EUROPEAN SEABASS
IN THE SOUTHERN NORTH SEA

A story of electronic tags, movement ecology and environmental policy

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Een miljoen vissen houden zich stil
en daardoor slaapt de zee.

Herman De Coninck

CONTENTS

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The journey of the past five years has brought me

from sleepless nights over a scholarship to restless months over finishing,
from writing sessions to dance breaks, from Ghent to Brussels,
from car trouble to conference, from tags to trajectories,
from *error* to *error* to *error* to *NICE GRAPH* to *ggsave* to *ugh, font size issue*,

from searching for answers to asking better questions,
from the North Sea's barely blue to the bluest blue of the Pacific,
from codes in red to narwhals in pink,
from purple to protest,
from friendship to love,

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SUMMARY

Fish populations are globally under threat, with the main cause for their depletion consisting of fisheries. On the level of the European Union (EU), the common fisheries policy has committed to restore fish populations and to reduce fisheries exploitation to rates considered sustainable. In light of this commitment, the alarm was raised in 2015 on the declines of European seabass, *Dicentrarchus labrax* L., a popular target species for both commercial and recreational fisheries. From 2015 onwards, emergency fisheries measures have been introduced to halt excessive fishing pressures. Slow growth, late reproductive maturity, aggregation at spawning areas and high residency add to seabass's vulnerability for overexploitation and local depletion.

The highly mobile European seabass is distributed across the continental shelf of the Northeast Atlantic and the Mediterranean Sea. In the Northeast Atlantic, seabass undertake seasonal migrations from summer feeding grounds along the coast and estuaries towards deeper offshore spawning grounds in colder months. Individual seabass can exhibit highly localized behaviour, residing in a specific location for a long period time (residency) and returning to that location after seasonal migrations (fidelity). An area with particularly limited knowledge on seabass movements and habitat use, is the North Sea. The objective of this PhD thesis has been to improve the understanding of the movement ecology of European seabass in the southern North Sea, in contribution to its conservation management.

The main technique used for this dissertation is electronic tagging. Individual fish are captured, anaesthetised, and fitted with a tag. Since the tagging research involves important methodological considerations, we investigate and elaborate different technicalities in part I, prior to detailing their application in our studies on seabass ecology.

The newly developed data storage tag (ADST) combines the features of an acoustic transmitter, emitting a signal that could be picked up by acoustic receivers, and of a data storage tag (DST), archiving depth and temperature sensor measurements on the tag itself. In chapter 2, we detail the use of the ADST on seabass, as well as Atlantic cod (*Gadus morhua* L.) and starry smooth-hound (*Mustelus asterias* L.) in the southern North Sea. Using archived data

series, we reconstruct migration trajectories with a geolocation modelling approach. The inclusion of the acoustic detection information in the geolocation model improves the timing of the daily position estimates. The combination of acoustic and archival tagging technologies provides highly complementary data, which we apply to investigate seabass migrations in chapter 6.

In chapter 3, we detail another technological advancement: a tripod frame developed to facilitate the deployment of acoustic receivers. The deployment and recovery protocol are proven to be practical and efficient in a field trial in sandy habitats in the North Sea. As the receiver is in a fixed position in the tripod frame, the frame provides more stability (less variation in tilt) than a commonly used cabled deployment design. Compared to the cabled set-up, the tripod results in higher performance of the instrument, whereby the detection probability is higher at greater distance and under louder ambient noise. The tripod frame is part of different receiver arrays used for gathering acoustic detection data throughout this dissertation.

Using the frame, we elaborate a new method to explicitly consider temporal resolution in detection range studies (Chapter 4). In acoustic telemetry studies, detection range is usually evaluated as the relationship between the probability of detecting an individual transmission and the distance between the transmitter and receiver. When investigating tagged fish presence within a time bin (e.g. per hour or day), few detections out of multiple transmissions suffice to establish presence. Using a cumulative probability calculation, we have developed and assessed a new method for evaluating detection range. The novel approach performs adequately in terms of accuracy and specificity, and demonstrates that a single transmission's detectability differs distinctly from the probability of determining presence. Detection range assessment should therefore be an integral part of the study design, whereby the temporal resolution is taken into account.

