed to different environmental pressures, including fisheries activity (Díaz López, 2005, 2006b; Giralt Paradell *et al.*, 2021) and aquaculture structures (Díaz López, 2006a, 2012; Díaz López and Bernal Shirai, 2008; Díaz López and Methion, 2017; Methion and Díaz López, 2019).

The combined use of boat-based and fixed PAM acoustic methods is another key contribution. The field of marine bioacoustics is expanding rapidly, and advances in fixed PAM now allow the continuous collection of large acoustic datasets that overcome many of the logistical constraints of visual surveys (Zimmer, 2011; Howe *et al.*, 2019; Webber *et al.*, 2022; Diego-Tortosa *et al.*, 2025). Yet passive acoustic data lack contextual information on species identity, group size, behaviour, or social composition, making behaviourally contextualised datasets such as those used within Objectives 1 and 2 essential for interpreting PAM outputs meaningfully (Simard *et al.*, 2015; Thompson, Brookes and Cordes, 2015; Frasier *et al.*, 2021). This thesis demonstrates that the two approaches are not only complementary but mutually reinforcing.

Together, these methodological frameworks provide a powerful model for integrating behavioural and ecological inference. This becomes particularly evident in the interpretation of the results from the fixed PAM objective, where the behavioural and group-size drivers of whistle production identified in the earlier sections of the research inform the ecological interpretation of whistle detections in the estuary. By linking the contextual foundation of supervised recordings with the scalable temporal coverage of PAM, this thesis illustrates a valuable framework for future research in marine mammal bioacoustics.

4.2.2 Behavioural and Ecological Insights

This thesis provides insight into how acoustic signals reflect both the behavioural dynamics and ecological context of a highly social marine top predator. Across the three research objectives, acoustic behaviour emerges as a bridge between social interaction and habitat use, clarifying how dolphins adjust their vocal output in response to activity, group composition, and environmental conditions.

Results from Objectives 1 and 2 offer additional evidence that social acoustic communication is closely tied to behavioural state and motivational context. As widely reported in the literature, vocal output increases during high-energy behaviours such as feeding and socialising, where calls may facilitate coordination, or cooperative foraging (Acevedo-Gutiérrez and Stienessen, 2004; Díaz López and Bernal Shirai, 2010; King and Janik, 2015; La Manna *et al.*, 2019). Resting, by contrast, is characterised by very low or absent vocal activity (Jones and Sayigh, 2002; Quick and Janik, 2008; Hawkins and Gartside, 2010). These results reinforce the established link between behavioural state and vocal production, showing that acoustic activity scales with social and energetic demands.

Beyond behavioural context, the results of these two first sections also emphasise the role of sound as a cohesion-related signal, particularly as group size increases. The positive association between group size and both whistle rate and signature whistle probability suggests that vocal communication becomes increasingly important as social units grow and individuals must maintain contact over greater spatial or sensory distances (Jones and Sayigh, 2002; Cook *et al.*, 2004; Quick and Janik, 2008). This pattern supports the idea that cohesion signals remain important even within stable groups and aligns with findings from other species (Insley, 1992; Bowmaker-Falconer *et al.*, 2022; Sun *et al.*, 2023).

A central contribution of the thesis lies in showing that acoustic behaviour is shaped not only by immediate behavioural context but also by ecological conditions that influence grouping patterns. The two study populations differ markedly in habitat productivity, prey distribution, and typical group sizes, and these ecological differences appear to modulate both the frequency and probability of whistle and signature whistle use. In this way, the analyses carried out within this work demonstrate that communication patterns emerge from the interaction between ecological constraints and social organisation, rather than from location alone (La Manna *et al.*, 2022; Pace *et al.*, 2025).

On the ecological front, the final objective provides further support for the use of fixed passive acoustic monitoring as an effective tool for assessing dolphin presence and habitat use, particularly in environments where visual surveys are limited (Ross *et al.*, 2023). This analysis presents the first evidence of year-round bottlenose dolphin presence in the Ulla estuary, confirming what had been anecdotally recorded by documenting it acoustically. The marked seasonal pattern in whistle detections suggests that habitat use is variable across the year and may be linked to seasonally available prey, consistent with patterns observed in other estuarine or river-influenced systems (dos Santos, Coniglione and Louro, 2007; Carmen, Berrow and O'Brien, 2021).

4.2.3 Specific Contributions to Cetacean Bioacoustics and Dolphin Whistle Research

This thesis brings together three complementary objectives that examine how bottlenose dolphins use whistles across different behavioural, social, and ecological contexts, offering distinct but interconnected contributions to cetacean bioacoustics. Each objective focuses on a different analytical scale and whistle metric, providing an understanding of the drivers of whistle rate, the contextual production of a specific whistle type, and how whistles can be used as indicators of habitat use in passive acoustic datasets.

Objective 1 focuses on overall whistle production rate (whistles per minute) in relation to group size, behaviour, and location. This analysis contributes to the field by quantifying how broad-scale whistle activity varies according to social and environmental conditions. The modelling approach used here highlights the interaction between group size and ecological setting, reinforcing that whistle use is jointly shaped by social structure and habitat characteristics. Importantly, this analysis underscores the consistency of behaviour-linked vocal production patterns across populations, strengthening previously established ideas about the behavioural drivers of whistle use (Quick and Janik, 2008; Hawkins and Gartside, 2010; Díaz López, 2011).

Objective 2 shifts from general whistle output to the contextual production of a specific whistle type, the signature whistles. By analysing when signature whistles occur (presence/absence per minute) in relation to group size, behaviour, and location, this analysis provides insight into how identity signals function within different social and ecological scenarios. The finding that signature whistle probability increases with group size, and that this relationship differs across populations, contributes to broader discussions in cetacean communication about cohesion signals in large and socially dynamic groups as well as social and ecological complexity and diversity driving vocal communication needs. These results echo patterns observed in other studies and how signature whistles vary between populations through adaptation (Luís *et al.*, 2021; Terranova *et al.*, 2021; La Manna *et al.*, 2022).

Objective 3 extends the scope of the thesis by applying whistle detections to a broader ecological question to understand how dolphins use a previously unstudied estuarine habitat. This analysis uses whistle presence as an indicator of dolphin occurrence, revealing clear seasonal patterns and potential links to prey availability, further supporting the role of passive acoustic monitoring for cetacean distribution and habitat use (Dede *et al.*, 2013; La Manna, Manghi and Sara, 2014; Tellechea, 2014; Simard *et al.*, 2015; Carmen, Berrow and O'Brien, 2021; Gregorietti *et al.*, 2021; Fleishman *et al.*, 2023). This final objective provides the first acoustic evidence of year-round use of the Ulla estuary, adding an ecological dimension to the whistle-based analyses in the preceding sections.

4.3 CONSERVATION AND MANAGEMENT IMPLICATIONS

The findings of this thesis provide several immediate contributions to the management and conservation of bottlenose dolphins in the Galician rías and comparable coastal systems. From a conservation perspective, the results of the Objective 3 analysis provide important context for a population already exposed to multiple anthropogenic pressures (Methion and Díaz López, 2018, 2019; Bridge, Methion and Díaz López, 2023). The Ulla estuary lies adjacent to Vilagarcía harbour, a major commercial port where vessel traffic, underwater noise, and associated risks are likely to overlap with dolphin habitat use. While this analysis did not directly assess anthropogenic impacts, identifying when dolphins are most likely to use this habitat offers a critical baseline for conservation planning. This is particularly relevant within European legislative frameworks. Bottlenose dolphins are listed under Annexes II and IV of the EU Habitats Directive (Council of the European Communities, 1992), requiring the designation of Special Areas of Conservation (SACs) and strict protection measures for populations within these areas. The Galician rías are also recognised as an Important Marine Mammal Area (IMMA) (Marine Mammal Protected Areas Task Force, 2024), and the Cortegada archipelago is included in the Atlantic Island National Park (Xunta de Galicia, 2025a), highlighting the need for site-specific management. Bioacoustic studies from other regions have shown how passive acoustic monitoring can directly inform conservation measures by identifying overlap with mussel farming activities (Valdés Hernández *et al.*, 2024) and in areas of high vessel traffic around busy ports (Marley, Salgado Kent and Erbe, 2016; Marley *et al.*, 2017). The findings presented in this section, although preliminary, could suggest several practical measures, including restrictions on vessel traffic or vessel noise through speed regulation or underwater noise level limitations or the installation of live anti-collision systems automatically alerting vessels of cetacean presence in critical areas of importance (Brunoldi *et al.*, 2016).

Finally, the ecological differences documented between the Galician and Sardinian populations also highlight that acoustic behaviour reflects local environmental conditions, further supporting the notion that whistle-based analyses could contribute to defining management units or informing regional conservation strategies in both study regions (La Manna *et al.*, 2020, 2022; Papale *et al.*, 2021; Fandel, Silva and Bailey, 2024).

4.4 FUTURE DIRECTIONS

The findings of this thesis provide several avenues for future research, both through direct extension of the datasets and methods presented here and in relation to broader overall concepts within the field of marine bioacoustics. The following sections outline these suggestions.

Abundance Estimation through Acoustic Parameters

One of the challenges that has been associated with the advances in passive acoustic techniques is animal abundance estimation (Mellinger *et al.*, 2007). Although there have been efforts in this field, there are still some challenges before acoustic methods can provide reliable abundance estimates (Caillat, Thomas and Gillespie, 2013; Fearey *et al.*, 2019; Longden *et al.*, 2020; Sharpe and Berggren, 2025). Converting acoustic detections into estimates of abundance is challenging because the link between the number of calls and the number of individuals is not straightforward, as some animals may vocalise repeatedly, while others remain silent, and vocalising individuals may repeatedly swim in the proximity of the hydrophone, effectively biasing the estimates (Mellinger *et al.*, 2007; Zimmer, 2011). It is therefore crucial to have a deep understanding of a species' vocal repertoire as well as the links between vocal production and behaviour before detection parameters and assumptions are made (Mellinger *et al.*, 2007; Zimmer, 2011). This is also to ensure that when passive acoustic detection is deployed in an environment where different cetacean species may occur, they can be properly recognised. The results from Objectives 1 and 2, showing predictable relationships between whistle rate, signature whistle presence and group size, provide one such behavioural parameter that could improve abundance estimates from passive (autonomous) acoustic methods in the future. The use of signature whistles as individual identifiers also offers potential for an acoustic identification tool, whereby the number of unique signature whistles detected in an area could provide a conservative estimate of the number of individuals present (Bazúa Durán, 2018; Longden *et al.*, 2020; Papale *et al.*, 2024; Sharpe and Berggren, 2025).

Using AI and Machine-learning for Signal Detection and Classification

Advances in automated detection and AI-assisted classification, such as Convolutional Neural Networks (CNNs), are rapidly expanding the scope of bioacoustics studies (Scaradozzi *et al.*, 2024; Di Nardo *et al.*, 2025). These methods, with increasingly accurate automatic detections, could therefore generate detailed information on the large datasets created by passive acoustic methods that would otherwise require prohibitive manual effort. Within the context of the populations studied in this thesis, future work could take advantage of AI-assisted technologies to analyse the entirety of the large 189 h dataset (collected over 15 years and used in Objectives 1 and 2) and integrate whistle metrics to better describe the respective population repertoires, leading to further opportunities for comparison between populations and furthering of acoustic communication knowledge. Furthermore, and moving beyond whistles, other acoustic signals like Burst-Pulsed sounds and echolocation clicks could be further investigated as well.

Including Clicks and Burst-pulsed Sounds in PAM Analyses

While this thesis focused on whistles for the fixed PAM ecological analysis within Objective 3, future work could also integrate burst-pulsed sounds and echolocation clicks to obtain a fuller picture of acoustic behaviour. Although whistles have been used in previous studies for dolphin habitat use detection (Gregorietti *et al.*, 2021), echolocation clicks are often used and are linked to foraging activities (Papale *et al.*, 2020; Carmen, Berrow and O'Brien, 2021). Some studies use a combination of whistles and clicks (Tellechea, 2014; Marley *et al.*, 2017) and some use all types of dolphin vocalisations (La Manna, Manghi and Sara, 2014; Rankin *et al.*, 2017). Integrating multiple sound types into PAM analyses and potentially comparing differences in their detections with respect to spatio-temporal variables would provide a more nuanced basis for interpreting acoustic presence in habitats where visual context is unavailable.

Developing Multi-Hydrophone PAM Networks

The results support the value of fixed PAM for detecting dolphin occurrence in challenging habitats. Building on this, a network of hydrophones integrated into existing oceanographic infrastructure could allow for continuous monitoring of a wider coastal area. Such networks could track spatio-temporal shifts in cetacean habitat use, provide early detection of changes in local populations, and support conservation management in high-use or high-risk areas. Additionally, a number of other cetacean species are present in Galician coastal waters (Díaz López and Methion, 2018; Giralt Paradell, Díaz López and Methion, 2019; Bland *et al.*, 2023; Methion, Mosca and Díaz López, 2023). A network of acoustic monitoring stations could therefore provide some novel information about their spatio-temporal patterns of distribution remotely, complementing the visual surveys, or replacing them if impractical or impossible due to accessibility or adverse conditions (Miksis-Olds *et al.*, 2021).

Long-term Monitoring to Quantify Noise Impacts

The hydrophone deployed by CETMAR (which provided the acoustic data used in Objective 3) is calibrated for underwater noise measurement, creating an opportunity for future research to build upon the initial results presented within this thesis and assess the influence of anthropogenic soundscapes on dolphin acoustic behaviour. Long-term monitoring could quantify baseline noise levels, evaluate temporal variation in noise exposure, and explore whether dolphins adjust their acoustic output with respect to vessel noise and overall underwater noise pollution (Marley *et al.*, 2017; Carmen, Berrow and O'Brien, 2021). Such analyses would be especially valuable in areas where vessel traffic and aquaculture activity are prominent.

Incorporating Active Space Concepts into Conservation

Finally, future work could provide further information to inform the extent of animals' active space, as little research has been conducted on dolphins (Vincent M. Janik, 2000). As indicated in Burnham and Duffus (2023), a better understanding of an individual or a species' active space could help evaluate how shifting soundscapes affect animals' perceptual and communication space. Applying this framework to both study regions could help identify periods or areas where noise compression of active space is most pronounced, guiding targeted mitigation measures.

CHAPTER 5:
CONCLUSIONS

5.1 THESIS CONCEPTUAL ROADMAP AND FRAMEWORK

This conceptual roadmap (illustrated in Figure 5.1) outlines a stepwise framework that was employed in this doctoral thesis, and links standardised data collection to ecological interpretation and, ultimately, to conservation application.

Overall Aims and Objectives

This thesis was designed to address one central challenge: to better understand the contextual role of whistles, and particularly signature whistles, in wild populations of bottlenose dolphins across contrasting ecological scenarios. Additionally, this research bridges the gap between acoustic and visual methodologies by integrating traditional supervised acoustic observations (boat-based hydrophone recordings collected concurrently with visual behavioural data), with fixed passive acoustic monitoring (PAM). This dual approach allowed for the exploration of both behavioural questions, such as the drivers of different whistle types in bottlenose dolphins, and ecological questions, such as how whistle occurrence relates to habitat use and environmental variability.

Data Collection, Methodological Consistency and Compatibility

A key strength of this work lies in the methodological consistency and complementarity of the datasets. Long-term acoustic recordings collected with standardised protocols in two wild populations provided a robust basis for comparing whistle use across ecological settings. In parallel, a multi-year fixed PAM dataset from the Ulla estuary extended this framework to continuous, unsupervised monitoring, allowing the contextual insights from supervised recordings to inform ecological interpretation.

Main Findings and Insights

The three main objectives addressed within this thesis collectively advance our understanding of the contextual use of dolphin whistles. The first two revealed how whistle and signature whistle production vary with behavioural state, group size, and location, illustrating that communication strategies differ between populations depending on their social organisation and ecological environment. The third objective expanded this understanding to a different temporal and spatial scale, demonstrating how whistles can be linked to environmental cycles and potential prey availability in an estuarine habitat previously unexplored through acoustic monitoring. Together, these findings emphasise that acoustic behaviour is both socially and ecologically adaptive, shaped by the dynamic interplay between group cohesion, environmental context, and anthropogenic influence.

Conservation Applications

From an applied perspective, this work highlights the growing potential of acoustic data as a tool for conservation and management in anthropogenically impacted coastal regions that host protected bottlenose dolphin populations with high site fidelity. By clarifying the contexts in which whistles are produced and identifying the environmental factors influencing their presence, this research provides a baseline for using acoustic monitoring as an ongoing, non-invasive means of population assessment. Continued deployment of fixed passive systems can enable long-term, cost-effective monitoring of dolphin occurrence and behaviour in key habitats, supporting early detection of changes in site use or disturbance. In the future, integrating such acoustic approaches into management frameworks could inform area-based protection measures, such as temporal restrictions on marine traffic or construction in high-use zones, thereby improving mitigation of acoustic and ecological disturbance.