As the tripod frame (Chapter 3) provides a useful deployment mechanism, its application has been extended to include a C-POD, an instrument for passive acoustic monitoring of echolocating cetaceans. In chapter 5, we make use of the combined deployment of the two technologies to explore how these can be applied to study the dynamics of different species. We analyse patterns in

occupancy and co-occurrence of seabass, cod, harbour porpoise (*Phocoena phocoena* L.) and dolphins (which can't be identified up to species level with a C-POD). By applying metrics and analysis types commonly used in co-occurrence studies, we demonstrate the value of these long-term, high-resolution data series, as different temporal resolutions can results in different outcomes. This study serves as a demonstrator application of how these multi-sensor observations can benefit research on ecosystem dynamics.

In part II of this PhD dissertation, we describe how electronic tags have been used to investigate the movement ecology of seabass in the southern North Sea on different spatiotemporal scales.

The large-scale migrations of seabass are addressed in chapter 6. We combine data from mark-recapture, acoustic telemetry, DST and ADST, originating from tagging project in French, Dutch, English and Belgian waters of the North Sea. Using these data, we have identified different migration strategies, whereby seabass head south-westwards to the eastern and western English Channel, the Celtic Sea and the northern range of the Bay of Biscay. Additionally, many seabass stay in the North Sea, undertaking migrations within the North Sea, or staying put in a port area or the warmth of cooling water outlets. Fidelity to the North Sea is evidenced for approximately half of seabass with an electronic tag. Our results show that current seasonal fisheries closures are not aligned with the ecology of seabass in the North Sea, and demonstrate the importance of accounting for fine-scaled populations structuring in fisheries assessment.

In chapter 7 we look into the habitat use of European seabass within the range of the Belgian part of the North Sea (BPNS) and the Scheldt Estuary, using acoustic telemetry. On this scale, the spatial connectivity of the area also varies among individual seabass. Seabass tagged in more offshore areas have been mainly detected at offshore receiver stations and have never been detected along the north-eastern coast or the Scheldt Estuary. This is in contrast with movement patterns from seabass tagged along the coast, who either stick to coastal areas or head offshore without having been detected along the south-western coast. Looking into seabass habitat use at artificial substrates in the BPNS (port infrastructure, offshore wind farm, radar tower and offshore wreck), we see differential patterns in presence on a seasonal scale.

In chapter 8, we zoom in on patterns of seabass habitat use and connectivity within the port of Zeebrugge. Seabass residency and site fidelity manifests to the smaller spatial scale of the inner and outer harbour area, whereby we distinguish two groups using the habitats within the port differently. By linking these patterns in movement to the prevailing spatiotemporal fisheries measures, we have seen individual seabass to be differentially protected from fisheries. By setting out from individual fish' vulnerability rather than from a fisheries' need, this study highlights the importance of taking into account movement behaviour when evaluating fisheries management measures.

As a third part of the PhD (Chapter 9), we investigate seabass fisheries policy. As it can be difficult to keep oversight of policy evolution, considering policy measures change on a yearly or more frequent basis, we make an overview of seabass fisheries policy on the EU-level from 2015 to 2022. In addition, we discuss the specific case of Belgium, where commercial seabass angling is at an administrative impasse due to indirect effects of a national fisheries policy system designed to accommodate demersal mixed fisheries. Key issues for both the EU and Belgian policy level relate to the opacity in decision-making procedures, the failure to apply the precautionary principle in its political definition, and the lack of the cultural framework of marine stewardship.

Across the different aspects of this research, we highlight the importance of scale and dimension. The information potential of tagging data is maximised by applying novel technologies and sharing data, as well by analysing at different spatiotemporal scales with explicit consideration of the individual dimension. The studies on seabass movement ecology at different spatial scales have demonstrated high residency and site fidelity. Different migration strategies and localized behaviour in different areas imply that seabass are grouped to some extent, indicating fine-scaled population structuring. A direct recommendation for fisheries management is to extend the seasonal closure to May or June, at least for the North Sea seabass fisheries. Despite having found relevant findings for fisheries assessment and management, we have identified the issues on the policy level to be of a political nature, not as a lack of knowledge.

Finally, my experience of the PhD endeavour cannot be decoupled from my experiences with sexism throughout the PhD process. In the epilogue, I discuss how sexism and its intersections persist in (marine) science environments. The essay serves as a personal testimony and a plea for change.

SAMENVATTING

Wereldwijd staan vispopulaties onder immense druk, waarbij visserij de belangrijkste oorzaak van de uitputting is. Op het niveau van de Europese Unie (EU) houdt het gemeenschappelijk visserijbeleid een engagement in om de vispopulaties te herstellen en de exploitatie van de visserij terug te leiden tot niveaus die als duurzaam worden beschouwd. In 2015 klonk het alarm over de achteruitgang van de Europese zeebaars, *Dicentrarchus labrax* L., een populaire doelsoort voor zowel de commerciële als de recreatieve visserij. Vanaf 2015 zijn er noodmaatregelen afgekondigd om de buitensporige visserijdruk een halt toe te roepen. Trage groei, late geslachtsrijpheid, aggregatie in paaigebieden en honkvastheid dragen bij tot de kwetsbaarheid van zeebaars voor overbevissing en lokale uitputting.

De mobiele Europese zeebaars is verspreid over het continentaal plat van het noordoostelijke deel van de Atlantische Oceaan en de Middellandse Zee. In de Atlantische Oceaan onderneemt de zeebaars seizoensgebonden migraties. Zeebaars gaat van forageergebieden langs de kust en estuaria in de zomer naar paaigebieden dieper in zee tijdens de koudere maanden. Individuele zeebaarzen kunnen een sterk gelokaliseerd gedrag vertonen. Zo kunnen ze gedurende lange tijd op een specifieke plaats verblijven (residentie) en na een seizoenstrek naar die plaats terugkeren (sitegetrouwheid). Een gebied met een beperkte kennis van het bewegingsgedrag en habitatgebruik van zeebaars, is de Noordzee. Dit doctoraatsonderzoek heeft het doel om de bewegingsecologie van de Europese zeebaars in de zuidelijke Noordzee beter te begrijpen in functie van het instandhoudingsbeheer van zeebaars.

Als voornaamste methode maakt dit doctoraatsonderzoek gebruik van elektronische zenders. Een vis wordt gevangen, verdoofd en voorzien van een zender. Het zenderonderzoek gaat gepaard met belangrijke methodologische overwegingen. Daarom onderzoeken we in deel I verschillende technische aspecten van de techniek zelf, alvorens die toe te passen in studies op de bewegingsecologie van zeebaars.

De recent ontwikkelde *acoustic data storage tag* (ADST) combineert twee technologieën. Enerzijds stuurt de zender een geluidssignaal uit dat door akoestische ontvangers kan worden opgepikt, en anderzijds slaat die

gegevens op (diepte- en temperatuurmetingen) op de zender zelf (*data storage tag*, DST). In hoofdstuk 2 duiden we hoe we de ADST gebruikt hebben bij zeebaars, Atlantische kabeljauw (*Gadus morhua* L.) en gevlekte gladde haai (*Mustelus asterias* L.) in de zuidelijke Noordzee. Aan de hand van de op zender opgeslagen metingen kunnen we migratietrajecten reconstrueren met een geolocatiemodel. Door de akoestische detectie-informatie op te nemen in het geolocatiemodel verbetert de temporele error van de geschatte trajecten. De twee zendertechnologieën leveren zeer complementaire gegevens op, die we in hoofdstuk 6 toepassen om zeebaarsmigraties te onderzoeken.

In hoofdstuk 3 beschrijven we een andere technologische vooruitgang: een tripode die is ontwikkeld om de installatie van akoestische ontvangers op de zeebodem te faciliteren. Uit onze studie in de Noordzee is het protocol van installatie en recuperatie praktisch en efficiënt gebleken. Gezien de akoestische ontvanger gefixeerd is op de tripode, biedt deze methode meer stabiliteit (minder variatie in tilt) dan een ander gangbaar ontwerp met vasthechting aan een kabel. Vergeleken met de bekabelde opstelling levert de tripode een betere werking van het instrument op, waarbij de kans om een geluidssignaal te detecteren groter is. De tripode maakt deel uit van verschillende netwerken van ontvangers die in dit proefschrift gebruikt worden.