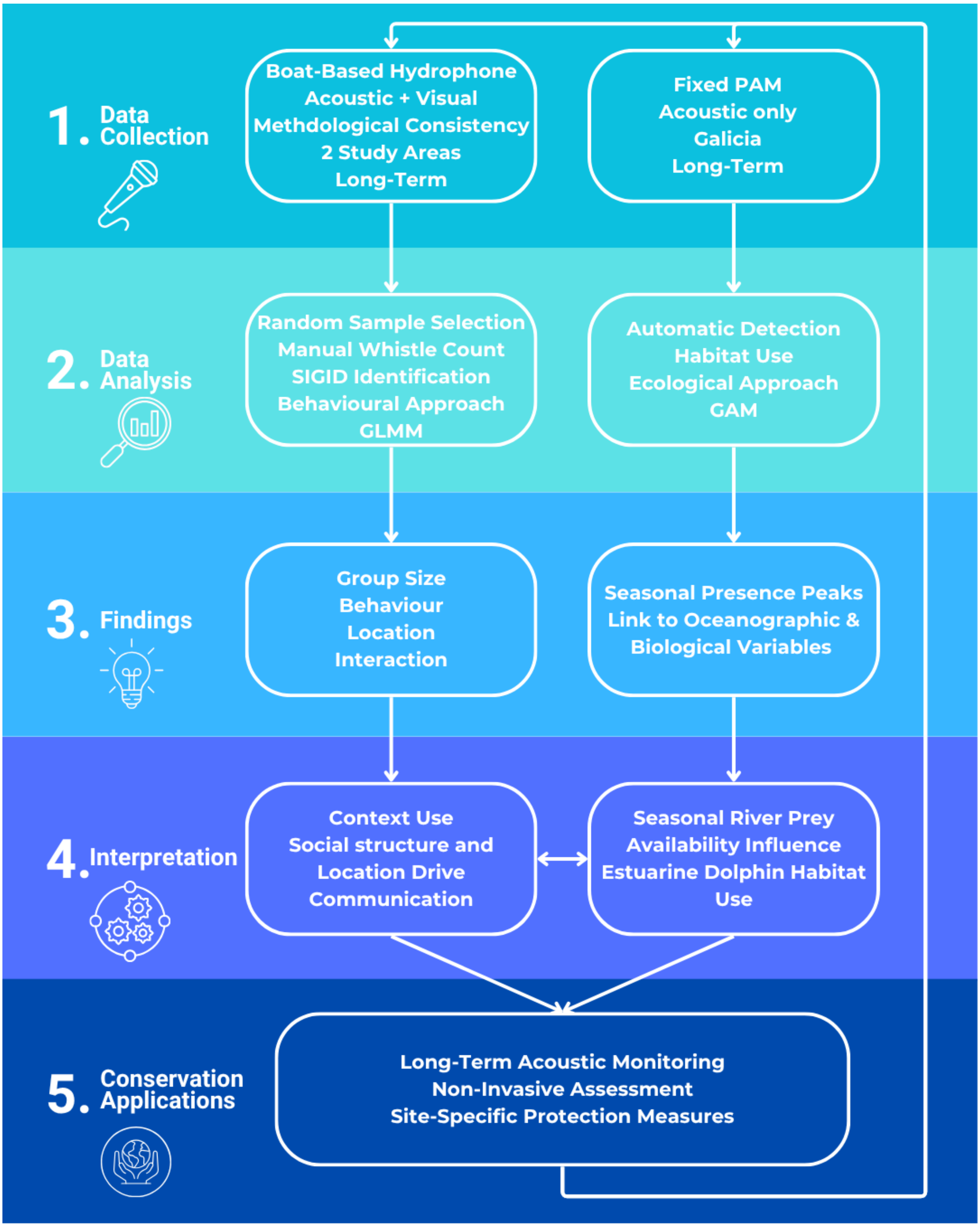


Figure 5.1 Thesis Conceptual Roadmap and Framework

5.2 PERSONAL INSIGHTS

This doctoral work has given me a deep appreciation for the scientific and practical challenges inherent to bioacoustic research, and to cetacean research overall. The process of collecting, processing, and interpreting acoustic data revealed how each stage requires both precision and flexibility to achieve reliable results.

In the field, obtaining usable acoustic data often depended on a combination of environmental and behavioural conditions beyond control. Sea state, animal movement patterns, and group behaviour all affected recording opportunities, while background and anthropogenic noise frequently masked the signals of interest. General fieldwork is already constrained by visibility and sea state, but acoustic data collection is even more limited. Even though I was fortunate to analyse a large dataset collected over many years, being part of the data collection process myself provided a clear understanding of how valuable each recording is, even when further selection must occur during visual and aural spectrogram analysis. In this sense, data collection in bioacoustics occurs twice: once at sea and again in the lab, when determining which parts of the recordings meet the standards necessary for quantitative and qualitative assessment.

Further stages of data processing and interpretation presented their own complexities. Random sampling to minimise bias, conservative selection criteria for signal classification, and the constant need to balance data quantity with quality all highlighted the rigour required in acoustic studies. Statistical analysis further underscored that models are simplifications of reality and are only useful when built and interpreted with care. Each stage of this work reinforced the iterative nature of science: refining hypotheses, revising analyses, and continuously adjusting interpretations as new perspectives emerge.

Communicating scientific results through academic writing also demands a different form of precision. Presenting findings clearly while providing details and maintaining strong links to existing literature is an essential skill in itself.

Altogether, this research has deepened my understanding of the demands and possibilities of cetacean bioacoustics, a field that combines technical expertise, analytical reasoning, and critical interpretation. The challenges encountered throughout the process reflect the complexity of studying communication in the marine environment, but also the growing potential of acoustic methods to contribute to behavioural ecology and conservation in meaningful ways. I look forward to continuing to refine and expand these skills in the future.

Ultimately, the research presented here reflects the open-ended nature of scientific inquiry and how each result can raise new questions. I hope this thesis contributes not only to our knowledge of bottlenose dolphin behaviour and ecology through sound, but also to the wider field of marine bioacoustics and to our collective effort to better understand, protect, and preserve the natural world for future generations.

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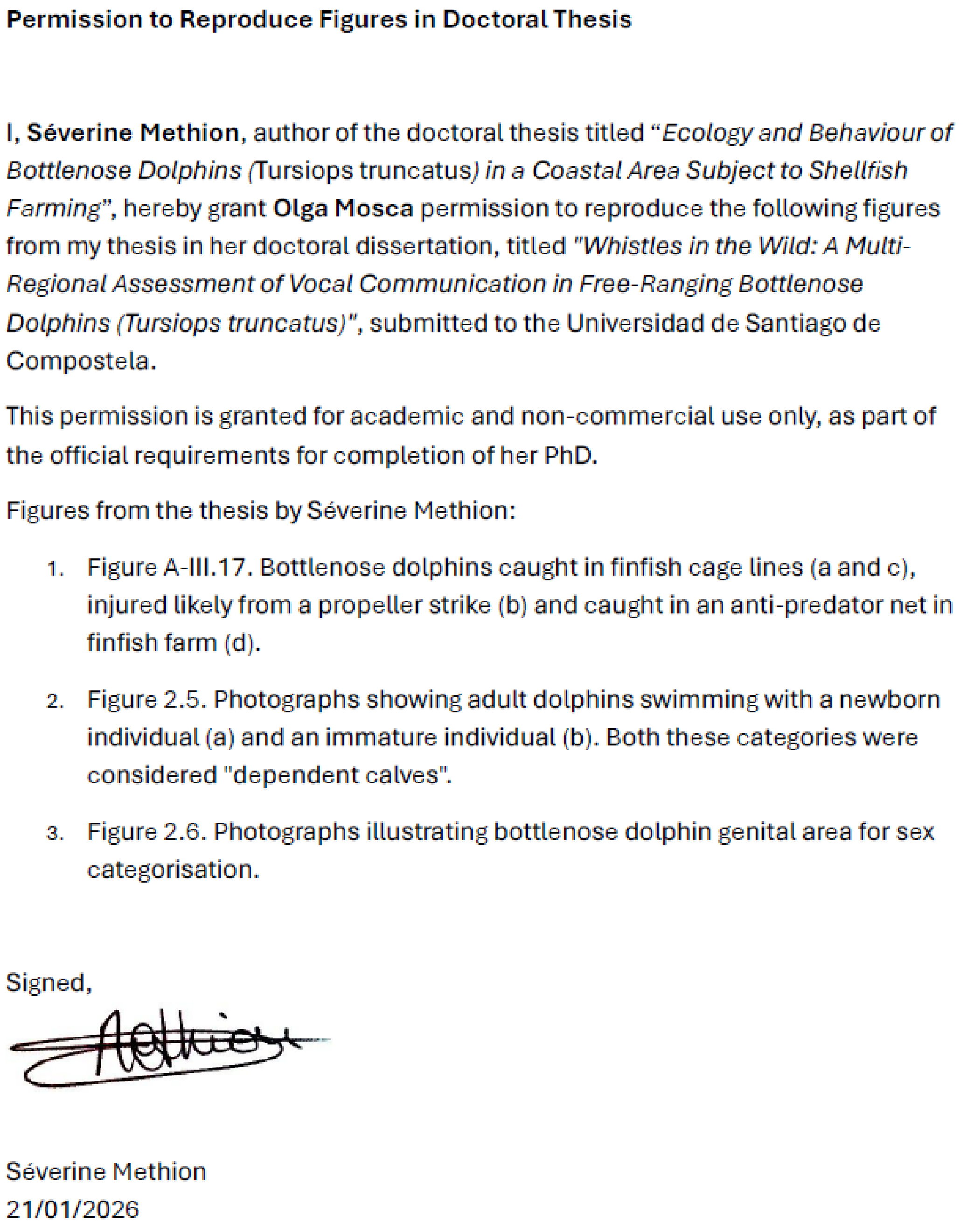

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1. Figure A-III.17. Bottlenose dolphins caught in finfish cage lines (a and c), injured likely from a propeller strike (b) and caught in an anti-predator net in finfish farm (d).
2. Figure 2.5. Photographs showing adult dolphins swimming with a newborn individual (a) and an immature individual (b). Both these categories were considered "dependent calves".
3. Figure 2.6. Photographs illustrating bottlenose dolphin genital area for sex categorisation.

Signed,

Séverine Methion
21/01/2026

ANNEX III :
GENERAL LITERATURE BACKGROUND AND CONTEXT

This Annex provides the theoretical background to contextualise the research presented in this thesis. It introduces key concepts for the study of communication in animals, starting with a general overview of communication as a field within behavioural ecology and its importance in social species. From there, the focus narrows to acoustic communication in the marine environment, with a review of the basic principles of bioacoustics and how sound is produced and perceived in odontocetes, and more specifically in dolphins. The main types of dolphin vocalisations are described, along with the contexts in which they are typically used, along with the main techniques used in marine bioacoustics research. The study species, the common bottlenose dolphin (*Tursiops truncatus*), is then introduced.

A. ANIMAL COMMUNICATION

The study of animal communication includes many disciplines, such as evolution, linguistics, neurobiology, biomechanics, and psychology, to name but a few (Naguib and Price, 2013). Communication can occur a number of ways, and some of them may not be intentional. “Cues”, for example, are a simple by-product of an animal’s activity, like tracks in the soil, or the rustling of leaves from movement; they are unintentional ways that an animal may communicate its presence or several other characteristics to others around them (Goodenough, McGuire and Jakob, 2010; Rossano and Kaufhold, 2021). A signal, on the other hand, is defined as a pattern, or a change in the environment, with the purpose of encoding and transmitting information from one animal to another (Martinelli, 2017; Rossano and Kaufhold, 2021) (Figure A-III. 1). The function of signals, however, has been debated over the years, with some arguing that signals are used to share information (Shannon, 1948; Wiener, 1961; Seyfarth *et al.*, 2010), and others proposing that signals act as a form of manipulation (Dawkins and Krebs, 1978; Seyfarth *et al.*, 2010). Information-sharing is seen as a cooperative activity where both sender and receiver benefit from the exchange (Goodenough, McGuire and Jakob, 2010; Seyfarth *et al.*, 2010), such as predator alarm calls (Cheney and Seyfarth, 1985; Wilson-Henjum *et al.*, 2019), or conveying the location of food (Brown, Brown and Shaffer, 1991; Seeley, 1998). The other perspective instead argues that signallers aim to manipulate receivers to perform behaviours that benefit the sender, such as in loud, aggressive, competitive displays that may affect the nervous system of the receiver directly (Morton, 1977; Rendall, Owren and Ryan, 2009). The manipulation theory was then criticised, because if signals were only beneficial for senders, then receivers would simply ignore them, eventually leading to the disappearance of such communication over time (Searcy and Nowicki, 2010; Seyfarth *et al.*, 2010). Signals are therefore believed to benefit both senders and receivers, and the reliability of such signals is ensured through “honest” signalling (Rossano and Kaufhold, 2021). What allows signals to be honest is the handicap principle, which suggests that costly, extravagant displays (like a peacock's plumage) indicate a signaller's strength, status, or genetic quality because only strong individuals can bear such a "handicap" (Zahavi, 1975). While honest signalling has been proven to be an evolutionarily stable strategy in which there are mutual benefits for both receivers to attend to signals and for senders to be "honest" about them (Grafen, 1990; Searcy and Nowicki, 2010), communication systems are also susceptible to deception, or "lies" where the sender breaks the association between a signal and its meaning and make the receiver believe something that is not true (Searcy and Nowicki, 2010; Martinelli, 2017). Examples of this include animals using fake alarm calls in order to secure mating opportunities (Bro-Jørgensen and Pangle, 2010). These cases illustrate the evolutionary pressures behind communication, where signal reliability, deception, and receiver responses shape how basic social interactions unfold.

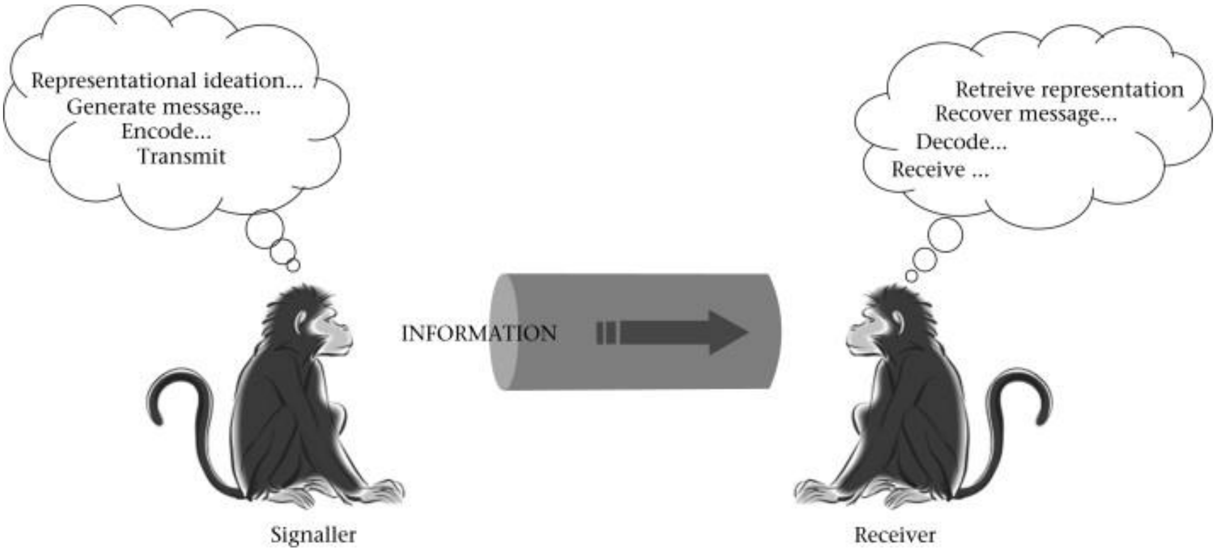

Figure A-III. 1 Schematic illustrating core features of classic information transmission approaches to animal communication. Reproduced with permission from Rendall, Owren and Ryan, 2009. Copyright 2009, Elsevier

Animal communication is crucial for an organism's fitness, influencing basic life functions such as courtship, parental care, defence, and foraging (Green and Marler, 1979; Gillooly and Ophir, 2010; Martinelli, 2017). Some of the most basic ways in which communication is used are to identify conspecifics (Losos, 1985; Charrier and Sturdy, 2005), a phenomenon that is also often linked to the concept of finding mates, especially in contexts where there may be a high number of individuals present (Ryan and Rand, 1993; Detto, 2007). Communication related to mating also includes mate attraction (Dweck *et al.*, 2015), sex broadcasting through colouration or mating displays (Dougherty, 2021), competition between males to ensure female choice (Candolin, 1999) and then mate guarding (Chaudhary, Mishra and Omkar, 2017) or maintenance of the mating bond is also observed (Sogabe and Yanagisawa, 2007). Communication is also of particular importance within a group setting, and communication in social groups has been shown to be more complex when compared to less social counterparts (Bouchet, Blois-Heulin and Lemasson, 2013).

The social complexity hypothesis posits that the complexity of a species' social structure is correlated with the complexity of its communication system. This concept suggests that as animals engage in more intricate social interactions and form more complex social organisations, their communication needs evolve, leading to more sophisticated and varied signal types and repertoire (Freeberg, Dunbar and Ord, 2012; Bouchet, Blois-Heulin and Lemasson, 2013; King, Connor and Montgomery, 2022). Socially complex species are characterised as ones with varied group member roles and hierarchies, which entail higher cognitive processing (Freeberg, Dunbar and Ord, 2012). Communication strategies within groups, also known as communication networks (Templeton and Carlson, 2019), include maintaining social bonds through touch with grooming (Dunbar, 1991), through sound by alerting others to danger (Cheney and Seyfarth, 1985; Hollén and Radford, 2009), or through the use of chemical compounds like pheromones for early neonatal feeding behaviour (Coureaud and Schaal, 2008). This concept highlights the role of communication not just as an exchange of information, but as a system that adapts and evolves to meet the demands of living in structured, dynamic groups (Freeberg, Dunbar and Ord, 2012).