Voor studies die het detectiebereik van een ontvanger onderzoeken hebben we een nieuwe methode uitgewerkt om expliciet rekening te houden met temporele resolutie (hoofdstuk 4). Bij akoestische telemetriestudies wordt het detectiebereik gewoonlijk geëvalueerd als de relatie tussen de waarschijnlijkheid van detectie van een individuele transmissie en de afstand tussen zender en ontvanger. Wanneer we echter de aanwezigheid van gemerkte vissen binnen de periode van een uur of dag onderzoeken, volstaat het om uit vele uitgezonden signalen er slechts een of enkele te detecteren. Aan de hand van een berekening van de cumulatieve kans hebben wij een nieuwe methode ontwikkeld en geëvalueerd voor het evalueren van het detectiebereik. Door deze nieuwe methode tonen we aan dat de detectiekans van een enkele transmissie verschilt van de kans om aanwezigheid vast te stellen. Studies naar het detectiebereik maken daarom best integraal

onderdeel uit van de onderzoeksopzet, waarbij rekening wordt gehouden met de temporele resolutie.

In hoofdstuk 5 wordt de toepassing van de tripode (uit hoofdstuk 3) uitgebreid met een C-POD, een instrument voor het observeren van echolocatiesignalen van walvisachtigen. De combinatie van C-POD en akoestische ontvanger laat toe om de technologieën te combineren en verschillende soorten tegelijkertijd te bestuderen. We analyseren patronen in ruimtegebruik en co-incidentie van zeebaars, kabeljauw, bruinvis (*Phocoena phocoena* L.) en dolfijnen (die met een C-POD niet tot op soortniveau kunnen worden geïdentificeerd). Door analyses toe te passen die gewoonlijk worden gebruikt in studies naar co-incidentie, illustreren we de waarde aan van deze tijdsreeksen met hoge resolutie en lange termijn. Analyses die gebruik maken van verschillende temporele resoluties kunnen zo tot verschillende uitkomsten leiden. Deze studie dient als een voorbeeld van hoe gelijktijdige observaties van meerdere sensoren onderzoek op een ecosysteemniveau kunnen vooruithelpen.

In deel II van dit proefschrift gebruiken we elektronische zenders om de bewegingsecologie van zeebaars in de zuidelijke Noordzee op verschillende schalen van tijd en ruimte in kaart te brengen.

De grootschalige migraties van zeebaars bekijken we in hoofdstuk 6. We combineren gegevens van projecten in Franse, Nederlandse, Engelse en Belgische wateren van de Noordzee, waarbij gebruik gemaakt wordt van merk-hervangst, akoestische telemetrie, DST en ADST. Aan de hand van deze gegevens stellen we verschillende migratiestrategieën vast, waarbij zeebaarzen zuidwestwaarts trekken naar het oostelijke en westelijke Engelse Kanaal, de Keltische Zee en het noordelijke deel van de Golf van Biskaje. Ook blijven veel zeebaarzen in de Noordzee, waarbij ze migreren binnen de Noordzee, of ze blijven in een havengebied of in de buurt van koelwateruitlaten. Voor ongeveer de helft van de zeebaarzen met een elektronische zender is getrouwheid aan de Noordzee aangetoond. Onze resultaten tonen aan dat de huidige seizoenale sluiting van de visserij niet in overeenstemming is met de ecologie van zeebaars in de Noordzee. Ook toont deze studie aan hoe belangrijk het is om bij de beoordeling van de visserijstocks rekening te houden met fijnschalige populatiestructuur.

In hoofdstuk 7 onderzoeken we het habitatgebruik van Europese zeebaars binnen het Belgische deel van de Noordzee (BDNZ) en het Schelde-estuarium, aan de hand van akoestische telemetrie. Ook op deze schaal varieert de connectiviteit in het gebied tussen individuele zeebaarzen. Zeebaarzen die vrijgelaten zijn op locaties dieper in zee (meer dan 6 nautische mijl van de kustlijn), zijn voornamelijk gedetecteerd op stations diep in zee en zijn nooit gedetecteerd langs de noordoostkust of het Schelde-estuarium. Dit staat in contrast met de bewegingspatronen van zeebaarzen gevangen langs de kust, die ofwel in de kustgebieden blijven, ofwel nooit langs de zuidwestkust zijn waargenomen. Wanneer we kijken naar het habitatgebruik van zeebaars op kunstmatige substraten in het BDNZ (haveninfrastructuur, windmolenpark, radartoren en wrak), zien we verschillende seizoenale patronen in habitatgebruik.

In hoofdstuk 8 bekijken we patronen van habitatgebruik en connectiviteit van zeebaars op een nog kleinere ruimtelijke schaal, namelijk de haven van Zeebrugge. Twee groepen zeebaarzen vertonen residentie en sitegetrouwheid aan enerzijds de voorhaven en anderzijds de achterhaven, wat de fijnschaligheid van de populatiestructuur aantoont. Door de bewegingspatronen te koppelen aan de visserijmaatregelen van kracht, hebben we vastgesteld dat individuele zeebaarzen een verschillende bescherming genieten door de wetgeving.

Als een derde onderdeel van het doctoraat (hoofdstuk 9) onderzoeken we het beleid van zeebaarsvisserij. Omdat het moeilijk kan zijn om zicht te houden op de evolutie van het beleid, aangezien beleidsmaatregelen jaarlijks of vaker veranderen, maken we een overzicht van het zeebaarsvisserijbeleid op EU-niveau van 2015 tot 2022. Ook bespreken we het specifieke geval van België, waar de commerciële zeebaarsvisserij zich in een administratieve impasse bevindt als gevolg van de indirecte effecten van een nationaal visserijbeleid dat gericht is op gemengde demersale visserij. Kernproblemen op zowel het EU als het Belgische beleidsniveau zijn het gebrek aan transparantie van de besluitvormingsprocedures, het niet toepassen van het voorzorgsbeginsel in de politieke definitie, en het ontbreken van een cultuur die zorg voor de mariene omgeving centraal stelt.

Het in acht nemen van schaal en dimensie is essentieel gebleken voor verschillende onderdelen van dit onderzoek. Nieuwe technologieën en het delen van gegevens, maar ook analyses op verschillende spatio-temporele schalen en op het individuele niveau, vergroten het informatiepotentieel van elektronische zenders. Op verschillende ruimtelijke schalen vertoont zeebaars een hoge residentie en honkvastheid. Verschillende migratiestrategieën en gelokaliseerd gedrag in verschillende gebieden impliceren een fijnschalige populatiestructuur. Een directe aanbeveling voor het visserijbeheer houdt de verlenging van de seizoenale sluiting in tot en met mei of juni, ten minste voor de zeebaarsvisserij in de Noordzee. Hoewel het onderzoek relevante resultaten opleverde voor de beoordeling en het beheer van de visserij, zijn de problemen op het vlak van visserijmanagement van een inherent politieke aard, en niet het gevolg van een gebrek aan kennis.

Tot slot kan mijn ervaring van het doctoraatsonderzoek niet worden losgekoppeld van mijn werkgerelateerde ervaringen met seksisme. In de epiloog bespreek ik hoe seksisme en intersecties blijven voortbestaan in (mariene) wetenschap. Het essay is een persoonlijke getuigenis en een pleidooi voor verandering.