While there are a number of different functions and contexts of communication, there are also different modalities in which animals communicate. These sensory modes are known as channels, and the main ones are: chemical, tactile, visual and acoustic (Goodenough, McGuire and Jakob, 2010; Freeberg, Dunbar and Ord, 2012; Martinelli, 2017) (Figure A-III. 2).

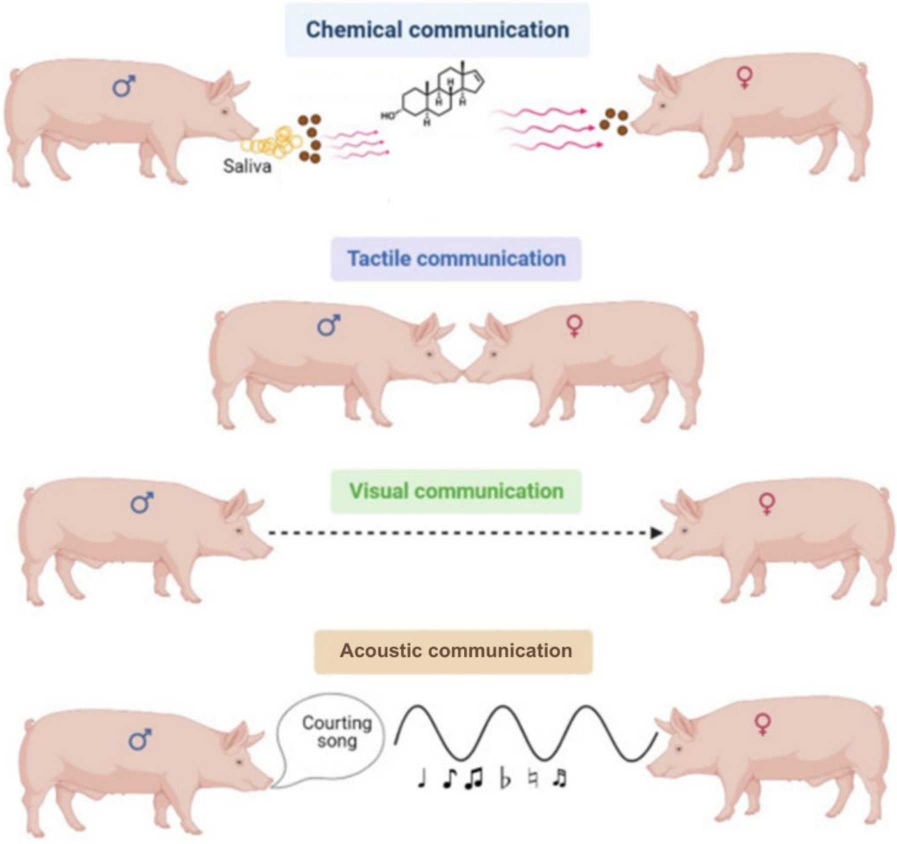

Figure A-III. 2 Illustration of the four primary channels of animal communication: chemical, tactile, visual, and acoustic. Adapted with permission from Sankarganesh et al., 2021. Copyright 2021, Elsevier

Chemical Channel

The chemical channel involves communication through smell and taste, utilising substances such as pheromones to convey messages, including territorial boundaries (Jaeger *et al.*, 1986) or mating readiness (Thomas, 2011). These signals often require little energy to produce, can persist over time, and may act over long distances. However, they are easily overwritten, one example being dog urine, marking a territory, which can easily be replaced by another individual’s scent (Martinelli, 2017).

Tactile Channel

The tactile channel, in addition to touch, includes thermic and electric forms of communication via direct body contact or vibrations near the receiver (Martinelli, 2017). Tactile signals can transmit a variety of messages, from lactation induction in whales (Videsen *et al.*, 2017) to “jerky-tapping” courtship displays in wolf spiders (Gibson and Uetz, 2008), and electric shocks as male-dominance display in gymnotid fish (Fugère, Ortega and Krahe, 2010). A major advantage of the tactile channel is its high variability in time and intensity, and the main disadvantage is the absence of distance transmission, requiring senders and receivers to be in direct contact or proximity (Goodenough, McGuire and Jakob, 2010).

Visual Channel

Visual signals can be extrinsic (outside the individual's body, like a nest), or intrinsic (part of the organism's body or behaviour, such as colour, or movement patterns) (Martinelli, 2017). Examples include mating displays in birds (Frith and Frith, 1988) or warning predators of toxicity through aposematic colouration in frogs (Roberts, Stuart-Fox and Medina, 2022). Visual signals can convey a vast amount of information and are often combined with other signal channels for multimodal signalling to ensure signal reception. The biggest limitation of this channel, however, is the need for light and line of sight, which restricts signal effectiveness in darkness or across great distances (Martinelli, 2017).

Acoustic Channel

Finally, the acoustic channel encompasses the production, emission, and reception of sounds, which can be produced through a vocal apparatus within the body, or by hitting parts of the body or the environment (Martinelli, 2017). Acoustic communication occurs across a wide range of taxa and is highly versatile in both function and complexity. Species occupy different acoustic frequency "niches" from the low infrasounds of blue whales (Mellinger and Clark, 2003) to the ultrasonic vocalisations in mice (Liu *et al.*, 2003), with frequency generally being inversely related to body size (Fletcher, 2004). Acoustic signals are used by animals in a multitude of ways for various life functions, ranging from courtship (Marconi *et al.*, 2020) and parental care (Briefer and McElligott, 2011) to defence (Wheeler, 2010; Dutour, Léna and Lengagne, 2017) and foraging (Brown, Brown and Shaffer, 1991; V. M. Janik, 2000). Acoustic signals also play a role in individual recognition, with signature vocalisations serving the role of group cohesion (Janik and Slater, 1998) and for contact with specific individuals, such as between mothers and offspring (Insley, 1992; Smolker, Mann and Smuts, 1993) or between individuals of a mated pair (Bowmaker-Falconer *et al.*, 2022; Sun *et al.*, 2023). Acoustic displays can also convey dominance and social status (Kitchen *et al.*, 2003) as well as self-promotion signals in singing birds (Catchpole, 1987), insects (Alexander, 1957), and amphibians (Bee, 2008). Communication within the acoustic channel has numerous advantages, as signals can be sent in darkness, around obstacles or in dense environments. Receivers are also able to directionally locate the sender, and the speed of sound transmission allows for quick response times (Goodenough, McGuire and Jakob, 2010; Martinelli, 2017).

B. BIOACOUSTICS

Bioacoustics is a rapidly advancing scientific field of study for how animals use sound. As with communication overall, bioacoustics too spans a wide range of disciplines, including anatomy, physiology, psychology, ethology, ecology, physics and mathematics, and seeks to understand how animals produce, transmit, perceive and interpret sounds, and how these processes evolved over time (Hopp, Owren and Evans, 1998; Megela Simmons, Popper and Fay, 2003; Au and Hastings, 2008).

The modern study of bioacoustics originated in the field of human speech science, with the development of two foundational theories: the “source-filter” theory of vocal tract resonances, which explains how sounds are shaped (Chiba and Kajiyama, 1941; Fant, 1960) and the “myoelastic-aerodynamic” theory of vocal fold vibration, explaining how sounds are produced and sustained (Van Den Berg, 1958). For many years, the technical and human-focused characteristics of these theories were a barrier to biologists because the main texts were either inaccessible or mathematically complex. However, these principles were then gradually extended to non-human animals in the 1980s and 1990s (Suthers *et al.*, 2016), particularly in bats, cetaceans, and birds, and have since expanded to a wide range of taxa (Suthers and Fattu, 1973; Cranford, Amundin and Norris, 1996; Goller and Larsen, 1997). Some broad fields of research today focus on the evolution of sound production in different taxa (Fitch and Hauser, 2003; Suthers *et al.*, 2016), the physics and physiology of sound production and propagation within the environment (Hopp, Owren and Evans, 1998; Bee, 2008, 2015), the neuroethology and cognition of sound reception and interpretation (Gentner and Margoliash, 2003), and the role of sound in animal communication and behaviour (Boughman and Moss, 2003; Erbe, 2022), including the effects of noise on acoustic communication (Brumm, 2013; Erbe *et al.*, 2025). While initially, much of the research focused on terrestrial habitats due to the relative ease of observation and data collection on land, since the 1940s, driven by naval sonar research, there have been advances in how sound is produced, transmitted and used by aquatic organisms, giving rise to marine bioacoustics (Hopp, Owren and Evans, 1998; Au, Fay and Popper, 2000; Erbe, 2022).

a. Marine Bioacoustics

The underwater environment is acoustically vastly different from the one on land. Sound travels approximately 4.5 to five times faster in water than in air, at a speed of approximately 1500 m/s (versus about 330 m/s in air), although this value can vary depending on parameters such as temperature, salinity, and pressure (Bass and Clark, 2003; Erbe *et al.*, 2025). The high speed of sound, coupled with the fact that low-frequency signals attenuate slowly, makes sound the most reliable way for organisms to communicate over long distances in aquatic habitats, particularly in comparison to other signals, such as chemical or visual ones, which dilute or scatter easily in these environments (Bass and Clark, 2003; Erbe *et al.*, 2025).

In simple physical terms, sound can be defined as a wave that travels through a medium. Unlike electromagnetic waves, sound requires a physical medium such as a solid, a liquid or a gas to propagate. Sound is essentially a change in pressure within the medium, and the particles of such a medium move in regions of alternating compression and rarefaction, propagating energy outwards from a given source (Bass and Clark, 2003; Erbe *et al.*, 2025) (Figure A-III. 3).

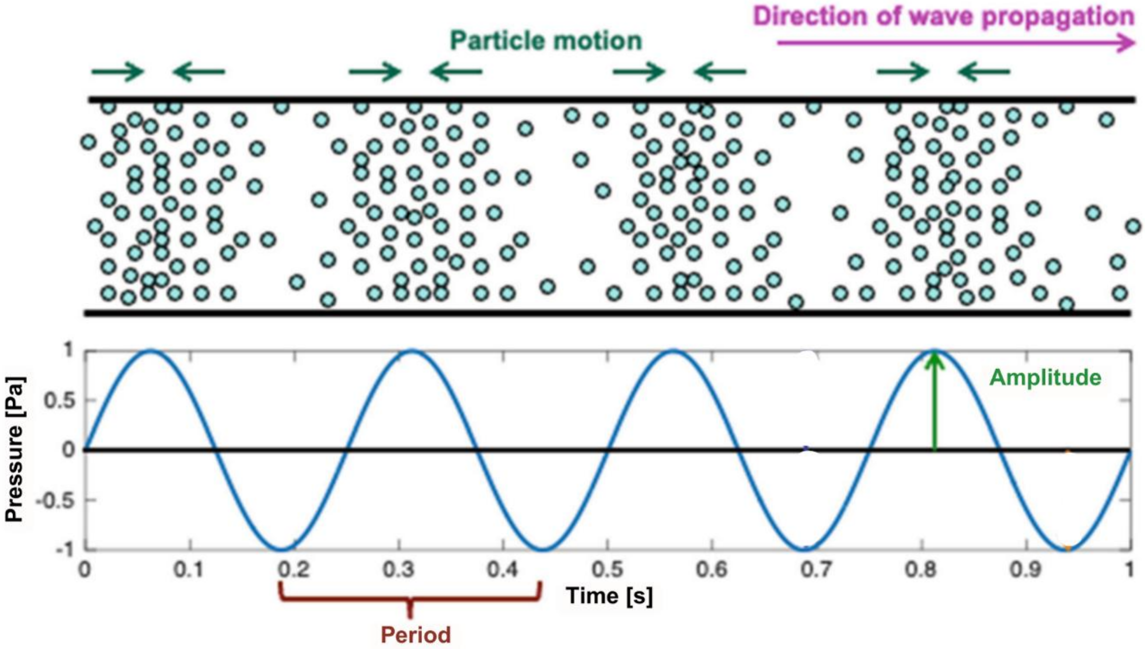

Figure A-III. 3 Sketch of alternating compression and rarefaction of water particles and the resulting pressure wave. Adapted from Erbe et.al., 2025 Springer, under the terms of the Creative Commons Attribution 4.0 International License (CC BY 4.0)

These waves can be described by several parameters, including period, frequency, wavelength, and amplitude (Bass and Clark, 2003; Au and Hastings, 2008). The period of the wave (Figure A-III. 3) is measured in seconds and refers to the time it takes for a wave to complete one full cycle (Bass and Clark, 2003). Frequency, measured in Hertz (Hz), is the inverse of the period, and represents the number of cycles a wave completes per second (Bass and Clark, 2003). In the example in Figure A-III. 3, four complete wave cycles occur within one second, resulting in a wave frequency of 4 Hz. Frequency is perceived as the pitch of the sound, with higher frequencies corresponding to higher-pitched sounds. Wavelength (λ) is the physical distance between two consecutive peaks of each wave (Bass and Clark, 2003), so it is similar to period, if the X axis (Figure A-III. 3) represented distance rather than time. Wavelength depends on both the frequency of the wave and the speed of sound in the medium. High-frequency sounds have shorter wavelengths, making the waves appear more “compressed”, whereas low-frequency sounds have longer wavelengths (Bass and Clark, 2003; Au and Hastings, 2008). Finally, amplitude represents the maximum displacement of the wave, and is related to the sound’s intensity or energy, perceived as its “loudness”. The amplitude of a sound is measured in decibels (dB), a logarithmic unit (Bass and Clark, 2003; Au and Hastings, 2008; Erbe *et al.*, 2025). These features influence how sound propagates in aquatic environments. High-frequency sounds (above 10 kHz), with shorter wavelengths, attenuate more rapidly and are better suited for short-distance signalling. In contrast, low-frequency sounds (below 1 kHz), with longer wavelengths, travel farther with less attenuation and are typically used for long-range communication (Erbe *et al.*, 2025). A particular example of this is the SOFAR (SOund Fixing And Ranging) channel (Figure A-III. 4).

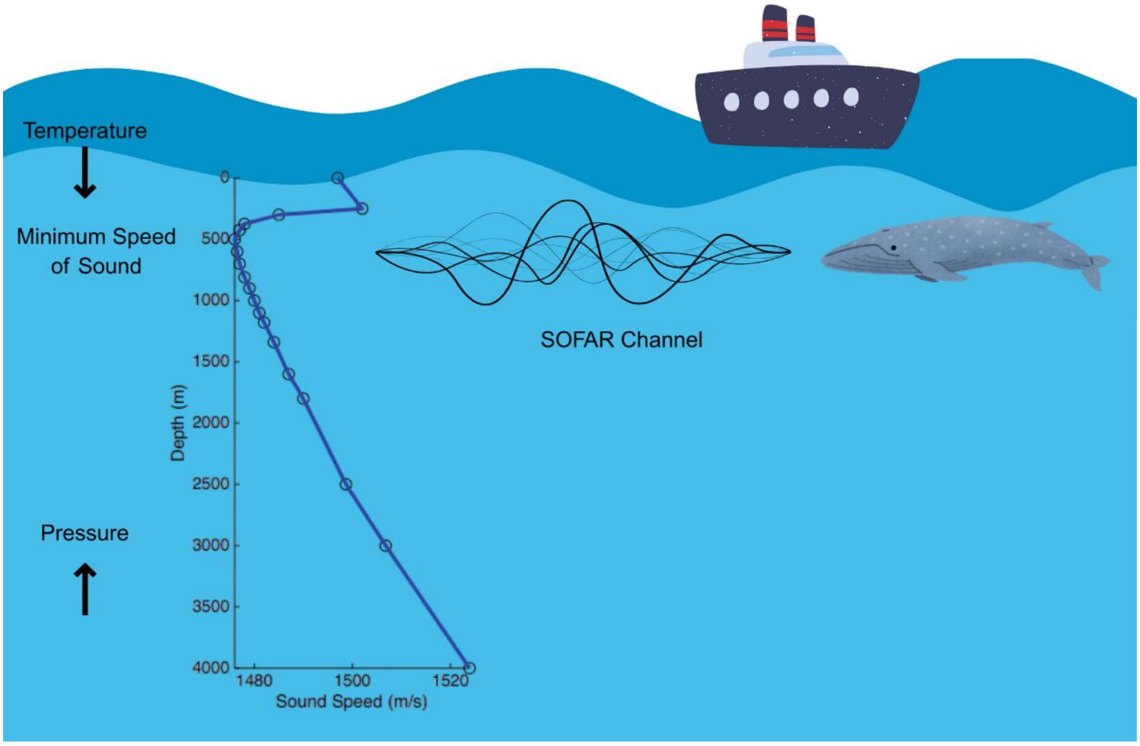

Figure A-III. 4 Visual Representation of SOFAR Channel. Modified from Erbe et al., 2025, Springer, under the terms of the Creative Commons Attribution 4.0 International License (CC BY 4.0)

The speed of sound in the ocean is primarily determined by temperature, salinity and pressure. Sound velocity decreases as temperature declines with depth, but rises again under the influence of rising pressures at even greater depths (Bass and Clark, 2003; Erbe *et al.*, 2025). This interaction produces a sound-speed profile in the water column, creating a zone where sound speed reaches a minimum. The depth of this "channel" depends on the local water mass thermocline. Within this layer, low-frequency sounds (usually below 100 Hz) are refracted back towards the channel axis, resulting in minimal transmission loss, and allowing them to propagate up to thousands of kilometres, a phenomenon that allows for many types of sounds to be detected across entire ocean basins (Bass and Clark, 2003; Erbe *et al.*, 2025).

The marine soundscape, or the ensemble of all sounds present in the ocean, can be characterised by three main sound groups: geophony, anthrophony, and biophony, which represent sounds from the natural environment, human activities, and biological sources, respectively (Erbe *et al.*, 2025) (Figure A-III. 5).

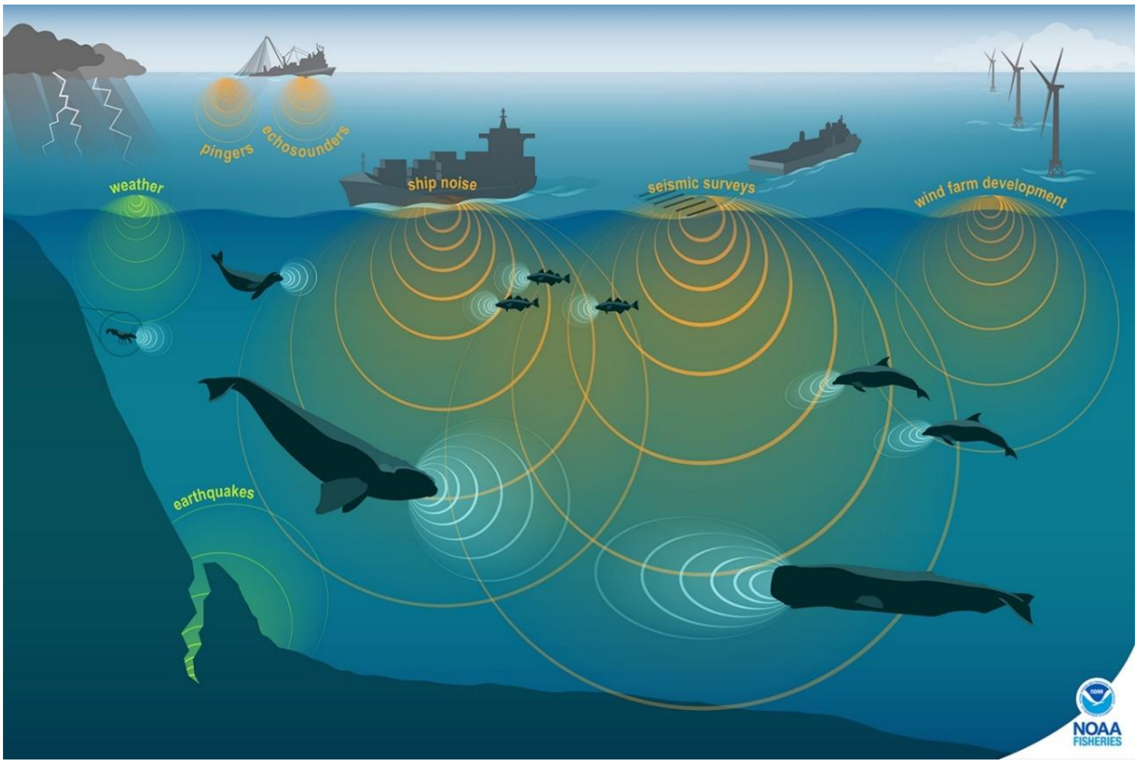

Figure A-III. 5 Marine Sound Sources: Geophony (Green), Anthrophony (Orange) and Biophony (Blue). Reproduced from Van Parijs et al., 2021, under the terms of the Creative Commons Attribution License (CC BY)

Geophony includes abiotic sounds such as rain, wind, seismic activity, ice, and volcanoes (Erbe *et al.*, 2025). Anthrophony comprises human-related sounds such as vessel noise, seismic surveys, underwater construction, and oil drilling (Erbe *et al.*, 2025). Anthropogenic noise has increased drastically over the past century and has now been recognised as a pervasive pollutant in marine ecosystems, with documented physiological and behavioural impacts on marine mammals, fish, invertebrates, and seabirds. These findings have prompted international calls for policies to address human-induced noise within the marine environment (Duarte *et al.*, 2021). Biophony comprises sounds produced by animals, with research focusing primarily on invertebrates, fish, and marine mammals (National Research Council, 2003; Erbe *et al.*, 2025). Invertebrate sounds are typically generated by mechanisms of crustacean exoskeleton stridulations or cavitation bubble formation, most commonly in shallow coastal environments (Erbe *et al.*, 2025). Snapping shrimps are among the loudest invertebrate sound producers and vary their snapping rates with abiotic factors such as temperature and time of day, although the underlying drivers of these variations remain poorly understood (Lillis and Mooney, 2016). Teleost fish represent another diverse group of sound producers, with acoustic mechanisms evolving independently multiple times. Most commonly, sounds are produced via swim bladder vibrations, although some species employ pectoral fin stridulation or bone striking (Bass and Clark, 2003; National Research Council, 2003). Fish use sounds primarily for territorial defence and competition (Hadjiaghai and Ladich, 2015; Parmentier and Fine, 2016; Rowell *et al.*, 2020), and in some species, they produce choruses, or synchronous calling by multiple individuals, which play an important role in mating and reproduction in shallow coastal environments (National Research Council, 2003; Amorim *et al.*, 2006; Rowell *et al.*, 2020). Finally, marine mammals represent the most extensively studied contributors to biophony. All species investigated to date have demonstrated the use of sound for a number of functions, supported by specialised adaptations for sound production and reception that are finely tuned to the marine environment (Herzing, 2000; National Research Council, 2003; Erbe *et al.*, 2025).

b. Cetacean Bioacoustics

Cetaceans are a specialised order of aquatic mammals, and have evolved complex acoustic communication systems that are closely linked to their ecology, physiology, and social structure (Herzing, 2000; Brumm, 2013; Erbe *et al.*, 2025). These adaptations are essential, as sound plays a critical role in their ability to navigate, forage, communicate, and maintain social cohesion in an environment where light penetration is limited and vision is often compromised (Au, Fay and Popper, 2000; Au and Hastings, 2008). Cetaceans are found in marine environments worldwide, from the equator to the poles, and are also found in some freshwater rivers and lakes. They vary widely in size from the small harbour porpoise (*Phocoena phocoena*) to the large blue whale (*Balaenoptera musculus*), with 90 presently recorded species (Au, Fay and Popper, 2000; Fordyce and Perrin, 2025).

Cetaceans produce sounds both through vocal mechanisms and non-vocal behaviours such as pectoral or fluke slaps, jaw claps, and breaching (Erbe *et al.*, 2025). The order Cetacea is divided into two suborders with different acoustic repertoires and sound production mechanisms: Mysticeti (baleen whales) and Odontoceti (toothed whales, including dolphins and porpoises). Both groups rely heavily on sound, but in different frequency ranges and for distinct ecological functions (Tyack, 1998; Janik, 2009). A key distinction between these two suborders lies in the frequency ranges used and in the directionality of sound production and reception. Because most mysticete species are larger in size than the odontocetes, they tend to produce lower frequency sounds which propagate omnidirectionally, and can travel hundreds of kilometres, facilitating long-range communication (Au, Fay and Popper, 2000; Erbe *et al.*, 2025). Odontocetes, on the other hand, use higher frequency sounds and use echolocation by emitting highly directional clicks into narrow beams and receiving returning echoes with high spatial resolution, an advanced biosonar that enables them to have detailed auditory images of their surroundings (Au, Fay and Popper, 2000; Erbe *et al.*, 2025). These functional divergences align with the social and ecological needs of the two groups.

i. Odontocete Sounds

Unlike terrestrial mammals or baleen whales that use vocal folds in the larynx, odontocete cetaceans generate sounds pneumatically within their nasal passages (Cranford, Amundin and Norris, 1996). Because of this, some researchers consider the term “vocalisation” incorrect, as this term is usually reserved for laryngeally-produced sounds, with “phonation” being more appropriate (Herzing, 2000; Au and Hastings, 2008). Despite this, the term is frequently used within the literature (Caldwell and Caldwell, 1968; Herzing, 1996, 2000; Jones *et al.*, 2019; King *et al.*, 2019), and will therefore be used throughout this thesis to refer to sounds produced by odontocetes.

Sound is produced when pressurised air is forced through specialised structures called "phonic lips", located just below the nasal plugs (Figure A-III. 6) (Cranford, 2000; Madsen, Siebert and Elemans, 2023). This action causes the phonic lips to rapidly open and close, causing vibrations that result in acoustic pulses (Ridgway *et al.*, 1980; Cranford, 2000; Madsen, Siebert and Elemans, 2023). Most odontocetes have two pairs of phonic lips (one on each side of the nasal passage), enabling them to generate complex acoustic patterns, and there is increasing evidence that the right pair is predominantly responsible for echolocation clicks (Ames, Beedholm and Madsen, 2020). Once air passes through the phonic lips, it is channelled into a set of air sacs where it can be recirculated back into the lungs. This mechanism allows animals to reuse the same air for sound production without needing to surface (Au, Fay and Popper, 2000).

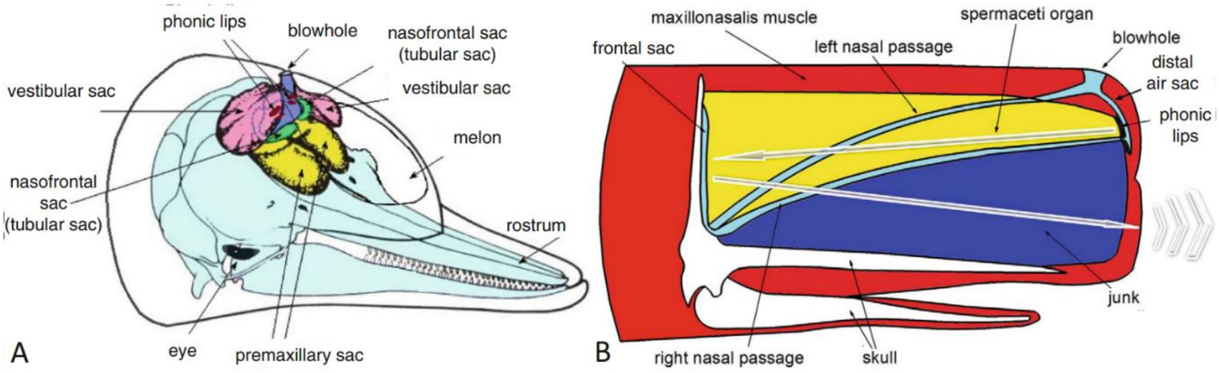

Figure A-III. 6 Sound production anatomy in the dolphin (a) and sperm whale (b). Reproduced from Erbe et al., 2025, Springer, under the terms of the Creative Commons Attribution 4.0 International License (CC BY 4.0)

Once the sounds are produced, they are then channelled through the melon, a lipid-rich structure in the front of the head. This organ acts as a sound amplifier, its unique acoustic fat composition helping to focus the sound and ensuring highly directional transmission (Cranford, Amundin and Norris, 1996; Au and Wei, 2017; Wei *et al.*, 2017). Sound reception in this suborder is equally specialised. Odontocetes do not rely on external ears ("pinnae"), although they do have vestigial ear canals that have filled with wax over evolutionary time and do not appear to have an active function in the reception of sounds (Ridgway, 2000). Instead, odontocetes receive sounds primarily through fat-filled channels in their lower jaw (Mandibular Fat Body, Figure A-III. 7), called the "pan" region, acoustic window, which then transmit vibrations to the middle ear bones (Ketten, 2000; Cranford, Krysl and Amundin, 2010) (Tympanoperiotic Complex, TPC, Figure A-III. 7). Further studies demonstrated the presence of two separate acoustic windows and that dolphins acquire sounds from the lower end of the frequency spectrum through highly specialised middle ear bones (Popov *et al.*, 2008). The physical separation of these two auditory pathways further enhances their sound localisation abilities, which are useful for echolocation (Brill *et al.*, 2001). Odontocetes are capable of producing and perceiving sounds across a very wide frequency range (Au, Fay and Popper, 2000), from below 30 Hz (Gridley *et al.*, 2015; Samarra, Deecke and Miller, 2016) to over 200 kHz (Verboom and Kastelein, 1995), although they typically operate in the “ultrasonic” range, or above the 20 kHz limit of human hearing (Hopp, Owren and Evans, 1998). Within the odontocete suborder (75 species), most species (38 species) belong to the *Delphinidae* family (Fordyce and Perrin, 2025), and small cetaceans are generally easier to study, particularly as some can be kept in captivity for experimental research (Au, Fay and Popper, 2000).

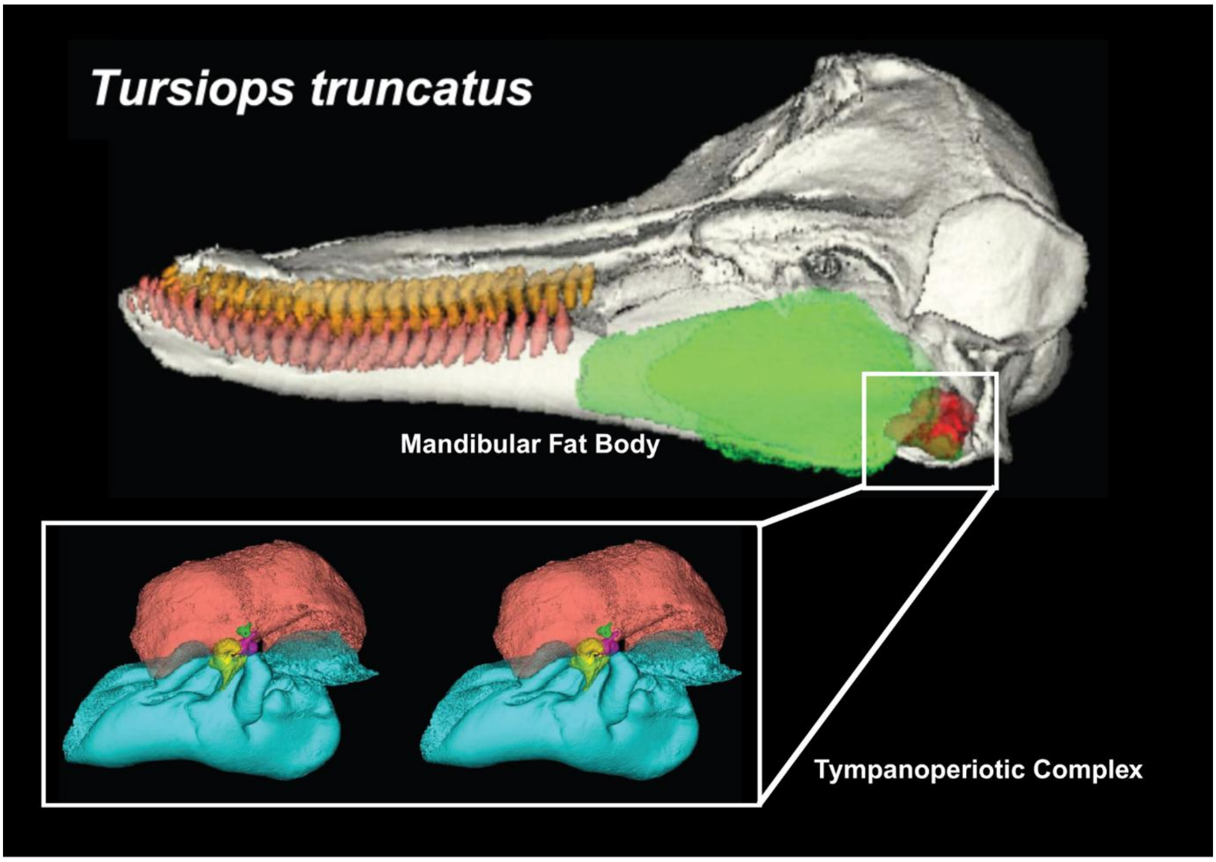

Figure A-III. 7 Left lateral view of the Atlantic Bottlenose Dolphin (Tursiops truncatus) from CT reconstructions (top) with left mandibular fat body (green) and left TPC (red). Stereogram of lateral view of the Tympanoperiotic Complex from Tursiops truncatus (bottom). The periotic bone is salmon coloured, the tympanic bone is coloured cyan, and the ossicles are coloured as follows: malleus = yellow, incus = magenta, stapes = green. Adapted from Cranford, Krysl and Amundin, 2010, PLoS ONE, under the terms of the Creative Commons International License

C. DOLPHIN SOUNDS

Acoustic communication in dolphins is among the most complex of any non-human animal (Herzing, 2000; Janik, 2009). This reflects these animals' advanced cognitive capacities and the demands of their complex societies that display fission-fusion dynamics (Connor *et al.*, 2000; Aureli *et al.*, 2008), where individuals frequently change associations and must maintain cohesion and coordinate activities (Connor *et al.*, 2000; J Mann *et al.*, 2000).