LIST OF ABBREVIATIONS

ADST	Acoustic data storage tag
AIC	Akaike information criterion
ANOVA	Analysis of variance
AT	Acoustic telemetry
BPAN	Belgian permanent acoustic network
BPNS	Belgian part of the North Sea
CA	Correspondence analysis
CFP	Common fisheries policy
CI	Confidence interval
DPD	Detection positive day
DPH	Detection positive hour
DST	Data storage tag
ECJ	European Court of Justice
EDMC	Empirical derived Markov Chain
ETN	European Tracking Network
EVC	Eigenvector centrality
F	Fishing pressure
GLM	Generalized linear model
GLMM	Generalized linear mixed model
HMM	Hidden Markov model
ICC	Intra-class correlation coefficient
ICES	International Council for the Exploration of the Sea
LL	Likely location
MAP	Multiannual management plan
MCRS	Minimum conservation reference size
MSY	Maximum sustainable yield
PAM	Passive acoustic monitoring
PBARN	Permanent Belgian acoustic receiver network
PVPM	Per vessel per month
PVPY	Per vessel per year
RI	Residence index
SD	Standard deviation
SE	Standard error
SSB	Spawning stock biomass
TAC	Total allowable catch
TAL	Time at large

CHAPTER 1
INTRODUCTION

ECOLOGICAL RESEARCH IN THE ANTHROPOCENE

At the time of writing, global biodiversity is under threat. The rate of biodiversity loss is 100 to 1,000 times higher than what is considered natural, with human activities being the main cause of the acceleration. This rate of loss is detrimental to ecosystem resilience and is - in combination with the transgression of other planetary boundaries (Fig. 1.1) - shifting the Earth out of its stable Holocene state (Rockström et al. 2009). Aside from the loss of species diversity (through extinction), biodiversity loss also translates in a loss of functional diversity, which effects remain poorly understood on a global level (Folke et al. 2021). The impact of the infamous terrestrial bipeds doesn't stop at the shoreline. Only 13.2% of the Ocean's surface area can be considered as wilderness, i.e. with low (cumulative) impacts of human activities (Jones et al. 2018). Anthropogenic impacts on the Ocean and the life they harbour include warming, acidification and deoxygenation due to rising CO_2 levels (Kwiatkowski et al. 2020), chemical, plastic, noise and light pollution (Landrigan et al. 2020), habitat loss (Stamp et al. 2022) and depletion of biomass (Christensen et al. 2014). Coastal ecosystems in particular are heavily affected by human presence and activities (Jones et al. 2018, Li et al. 2018, He & Silliman 2019).

Within the range of human activities in the marine environment, fisheries is considered to be the main cause of the depletion of fish populations (Pauly 2018). Biomass of marine fish is estimated to have declined by 38% since 1970 (Hutchings et al. 2010), with the predatory fish biomass ranging from one third (Christensen et al. 2014) to ten percent (Myers & Worm 2003) of its biomass levels of a century ago. Despite the international commitment to fish within sustainable limits by 2020 at the latest (United Nations 2015), overfishing is still increasing with 92.2% of fisheries considered to be fully exploited, overexploited or depleted (FAO 2022). Aside from pleas for systemic change to renounce capitalist exploitation of fish populations (Clausen & Clark 2005), the way forward is generally considered to be ecosystem-based management