The complexity of dolphin communication is reflected in their cognitive and behavioural capacities, including problem-solving, adaptability, and long-term memory (Herzing, 2000; Janik, 2013). Dolphins are capable of integrating signals from different communication channels (e.g., visual, tactile and acoustic), showing cross-modal perception (Herzing, 2000) and displaying potential for "Theory of Mind", by recognising the intentions and beliefs of conspecifics, although more information is needed to confirm this (Janik, 2009, 2013). A particular ability shown by dolphins that is not widespread in the animal kingdom is the concept of vocal learning, which encompasses both production learning and social adaptation. Dolphins not only learn to produce novel sounds and mimic them, but can also adapt their vocalisation according to social context and feedback (Tyack and Sayigh, 1997; Herzing, 2000; Janik, 2009). This ability is clearly illustrated by the development of signature whistles (discussed further in section ii), where individuals create unique frequency-modulated contours in their first months of life from other individuals around them, use them for individual recognition, and can even address one another by imitating conspecifics' whistles in a form of referential labelling analogous to the use of names (Tyack and Sayigh, 1997; Janik and Slater, 2000; Janik, 2013). Beyond individual recognition, the functional use of vocal signals plays a crucial role in facilitating group organisation, cohesion and the ability to listen in on conspecific signalling through eavesdropping (Herzing, 2000; Janik, 2009, 2013).

Dolphin sounds can broadly be categorised into two functional groups: echolocation, used primarily for navigating and foraging, and communication or social sounds, which support a range of social and behavioural interactions (Herzing, 2000; Au and Hastings, 2008; Erbe *et al.*, 2025). Within this framework, there are three main categories of vocalisations recognised: echolocation clicks, burst-pulsed sounds, and tonal sounds, also known as whistles (reviewed in Jones *et al.*, 2019). The basic sound production mechanism for all three sound types is the same, and is the pneumatic ”click” (described in section i), and it is the inter-click interval (ICI), or the speed at which the clicks are produced, that determines whether the sound will acquire a "tonal" quality (Jones *et al.*, 2019). These sound types differ in their physical and spectral characteristics and in the context in which they are produced, with echolocation clicks being mainly used for orientation and foraging, and whistles and burst-pulsed sounds making up the communication category (Herzing, 2000; Janik, 2009; Jones *et al.*, 2019), although some species do not use whistles, and echolocation clicks might also serve social or communication purposes (Dawson, 1991). The following sections will outline these major sound categories, their characteristics, and their known or hypothesised functions, highlighting the role they play in dolphin communication and behaviour.

a. Echolocation

Echolocation or biosonar is one of the defining characteristics of odontocete cetaceans, a trait they share with bats, and some species of birds and rodents (Brinkløv, Jakobsen and Miller, 2022). By emitting discrete high-frequency clicks and analysing the returning echoes that reflect off objects or other animals, dolphins have developed a sophisticated way to sense their surroundings through sound (Au, 2000; Au and Hastings, 2008). Echolocation likely evolved as an adaptation to navigate environments with limited visibility, enabling animals to locate barriers, objects, and their distance from them, as well as determine whether these objects are in motion (Brinkløv, Jakobsen and Miller, 2022). In dolphins, echolocation is particularly advanced due to specialised adaptations for producing and receiving high-frequency sounds, and the process can be divided into three phases: transmission, reception, and signal processing (Au, 1993, 2000; Au and Hastings, 2008). As described previously, dolphins produce echolocation clicks with their phonic lips, projecting them through the melon as highly-directional beams (Au and Wei, 2017; Madsen, Siebert and Elemans, 2023). These broadband pulses are short, lasting 40-70 µs, and span 40-150 kHz depending on context and species (Au, 1993; Au and Hastings, 2008; Au and Wei, 2017) (Figure A-III. 8).

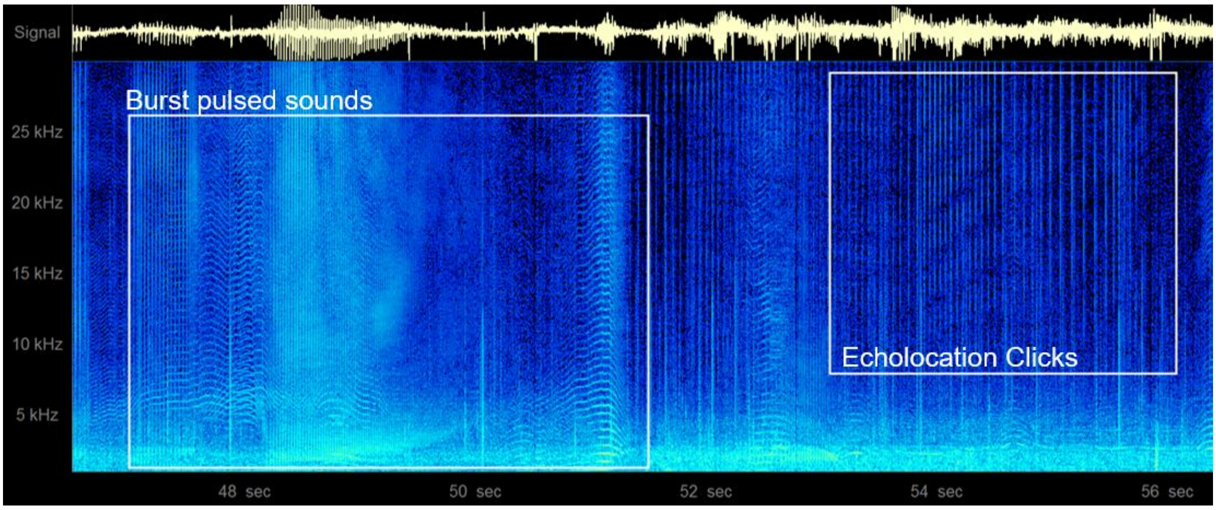

Figure A-III. 8 Spectrogram showing bottlenose dolphin burst pulsed sounds and echolocation clicks, displayed using SPECTROGRAM © version 6.2.3. FFT=4096, display frame duration= 10 s. This image was generated from an acoustic recording collected by the Bottlenose Dolphin Research Institute (BDRI) and processed by the author for this thesis

The temporal spacing of clicks (inter-click interval, ICI) is actively modulated depending on the task. During foraging, ICI usually decreases with prey detection and pursuit, terminating in "buzzes" before capture (Madsen and Surlykke, 2014; Erbe *et al.*, 2025) and "victory squeals" after prey capture (Ridgway *et al.*, 2014, 2015), although this vocalisation is thought to belong in the Burst-pulsed category (Jones *et al.*, 2019). What makes dolphin echolocation successful is the complex neural and sensory processing, with their auditory system capable of detailed spectral analysis, spatial resolution, and temporal pattern recognition (Au, 1993; Au and Hastings, 2008). Dolphins process echoes in real time, timing each click to the receipt of the previous echo, allowing them to discriminate between objects with great precision (Au, 2000; Madsen and Surlykke, 2014) (Figure A-III. 9).

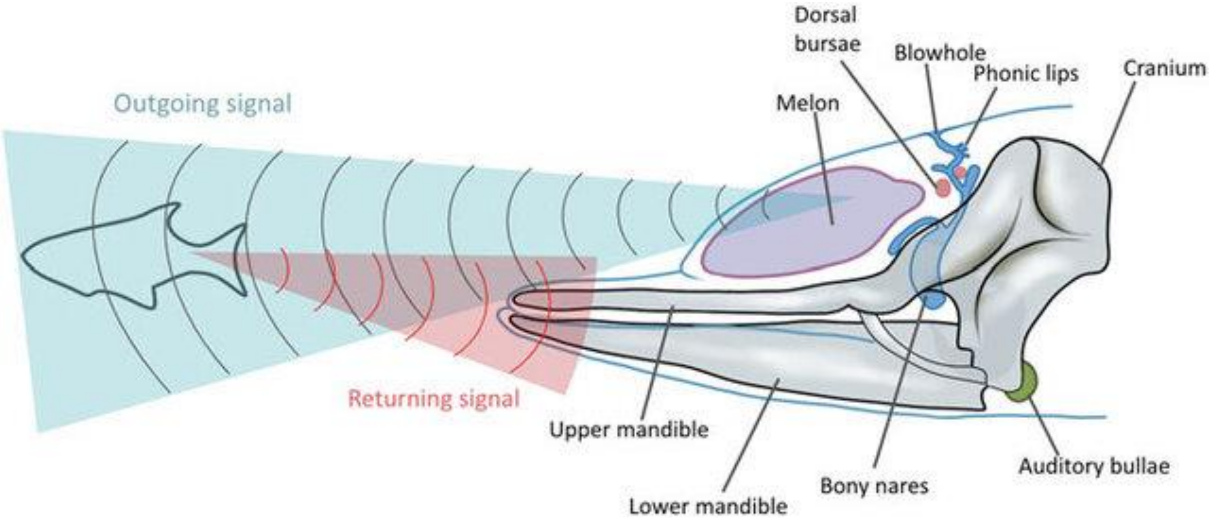

Figure A-III. 9 Schematic of Echolocation in Odontocetes with outgoing clicks represented in blue and the returning echo in red. Reproduced from Natoli and Al Hameli, 2024, Springer, under the terms of the Creative Commons Attribution 4.0 International License (CC BY 4.0)

In addition to identifying and pursuing prey, echolocation functions include navigation and orientation in low-visibility environments, as well as detecting potential predators (Au, 1993, 2000; Au and Hastings, 2008).

b. Burst-Pulsed Sounds

Burst-pulsed sounds (BPs) are among the most commonly produced yet least studied and standardised dolphin vocalisations, and are often the default category for sounds that do not have the characteristics of whistles or echolocation clicks (Herzing, 2000; Janik, 2009; Jones *et al.*, 2019). Structurally, BPs consist of rapid sequences of broadband clicks, produced at inter-click intervals of less than 10 ms, with frequency elements exceeding 100 kHz (Lammers *et al.*, 2004; Jones *et al.*, 2019) (Figure A-III. 8). Although they are produced with the same mechanism as echolocation clicks, the rapid repetition rate produces an apparent tonal quality to human listeners (Jones *et al.*, 2019). A main challenge in the study of BPs lies in their classification. Historically, they have been described using subjective, human-auditory labels such as “barks”, “brays”, “squawks”, “chirps”, etc., with researchers often developing their own terminology, complicating cross-study comparisons (Luís, Couchinho and dos Santos, 2016; Jones *et al.*, 2019). Other approaches have relied on signal duration, by labelling sounds “short” or “long”, based on a cutoff value (Díaz López and Bernal Shirai, 2010). Given these limitations, a standardised framework based on measurable acoustic parameters such as pulse interval, duration, and spectral features would advance the comparability and interpretation of future studies (Janik, 2009; Luís, Couchinho and dos Santos, 2016; Jones *et al.*, 2019).

Functionally, BPs are considered social signals used to mediate interactions and convey emotional states. Several studies have linked BPs to contexts of aggression and competition where sounds such as "squawks", "barks", and "screams" co-occur with visual and tactile signals like open mouth displays and body charges (Caldwell and Caldwell, 1966; Overstrom, 1983; Herzing, 2000), or as disciplinary signals between mothers and calves (McCowan and Reiss, 1995). Seasonal variation in their occurrence (Díaz López, 2022), the use of genital buzzes as both acoustic and tactile signals (Herzing, 2000), and their association with mate guarding in herding males (King *et al.*, 2019) highlight the role of BPs in mating contexts. BPs are also produced in foraging contexts, in the form of "victory squeals" following prey capture (Ridgway *et al.*, 2014, 2015), and for prey behaviour manipulation (V. M. Janik, 2000).

c. Tonal Sounds - Whistles

Whistles are the most frequently studied dolphin vocalisation, largely because they are relatively easy to record with good signal quality and allow for detailed acoustic measurements compared to other sound types (Caldwell, Caldwell and Tyack, 1990; Boisseau, 2005; Janik, 2009). Whistles are defined as narrow-band tonal signals lasting longer than 0.1 s (often up to a few seconds), with a modulated contour and at least part of the fundamental frequency above 3 kHz, typically ranging between 2 and 35 kHz (Janik, 2009; Janik and Sayigh, 2013a; Kriesell *et al.*, 2014; Jones *et al.*, 2019) (Figure A-III. 10). The fundamental frequency is the lowest and dominant contour of each whistle, and there are reflections of the contour at higher frequencies, called "harmonics" (Lammers and Au, 2003; Janik, 2009). Harmonics can reach frequency ranges beyond 100 kHz, and it is sometimes difficult to determine how many harmonics are present for a whistle, and this is sometimes due to the recording equipment and the nature of these sounds (Jones *et al.*, 2019). Given the difference in frequency, the fundamental frequency tends to propagate more omnidirectionally, whereas the higher-frequency harmonics are more directional, potentially encoding information about the sender's location and orientation, and only being recorded if the equipment is right in front of the animal producing the sound (Lammers and Au, 2003; Branstetter *et al.*, 2012).

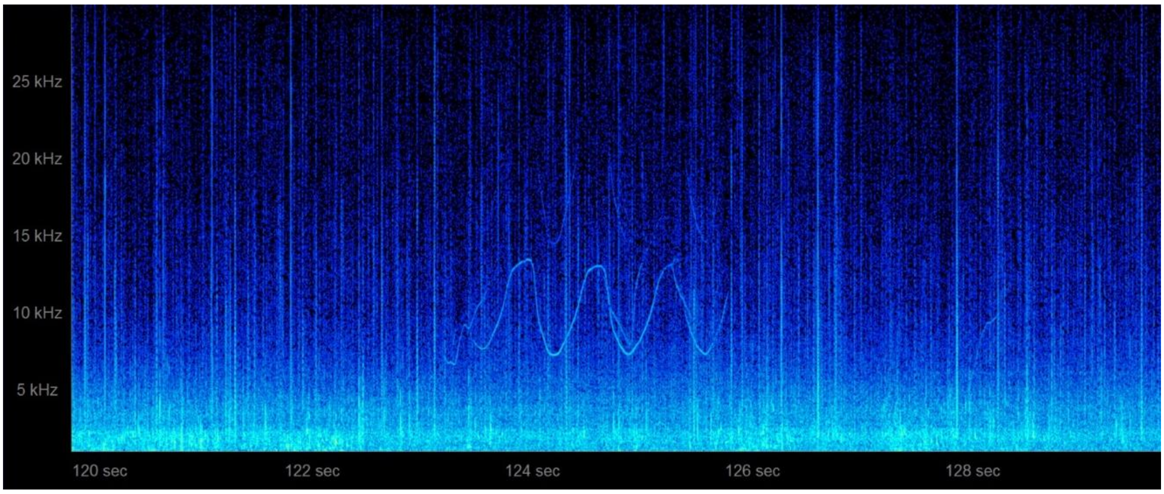

Figure A-III. 10 Spectrogram of a bottlenose dolphin whistle, displayed using SPECTROGRAM © version 6.2.3. FFT=4096, display frame duration= 10 s. This image was generated from an acoustic recording collected by the Bottlenose Dolphin Research Institute (BDRI) and processed by the author for this thesis

Whistle contours are extensively studied by analysing the shape of the signal, the inflection points, and a number of other characteristics. The fundamental frequency is the one studied, and it is done visually, and whistles are usually broadly divided into "type" based on the characteristics of their modulation patterns (Janik, 2009; Díaz López, 2011; Sayigh *et al.*, 2022). Whistles also vary across populations, with different degrees of production rates, frequency modulation, and contour complexity reported (Jones and Sayigh, 2002; Morisaka *et al.*, 2005; May-Collado and Wartzok, 2008; Luís *et al.*, 2021).

Whistles play a central role in dolphin social communication. They contribute to group cohesion (Janik and Slater, 1998), act as contact calls between mothers and calves (Sayigh *et al.*, 1990; Smolker, Mann and Smuts, 1993; Fripp and Tyack, 2008) and occur in a variety of emotional contexts (Herzing, 2000; Janik, 2009; Janik and Sayigh, 2013a; Sayigh *et al.*, 2022). Whistle production is also behaviour-dependent, with higher rates observed during socialisation and high-activity behaviours (Quick and Janik, 2008; Hawkins and Gartside, 2010; Hernandez, Solangi and Kuczaj, 2010; Díaz López, 2011).

There are two broad categories of whistles recognised in the literature: the more well-studied signature whistles (Caldwell and Caldwell, 1965; Caldwell, Caldwell and Tyack, 1990; Janik and Sayigh, 2013a), which are stereotyped and individually distinctive, and variant whistles, which are less well understood and may be more associated with certain behaviours (Sayigh *et al.*, 1990, 2025; Lopez-Marulanda *et al.*, 2020; Patiño-Pérez *et al.*, 2024).

ii. Signature Whistles

Signature vocalisations, or individually distinctive sounds, have been identified in numerous species (Shapiro, 2006, 2010; Elie and Theunissen, 2018; Marconi *et al.*, 2020; Bowmaker-Falconer *et al.*, 2022; Lehmann *et al.*, 2022), but the best-documented example likely is the bottlenose dolphin, with more than 60 years of research on the subject (Janik and Sayigh, 2013a). Most vocally active animals can be recognised through "byproduct distinctiveness" or "voice cues" that arise from individual anatomical differences in the vocal apparatus (Sayigh, Wells and Janik, 2017). Dolphins, however, produce sounds pneumatically in the nasal passages rather than through vocal folds, and therefore lack such inherent distinctiveness, and have evolved individualised calls that function as acoustic identifiers (Caldwell and Caldwell, 1965; Caldwell, Caldwell and Tyack, 1990; Sayigh, Wells and Janik, 2017; Sayigh *et al.*, 2022). Signature whistles are frequency-modulated, stereotyped calls that are unique to each individual and remain stable over many years (Sayigh *et al.*, 1990; Luís, Couchinho and dos Santos, 2015; Rachinas-Lopes *et al.*, 2017). Early studies on captive animals defined signature whistles as the most common whistle produced by a dolphin when isolated from its group (Caldwell and Caldwell, 1965, 1968), making up to 90% of vocalisations in each dolphin. (Sayigh *et al.*, 2007). In free-swimming individuals, this proportion decreases with production rates ranging between 38 and 70% (Cook *et al.*, 2004; Watwood *et al.*, 2005). A defining feature of signature whistles is the presence of repetitive elements or "loops". Contours without a repetitive unit are "single-loop" whistles, whereas those with repeated elements are "multi-loop" whistles (Caldwell, Caldwell and Tyack, 1990). These loops can vary slightly in frequency between the "starting" and "ending" loops and the repeated units in the middle, and are considered part of the same whistle when separated by less than 250 ms, on average 100 ms apart (Figure A-III. 11) (Esch, Sayigh and Wells, 2009).

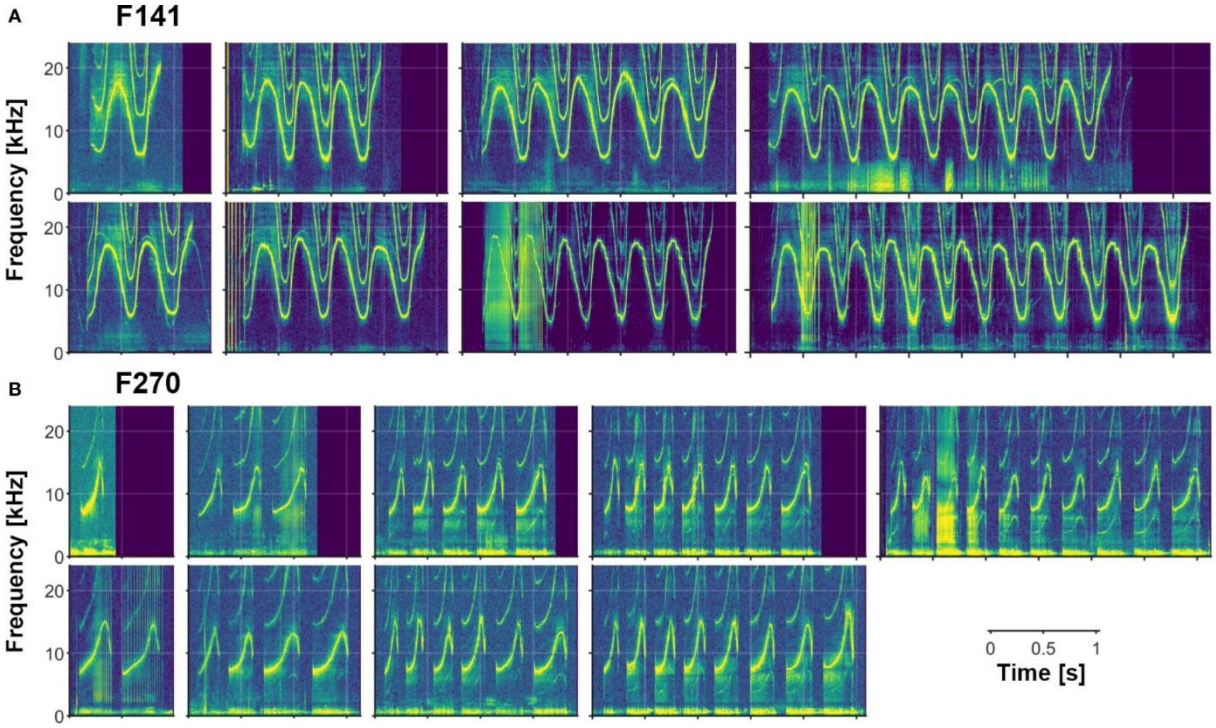

Figure A-III. 11 Examples of varying numbers of loops in multi-loop signature whistles from two different individuals (A and B) from the Sarasota Bay Dolphin Project Catalogue. Reproduced from Sayigh *et al.*, 2022 under the terms of the Creative Commons Attribution License (CC BY)

Signature whistles often occur in bouts or sequences. An established identification technique was proposed by Janik (2012) (SIGID), which considers a whistle a signature if it occurs at least 75% of the time within a bout with inter-whistle intervals of 1-10 s. This allows for the identification of about 50% of signature whistles correctly, with no false positive detections (Janik and Sayigh, 2013a). Although conservative, this approach reliably distinguishes signature whistles from other whistle types, which are otherwise structurally similar (Janik and Sayigh, 2013a). Signature whistles typically span frequencies of 1-30 kHz and last between 0.1 and 4 s (Buckstaff, 2004; Janik and Sayigh, 2013a). As with the broader category of whistles, signatures are also often grouped into "types" based on contour similarities, and although there are technological advances in automated classification tools, human visual classification remains the best, though more time-consuming, approach (Sayigh *et al.*, 2022).

Dolphins develop their own signature whistles within the first few months of life through vocal production learning (Tyack and Sayigh, 1997; Janik and Slater, 2000; Janik and Sayigh, 2013a). Mothers increase whistle output in the weeks post-partum (Fripp and Tyack, 2008), and evidence from cross-fostering experiments and captive studies shows that calves do not simply copy their mother's whistle, but instead incorporate acoustic elements from their social group and surroundings (Caldwell and Caldwell, 1979; Tyack and Sayigh, 1997). Once crystallised, a signature whistle typically remains stable for years, enabling the creation of catalogues for known individuals in well-studied populations like Sarasota Bay, Florida (Sayigh *et al.*, 1990, 2022; Luís, Couchinho and dos Santos, 2015). Some individuals, however, may alter their contour over time (Sayigh *et al.*, 2022), and within-individual variation (eg, number of loops used, and why this variation may occur) remains an active research topic (Sayigh *et al.*, 2022). Beyond self-identification, dolphins also exhibit "whistle matching", in which one dolphin reproduces another's signature. This behaviour, most often observed in closely affiliated individuals, is thought to function as a form of referential labelling, similar to using names, and requires memory of other individuals' signatures (Sayigh *et al.*, 1990; King, Harley and Janik, 2014). Copied whistles often contain slight contour modifications, distinguishing them from the original, and although more research is needed, their function appears to be to initiate contact with the individual in question (King, Harley and Janik, 2014). In some cases, groups with long-term alliances may even share signature whistles (Jones *et al.*, 2020), and additional information may be encoded in amplitude modulation in addition to the frequency (Jones *et al.*, 2021).

Signature whistles are used in diverse social contexts, but their primary role appears to be maintaining contact between separated individuals, such as mothers and calves (Sayigh *et al.*, 1990; Smolker, Mann and Smuts, 1993) and promoting group cohesion through reunion (Janik and Slater, 1998). Elevated production of signature whistles during capture events further supports their role as cohesion or distress signals (Esch *et al.*, 2009).

iii. Non-Signature Whistles

In addition to signature whistles, bottlenose dolphins produce other frequency-modulated tonal vocalisations that lack the stereotyped characteristics. Historically referred to as “variant” or “aberrant” whistles, they are now referred to as non-signature whistles (NSW) (Sayigh *et al.*, 2022). These signals can account for 40-70% of whistles in free-swimming population (Buckstaff, 2004; Cook *et al.*, 2004; Watwood *et al.*, 2005), and despite their ubiquity and decades of research on dolphin vocalisations, NSW remain relatively underexplored compared to signature whistles, and their functions are still poorly understood (Janik and Sayigh, 2013a; Sayigh *et al.*, 2022, 2025). In captivity, NSW can also represent a substantial proportion of an individual’s vocal output, ranging from 6% to over 50% depending on the age and sex of individual, and the context (Caldwell, Caldwell and Tyack, 1990; Tyack and Sayigh, 1997; Rachinas-Lopes *et al.*, 2017).

Non-signature whistles are also often divided into types or categories based on shape, such as “upsweep”, “downsweep”, “sine” (Lopez-Marulanda *et al.*, 2020; Sayigh *et al.*, 2025), and some whistle types have been associated with specific behavioural contexts, including social interactions or foraging (Díaz López, 2011; Sayigh, 2013). Studies in captivity further suggest that NSW may be associated with different behavioural contexts (Lopez-Marulanda *et al.*, 2020), while research on free-ranging populations has reported geographical variation in NSWs. Such variation may be shaped by acoustic adaptation to local environments, social factors such as calf presence or social complexity, and cultural transmission within isolated populations (Patiño-Pérez *et al.*, 2024). The Sarasota study further suggests that NSW may themselves be learned and referential signals, with functions ranging from alarm to query. Their occurrence across highly variable contexts points to a context-dependent role, reinforcing both the complexity of dolphin communication systems and their potential to exhibit language-like properties (Sayigh *et al.*, 2025).

D. COLLECTING BIOACOUSTICS DATA

The field of cetacean bioacoustics began in the 1950s when the first beluga sound was recorded in 1949 (Schevill and Lawrence, 1949). Much of the early research was initially funded and supported by Navy programs interested in understanding sonar effects and developing knowledge of biosonar and echolocation, advancing the development of related equipment (Hopp, Owren and Evans, 1998). These early efforts, often referred to as the “analogue era”, relied on bulky equipment, limited recording times, cassette tape recorders, and hard copies of spectrographs on which measurements were made manually with rulers (Pavan *et al.*, 2022). In the 1980s, technological advances such as the compact disc brought about a “digital revolution” in the field, with more sophisticated digital processing capabilities, which led to more precise and efficient processing of acoustic data (Pavan *et al.*, 2022).

Collecting sounds underwater requires two main tools: the hydrophone (an underwater microphone) and a recorder to store sounds, so they can be later processed and analysed. A hydrophone is a transducer that converts the mechanical pressure of sound waves in the water into electrical signals (Au and Hastings, 2008; Erbe, 2022). This is achieved through piezoelectric ceramics, which are materials that generate an electrical charge when subjected to mechanical stress, in proportion to the applied pressure (Au and Hastings, 2008; Erbe, 2022; Erbe *et al.*, 2025). The recorder then captures these signals by converting continuous analogue information into digital samples. The sampling frequency or sampling rate is the number of times that the signal’s amplitude is measured and converted to a digital number (44 kHz means

44000 samples taken per second) (Clements, 1998). The Nyquist frequency, which is half the sampling frequency, is the maximum frequency that can accurately be represented in a digital signal (Stoddard, 1998), so if a recorder has a sampling frequency of 96 kHz, the maximum frequency that can be visualised is 48 kHz. Once digitised, the signal is then processed with a mathematical algorithm called the Fast Fourier Transformation (FFT) (Clements, 1998; Au and Hastings, 2008), which allows the sounds to be visualised as a "spectrogram", visually representing the sound's energy (amplitude, shown as colour) as a function of frequency (y axis) and time (x axis) (Figure A-III. 12). Spectrograms allow researchers to visualise recordings, as well as collect additional information about the sounds recorded within them.

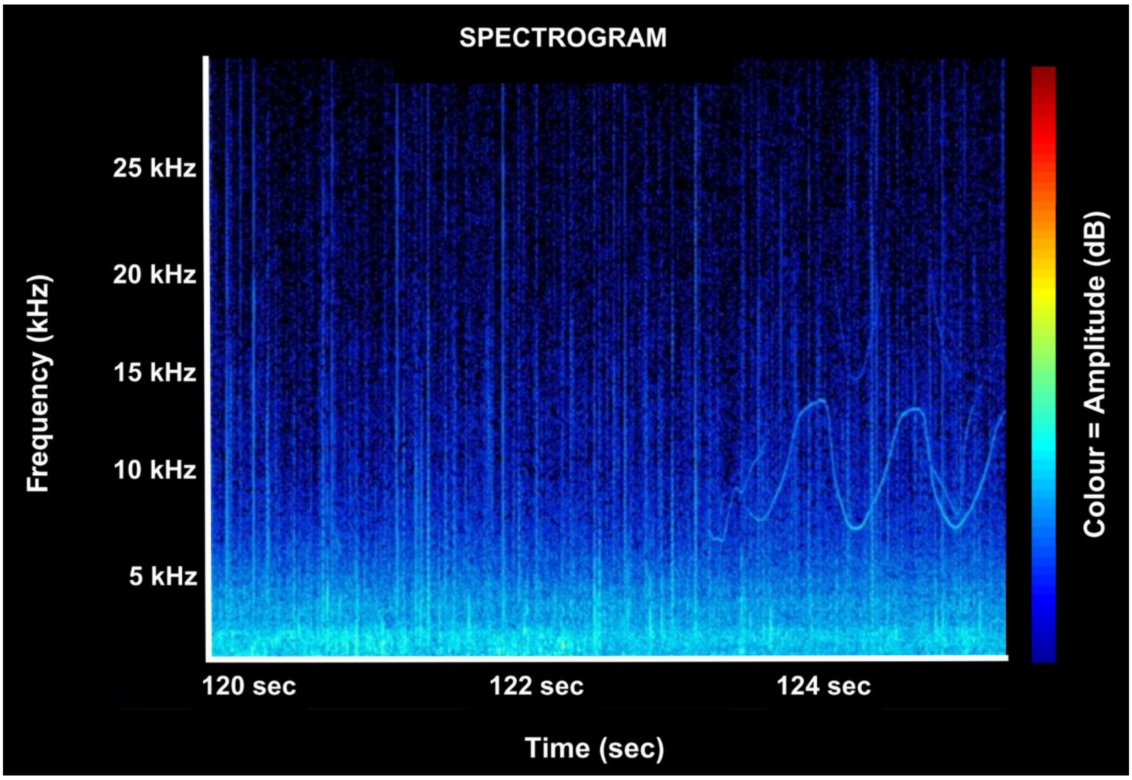

Figure A-III. 12 Illustration of a Spectrogram, displayed using SPECTROGRAM © version 6.2.3. This image was generated from an acoustic recording collected by the Bottlenose Dolphin Research Institute (BDRI) and processed by the author for the purposes of this thesis

In the field, there are a number of ways to collect bioacoustics data (Figure A-III. 13). These range from biologging tags attached directly to animals (Johnson, Aguilar De Soto and Madsen, 2009; Clayton *et al.*, 2023), to stationary, bottom-mounted devices, gliders, or free-floating buoys and equipment deployed from vessels, whether stationary or underway (Zimmer, 2011; Van Parijs *et al.*, 2021). Some approaches require the presence of observers and are coupled with visual monitoring, while others operate autonomously. Each technique has strengths and limitations, and the choice depends on the research questions, logistical feasibility, and the spatial and temporal scales of monitoring.

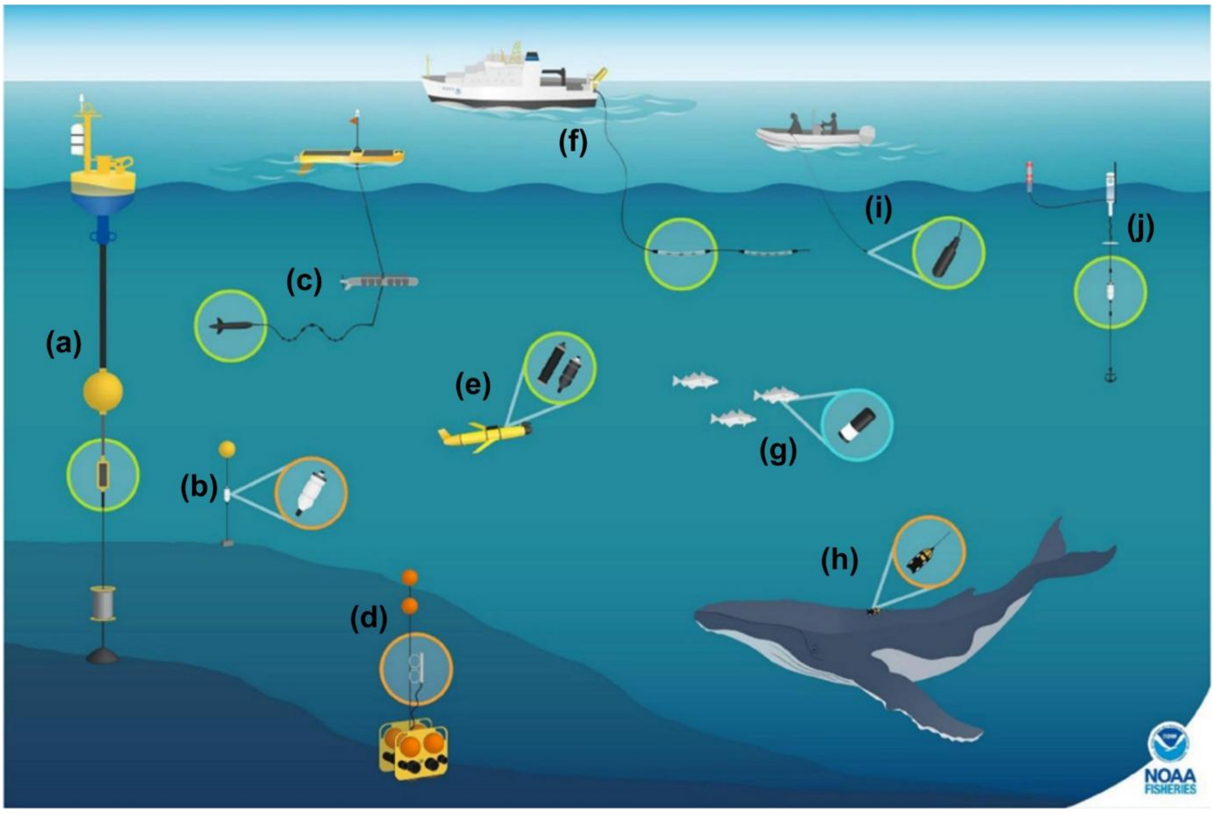

Figure A-III. 13 Examples of different types of acoustic technologies. (a) moored surface buoy, (b) SoundTrap on the seafloor, (c) wave glider, (d) bottom-mounted acoustic recorder (High-frequency Acoustic Recording Package [HARP]), (e) Slocum glider, (f) ship towing a hydrophone array, (g) Atlantic cod with telemetry tag, (h) humpback whale with an archival tag, (i) drop hydrophone deployed from a small boat, (j) autonomous, free-floating acoustic recorder (Drifting Acoustic Spar Buoy Recorder [DASBR]). The different technologies are highlighted with colored circles that show a zoomed-in view of the instruments and colors that represent the type of data collected: green for real-time data capabilities, orange for archival data, and blue for active acoustics. Adapted from Van Parijs *et al.*, 2021, under the terms of the Creative Commons Attribution License (CC BY)

E. THE COMMON BOTTLENOSE DOLPHIN (*TURSIOPS TRUNCATUS*)

The following sections present background information on the model species studied in this thesis, the common bottlenose dolphin (*Tursiops truncatus*, Montagu 1821, hereafter referred to as bottlenose dolphin).

a. Characteristics and Life History

The bottlenose dolphin (*Tursiops truncatus*) is a marine mammal species within the order Cetacea, suborder Odontoceti (toothed whales), and family Delphinidae (Jefferson *et al.*, 2015). It has a robust, streamlined body, a noticeable melon, a short and well-defined rostrum, and a tall, falcate dorsal fin (Wells and Scott, 2009) (Figure A-III. 14). This animal's colouration exhibits countershading, with a dark grey colour typically found on the dorsal side, fading to lighter grey on the sides, and a pale white colour on the ventral surface, which can sometimes have pink hues (Wells and Scott, 2009; Jefferson *et al.*, 2015). Some individuals display a lighter blaze along the sides, faint cape patterns on the back, or even subtle striping from the blowhole to the melon and around the eyes. Individual and regional colour variation is common and may be related to age, sex, or habitat (Wells and Scott, 2009; Jefferson *et al.*, 2015).

Figure A-III. 14 A bottlenose dolphin in Galicia, Spain. Photo credit: Olga Mosca – BDRI

Adults can measure from 1.9 to 4.1 m in length and weigh between 150 and 650 kgs. Males tend to be larger than females, a form of sexual dimorphism that can vary geographically and by ecotype (Tolley *et al.*, 1995; Wells and Scott, 2009). For example, individuals inhabiting colder waters, such as the eastern North Atlantic, tend to be larger than those in warmer, tropical regions (Wells and Scott, 2009). Individuals typically have 18 to 27 pairs of teeth in each jaw, used for grasping their prey rather than chewing it. In older individuals, teeth may be significantly worn down, or some may be lost altogether (Jefferson *et al.*, 2015).

Females tend to reach sexual maturity before males, between the ages of five and 13, while males mature between nine and 14 years of age (Wells and Scott, 2009; Barratclough *et al.*, 2024; Wells *et al.*, 2025). Life expectancy also differs on average between sexes, with females living over 50 years, and males beyond 40 years (Wells and Scott, 2009). A recent study on one of the longest-monitored bottlenose dolphin populations reports maximum recorded ages of 67 years for females and 52 years for males (Wells *et al.*, 2025). These values, however, may reflect population-specific patterns, and survival rates and longevity may vary across regions (Wells and Scott, 2009), and may be influenced by environmental contexts (Booth and Thomas, 2021) and anthropogenic pressures (Corr *et al.*, 2024).

The bottlenose dolphin exhibits a gestation period of about 12 months, after which a single calf is born. At birth, calves typically measure 1.0–1.3 m in length and weigh approximately 10–20 kg (Wells and Scott, 2009; Jefferson *et al.*, 2015). Females have been observed to be reproductively active from six to 48 years of age, producing an average of 12 calves across their lifetimes, although only fewer than half of these were sighted alive after calf–mother separation. Males, in turn, have been documented to sire offspring from around 10 to 43 years of age, with individual males fathering up to seven calves (Wells *et al.*, 2025). The average calving interval in females is 3.5 years, although this is influenced by factors such as maternal age, birth order, and calf survival rates. Seasonal reproduction is also evident, with 81% of births occurring between May and July (Wells *et al.*, 2025), although these parameters may differ across populations based on several factors, including food and energetic availability (Reddy *et al.*, 1994; Eskelinen, Richardson and Wendt, 2020). Calves typically nurse for up to three to six years, though this parameter can vary based on ecological and social context as well. Interbirth intervals also vary widely, ranging from two to six years, depending on calf survival and maternal condition (Connor *et al.*, 2000; Wells and Scott, 2009).

b. Distribution

The bottlenose dolphin is a widely distributed cetacean, with a range spanning both temperate and tropical waters worldwide. The limits of this range are mainly linked to water temperature, which can be a proxy for their prey distribution. In North America, they are found in waters with a surface temperature between 10ºC and 32ºC (Wells and Scott, 2009). This species is observed in both coastal and offshore environments, including semi-enclosed seas such as the Mediterranean, Black Sea, Gulf of Mexico, and the Red Sea (Wells and Scott, 2009; Jefferson *et al.*, 2015). Bottlenose dolphins are known to inhabit a variety of marine habitats, from shallow bays and estuaries to the deep pelagic zone. Their occurrence is, however, usually more frequent in continental shelf waters, where population densities are normally higher compared to open-ocean regions (Jefferson *et al.*, 2015) (Figure A-III. 15).

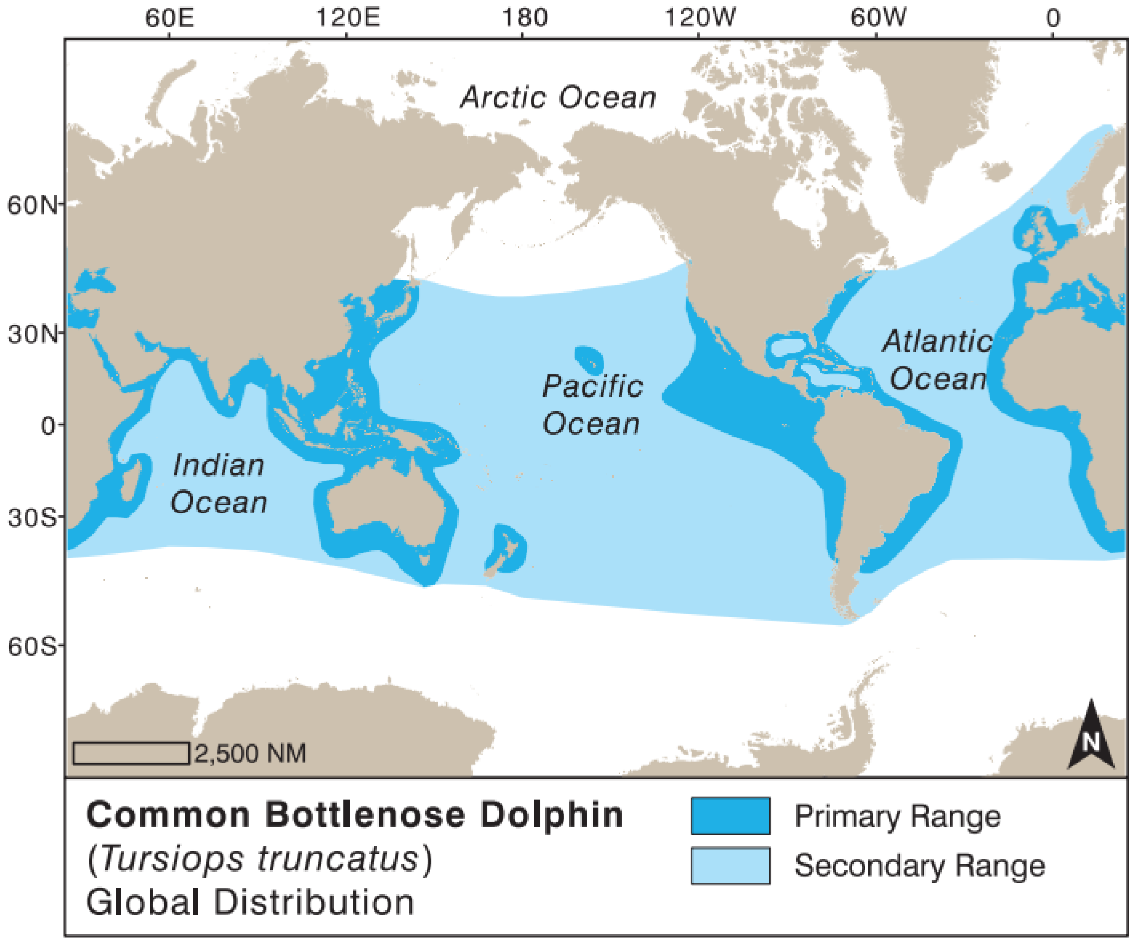

Figure A-III. 15 Bottlenose dolphin (*Tursiops truncatus*) Global Distribution Map. Reproduced with permission from Jefferson et al., 2015. Copyright 2015, Elsevier

Within the more coastal primary range, bottlenose dolphins exhibit significant ecological plasticity. They often inhabit bays, estuaries, and lagoons, and have also been documented travelling upriver (Connor *et al.*, 2000; Fury and Harrison, 2008; Chabanne *et al.*, 2012). This ecological plasticity has also resulted in the differentiation of ecotypes in several populations around the world (Louis *et al.*, 2021), where distinct inshore and offshore forms coexist but differ in morphology, colouration, social behaviour, and diet (Wells and Scott, 2009; Perrin *et al.*, 2011; Díaz-Gamboa, Gendron and Busquets-Vass, 2018; Costa *et al.*, 2022). While inshore dolphins form smaller groups adapted to structured habitats and localised prey availability, offshore dolphins are generally found in larger aggregations and tend to range more widely (Scott and Chivers, 1990; Oviedo Correa *et al.*, 2020).

c. Diet, Foraging Techniques, and Interactions with Human Activities

Bottlenose dolphins are generalist predators, and their diets are mainly composed of various demersal and pelagic fish species, including species from the Scombridae, Gadidae, Merluccidae, Clupeidae, Sciaenidae, and Mugilidae families (Wells and Scott, 2009; Jefferson *et al.*, 2015). They also prey on cephalopods such as squid and octopus, and, less frequently, on crustaceans as well. As a generally opportunistic species, most individuals target the most abundant or accessible prey; however, there are records of individuals or groups exhibiting specialised foraging techniques to access preferred prey (Wells and Scott, 2009; Jefferson *et al.*, 2015).

The breadth of potential prey species targeted by bottlenose dolphins is also accompanied by behavioural plasticity in the foraging strategies they display. Dolphins hunt both individually and cooperatively, employing diverse techniques that are often shaped by local ecological conditions and social dynamics (reviewed in Wells, 2019). Dolphin foraging strategies are highly adaptable and vary depending on prey availability, environmental conditions, and individual learning. Detection of prey may involve passive listening (especially for soniferous fish, Gannon *et al.*, 2005), visual cues in clear waters, or more commonly, through biosonar, or active echolocation (Wells, 2019) (described in more detail in section a). The most common foraging techniques involve the pursuit and capture of a single prey item, but within this species, there are also observed behaviours that include cooperative techniques such as herding, chasing, and strand feeding, especially in coastal environments where prey can be corralled efficiently (Fox and Young, 2012; Eierman and Connor, 2014). Studies have also shown that dolphins can have individual prey preferences and foraging specialisation, possibly reflecting age, experience, or social learning (Gazda *et al.*, 2005; Methion and Díaz López, 2020). Some techniques appear to be culturally transmitted within communities and may involve role differentiation or coordinated movements (Wells, 2019). Additionally, foraging is often affected by habitat structure, which may result in higher prey densities that dolphins can then take advantage of (Eierman and Connor, 2014).

Altered prey distributions can also result from man-made structures, such as aquaculture facilities (Díaz López, Marini and Polo, 2005; Díaz López, 2006a, 2012, 2019; Díaz López and Methion, 2017) or fishing operations (Díaz López, 2006b, 2019; Bearzi, Fortuna and Reeves, 2009), which can concentrate fish and create foraging opportunities. These conditions often result in interactions between dolphins and human activities, which can go from mutually beneficial to conflictual. Human–dolphin interactions have been documented since antiquity, with early records from Greek and Roman sources describing cooperative fishing between dolphins and fishers (Fögen and Thomas, 2017). Such interactions are still observed and continue to illustrate the capacity of bottlenose dolphins to exploit anthropogenic activities in opportunistic ways. For example, there are observations of dolphins following trawlers to feed on discarded fish (Gonzalvo *et al.*, 2008; Jaiteh *et al.*, 2013; Bonizzoni, Furey and Bearzi, 2021; Bonizzoni *et al.*, 2022). Furthermore, dolphins have been reported to remove fish directly from fishing gear, a practice referred to as "depredation" (Díaz López, 2006b; Zollett and Read, 2006; Powell and Wells, 2011; Rechimont *et al.*, 2018; Chávez-Martínez *et al.*, 2022) These interactions not only pose threats to the dolphins, which may cause entanglement and potentially even mortality (Díaz López and Bernal Shirai, 2007), but also lead to gear damage, economic losses for fishers, and occasionally provoke retaliation against dolphins (Bearzi, Saylan and Hwang, 2009; La Manna *et al.*, 2024).

d. Social Structure

Bottlenose dolphins have a highly flexible and complex social structure characterised by fission–fusion dynamics, where group composition changes over short temporal scales as individuals join and separate (Connor *et al.*, 2000; Aureli *et al.*, 2008). These flexible dynamics indicate that group size is not fixed, but is dependent on ecological, social, and anthropogenic conditions (Louise Chilvers and Corkeron, 2001; Gowans, Würsig and Karczmarski, 2007; Díaz López and Bernal Shirai, 2008; La Manna *et al.*, 2023; Methion *et al.*, 2023). Prey distribution is one of the main determinants of grouping patterns: patchy or unpredictable prey leads to smaller groups to minimise competition, while abundant or concentrated prey resources can support larger aggregations and facilitate cooperative foraging (Gowans, Würsig and Karczmarski, 2007; Díaz López and Bernal Shirai, 2008; Methion and Díaz López, 2019). Environmental proxies for prey availability, such as water temperature, dissolved oxygen, and chlorophyll concentration, have also been linked to group size, with larger groups predicted in more productive conditions (La Manna *et al.*, 2023; Methion *et al.*, 2023).

Social drivers also influence group size and composition. The presence of dependent calves is a consistent predictor of large groups, indicating the importance of protection and cooperative care (La Manna *et al.*, 2023; Methion *et al.*, 2023). The mother-calf bond can last for several years, during which calves acquire essential social and foraging skills (Wells, Scott and Irvine, 1987; Connor *et al.*, 2000). Females may also form nursery groups, and calves are sometimes cared for temporarily by young, less experienced females. This arrangement offers protection for the calves, while providing younger females “mothering” experience (Wells, Scott and Irvine, 1987; Mann and Smuts, 1998; Mann, 2019). Male alliances add another dimension, often in the form of closely-associated pairs or trios that are linked to cooperative behaviours such as herding and sequestering females for mating opportunities (Wells, Scott and Irvine, 1987; Connor, Smolker and Richards, 1992; Wells and Scott, 2009; Connor *et al.*, 2022). Feeding preferences can further influence associations through cooperative feeding strategies (Wells and Scott, 2009; Leatherwood and Reeves, 2012; Wells, 2019), with individuals who favour similar strategies tending to associate more closely (Methion and Díaz López, 2020). In addition, personality traits play a role in social positioning, with bold individuals often occupying more central roles within the social network, fostering cohesion and facilitating information transfer, while shy individuals are more peripheral (Díaz López, 2020) (Figure A-III. 16).

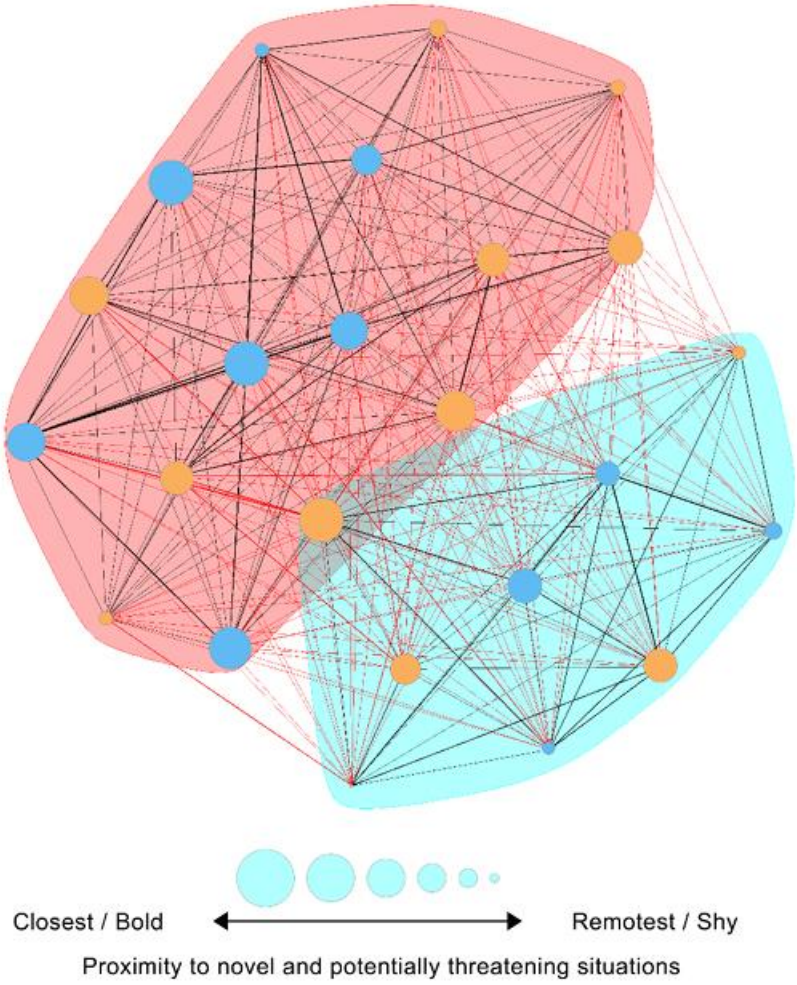

Figure A-III. 16 Network diagram for bottlenose dolphins using general affiliation indices (GAIs). The colour of each node indicates its sex (blue: males; orange: females). The size of coloured nodes represents the inverse of the personality score ranging from bold individuals with a larger node to shy individuals with a smaller node (N = 24). The thickness of the edges indicates the strength of association between individuals. Coloured polygons represent the two clusters assigned by the leading eigenvector algorithm for community detection. The colour of the edges represents connections between (red) and within (black) clusters. Reproduced with permission from Díaz López, 2020. Copyright 2020, Elsevier

Anthropogenic factors can also modulate grouping patterns: opportunistic feeding at aquaculture sites can reduce the need for cooperative foraging, leading to smaller or more transient groups (Díaz López and Bernal Shirai, 2008), while elevated noise levels may cause dolphins to reduce group size to avoid acoustic masking and maintain communication (La Manna *et al.*, 2023). Taken together, these factors contribute to the high variability in bottlenose dolphin group sizes, which vary globally and with the definition of the term "group", but typically range from four to 20 individuals in coastal areas, although larger aggregations can be observed offshore (Connor *et al.*, 2000; Jefferson *et al.*, 2015; Methion and Díaz López, 2018; Díaz López, 2019; Oviedo Correa *et al.*, 2020).

e. Predation, Threats, and Conservation

Bottlenose dolphins have few natural predators, and the majority of them are large sharks such as tiger sharks (*Galeocerdo cuvier*), bull sharks (*Carcharhinus leucas*), dusky sharks (*Carcharhinus obscurus*), and great white sharks (*Carcharodon carcharias*). Evidence on their predation on dolphins shows they mainly target calves or injured individuals (Heithaus, 2001; Celona, De Maddalena and Comparetto, 2006; Wells and Scott, 2009). In addition to sharks, killer whales (*Orcinus orca*) have also been documented attacking dolphins in some regions (Wells and Scott, 2009).

Bottlenose dolphins face numerous anthropogenic threats given the increasing overlap between human activities and coastal marine habitats (Figure A-III. 17). By-catch in fishing gear such as gillnets, trawlers and longlines can cause significant injury and mortality across their range (López *et al.*, 2003; Díaz López, 2006b; Read, 2008; Barnhill *et al.*, 2022). Additionally, collisions with vessels (Wells and Scott, 1997; Bechdel *et al.*, 2009), underwater noise (Buckstaff, 2004; Perez-Ortega *et al.*, 2021), and chemical pollution (Vos *et al.*, 2002; Bridge, Methion and Díaz López, 2023) may disrupt their habitat, have behavioural effects and can alter reproductive success (Wells and Scott, 2009). Studies have also reported negative effects on behaviour, group size and range from marine traffic (Nowacek, Wells and Solow, 2001; Papale, Azzolin and Giacoma, 2012), tourism (Barnhill *et al.*, 2022), and global warming (Gabriella La Manna *et al.*, 2023).

Figure A-III. 17 Bottlenose dolphins caught in finfish cage lines (a and c), injured likely from a propeller strike (b) and caught in an anti-predator net in finfish farm (d). Reproduced with author permission from Methion, 2019

Although the species is globally listed as "Least Concern" by the IUCN, specific populations may be threatened (Wells, 2019). Conservation strategies include inclusion in protected species lists and regulations governing boat approaches, fishing practices and coastal development, aimed at mitigating threats in high-pressure environments (Wells and Scott, 2009).

ANNEX IV:
ADDITIONAL GRAPHS

SUPPLEMENTARY FIGURES FOR SECTION 3.1

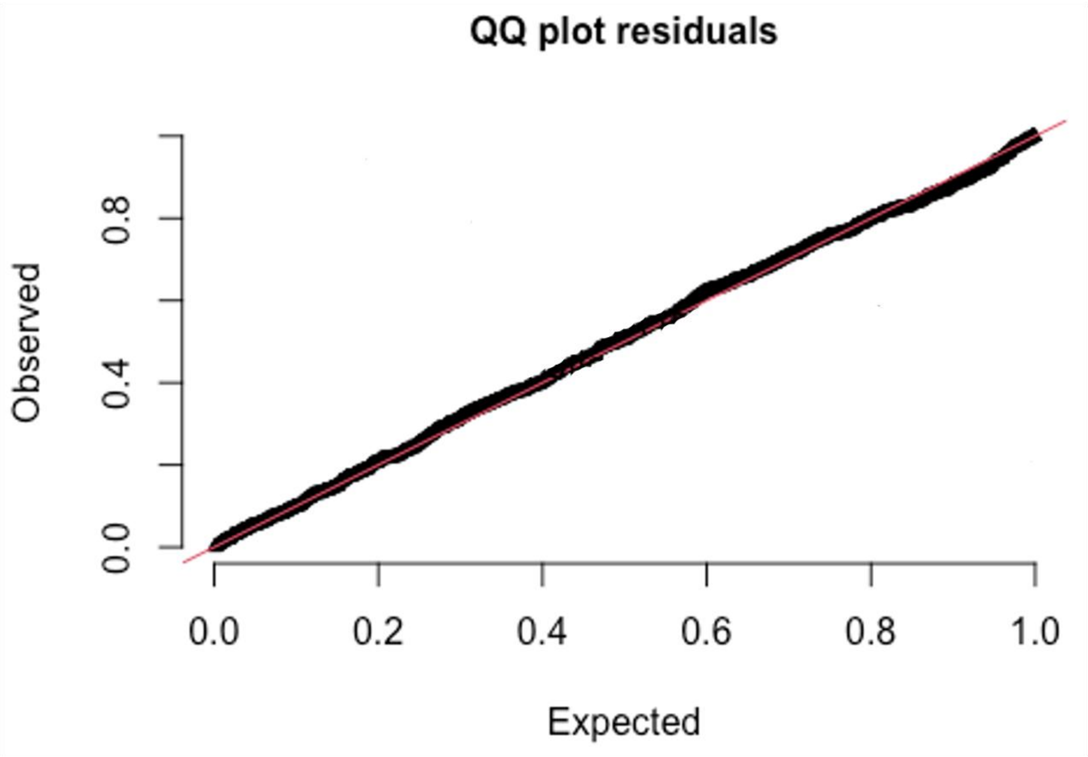

Figure A-IV. 1 Residual Diagnostics (DHARMa package, R) for Whistle Rate GLMM (Objective 1). QQ plot Residuals of the best GLMM model. KS Test: p=0.56964 Deviation n.s., Dispersion Test: p= 0.704 Dispersion n.s., Outlier Test: p=0.71561 Deviation n.s.

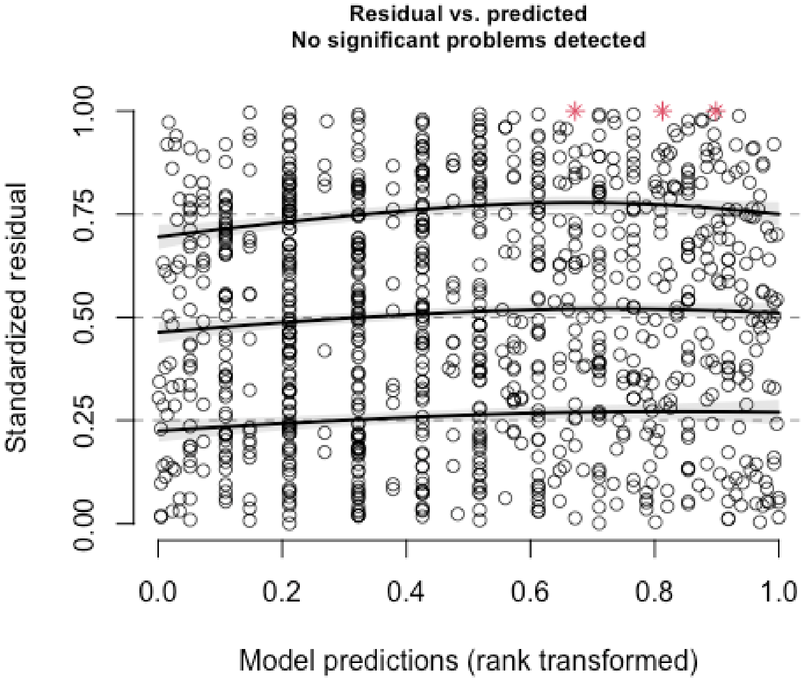

Figure A-IV. 2 Residual Diagnostics (DHARMa package, R) Whistle Rate GLMM (Objective 1). Residuals vs. predicted graph of the best GLMM model. No significance problems detected

SUPPLEMENTARY FIGURES FOR SECTION 3.2

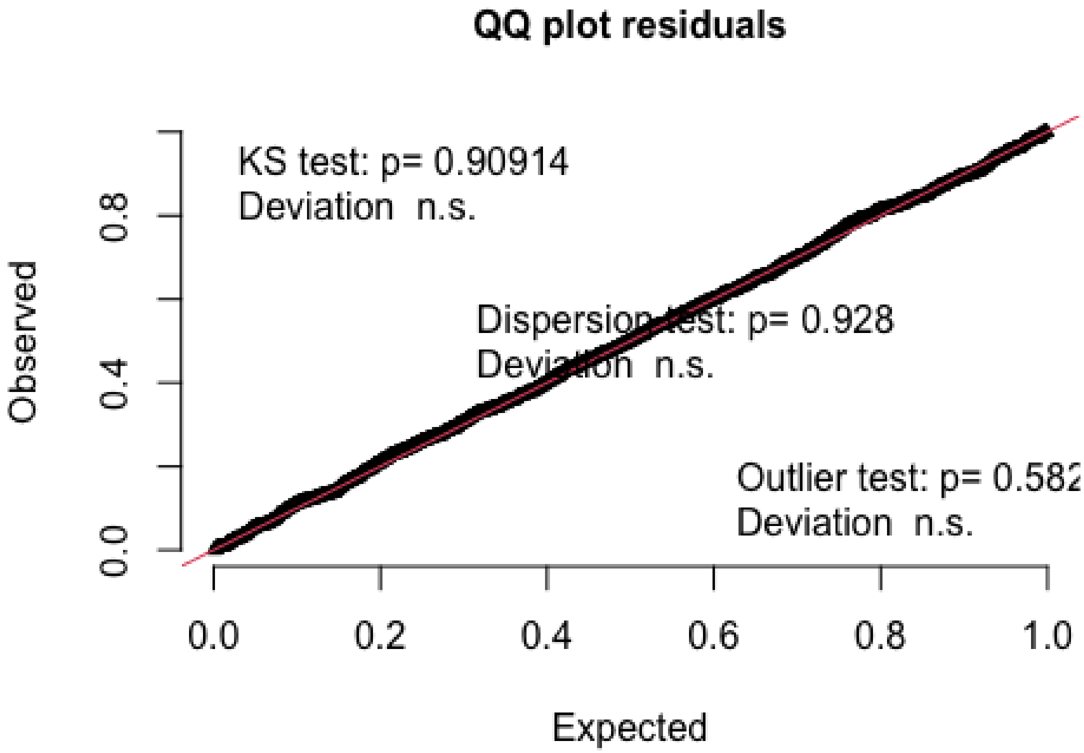

Figure A-IV. 3 Quantile-quantile (QQ) plot of the simulated residuals from the best-fit GLMM model, generated using the DHARMa package (Hartig, 2016)

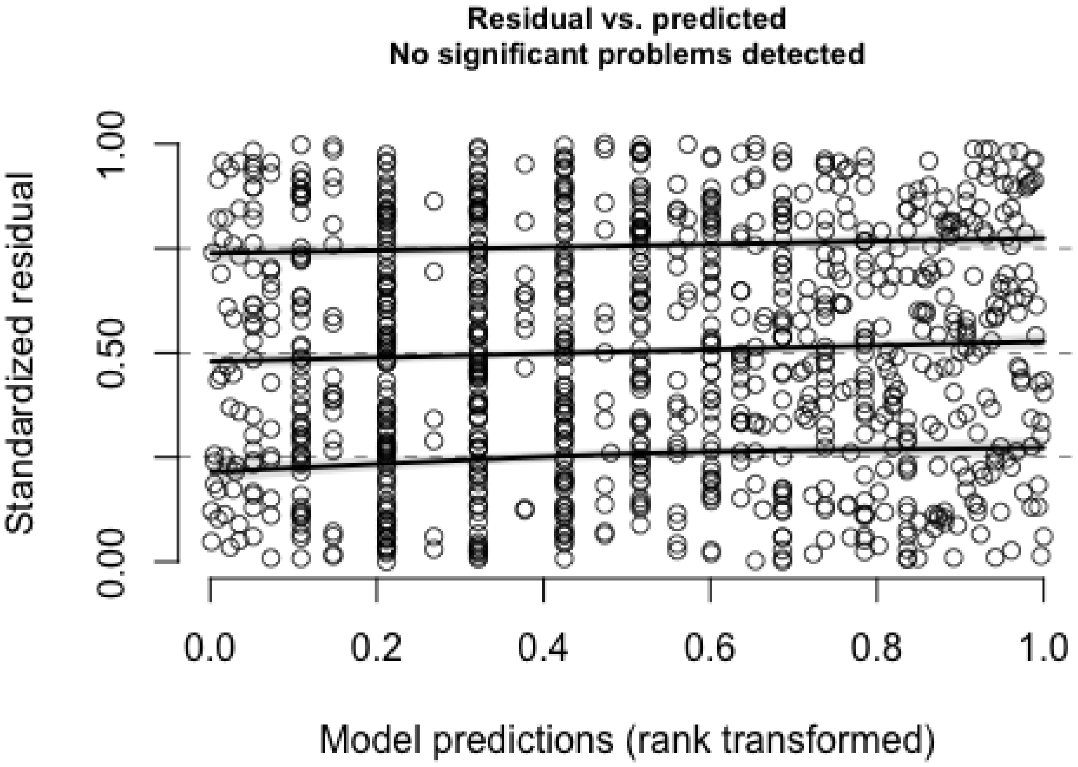

Figure A-IV. 4 Plot of residuals versus predicted values from the best-fit GLMM model, generated using the DHARMa package (Hartig, 2016).

ANNEX V :
ADDITIONAL STATEMENTS

Ethics Statement

All studies within this thesis were observational studies, and no ethical approval was required. Data collection complied with all current laws and regulations from each country (Italy and Spain) under the research permits granted to the Bottlenose Dolphin Research Institute (BDRI) and the Centro Tecnolóxico do Mar (CETMAR).

AI-assisted technologies in the writing process

During the preparation of this thesis, I used AI-based language tools (ChatGPT, OpenAI) to improve language and readability. After using this tool, I reviewed and edited the content as needed and take full responsibility for the content of this thesis.

This thesis investigates the acoustic communication of bottlenose dolphins using long-term datasets from two coastal regions. By combining long-term vessel-based recordings and passive acoustic monitoring, it examines how whistle production is influenced by behaviour, group size, and ecological context. Results show that whistle rate rises with behaviour and group size, and varies across populations due to social structure and environment. Signature whistles, unique identity signals, were linked to cohesion in large groups, and passive monitoring in an estuary provided the first systematic evidence of dolphin acoustic presence there, tied to seasonally variable predictors and prey availability. Together, these findings advance understanding of dolphin communication and inform conservation in human-impacted habitats.