(EBM) (UNEP 2011, EU 2013). Although many interpretations of EBM exist, the general concepts entail to consider the interconnectedness of different components and functions within an ecosystem, while taking into account the full social-ecological system (Fig. 1.2) (Curtin & Prellezo 2010, Langhans et al. 2019). For marine fisheries, this means moving away from optimizing single species yield towards a more sustainable and equitable use of the ocean (Berkes 2012, Hornborg et al. 2019). One aspect considered key to tackling the multidimensionality of the EBM's 'wicked problem' is movement ecology (Lowerre-Barbieri et al. 2019a).
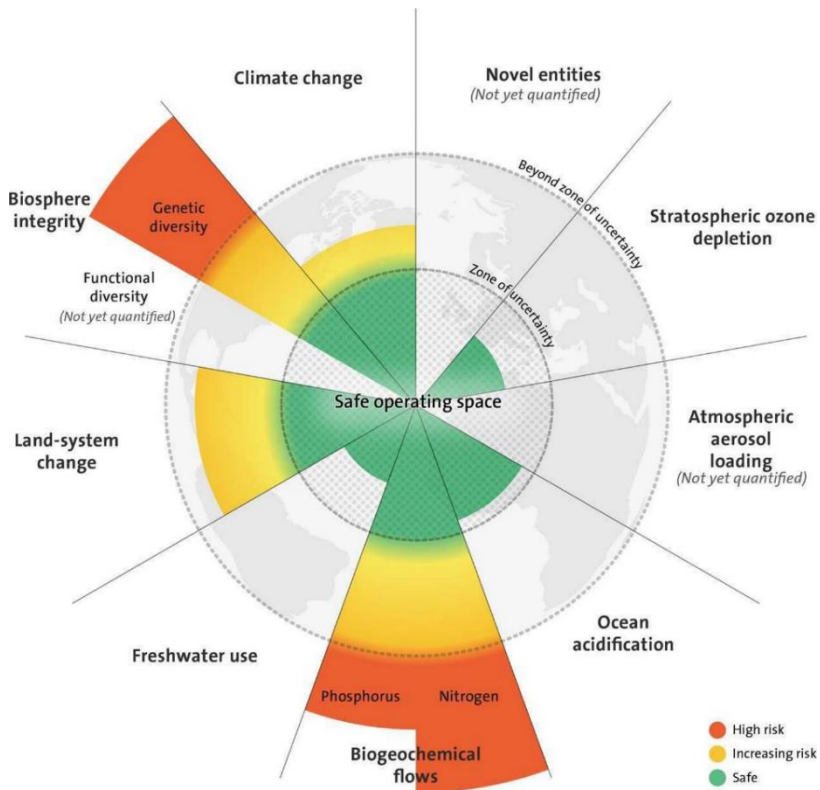
Figure 1.1. The model for a safe operating space for human activities, as developed by Rockström et al. (2009). The nine identified planetary boundaries serve as tipping points beyond which the Earth system could be pushed outside of the Holocene's stable environmental state. In terms of biosphere integrity, the loss of genetic diversity is quantified as high-risk (red), which means it has crossed the safe operating space (green) as well as the zone of uncertainty (yellow). The loss of functional diversity has not yet been quantified on a global scale. Adopted from Folke et al. (2021).

MOVEMENT ECOLOGY & ELECTRONIC TAGGING

Movement is one of the key mechanisms shaping biodiversity as it drives the distribution of species, individuals and genes in space and time (Jeltsch et al. 2013). By changing its spatial location over time, movement allows an organism (whether moving solitary or collectively) to make use of patchy and seasonally variable resources and hence increase its fitness (Nathan et al. 2008, Lennox et al. 2019). To undertake different life-history stages, fish move in between distinct essential habitats used for feeding, spawning, nursery, shelter and migration (Secor 2015). The movement path of an individual is driven by four fundamental mechanisms: the internal state, the motion capacity and the navigation capacity of the individual, in addition to external factors of the abiotic and biotic environment (Fig. 1.3) (Nathan et al. 2008). These processes and their interactions act at multiple spatiotemporal scales (e.g. Lohmann et al. (2008) described animals using geomagnetic information for large-scale navigation and chemical cues for small-scale navigation). Likewise, anthropogenic activities impact movement processes at these different scales (e.g. a basin-wide increase of temperature versus local habitat alterations) (Nathan et al. 2008, Lowerre-Barbieri et al. 2019a). The field of movement ecology has vastly benefited from electronic tagging studies (Lennox et al. 2017, Meyer 2017). Building on the principle of mark-recapture studies, a tag is attached – internally or externally – to an individual animal. The individual dimension (Villegas-Ríos et al. 2020) allows us to study habitat use and selection (Reubens et al. 2013b), spatial (Jacoby et al. 2012) and social networks (Winter et al. 2021a), migration routes and strategies (de Pontual et al. 2023), and importantly: the individual variability in all these aspects (Tyler & Rose 1994, Bolnick et al. 2011, Taylor et al. 2017). Individual fish move in ways that exceed simplistic explanations of habitat suitability (Petitgas et al. 2006), whereby animal personalities shape species dynamics (Spiegel et al. 2017, Villegas-Ríos et al. 2018). The findings from tagging research have contributed to conservation management in various ways (Lowerre-Barbieri et al. 2019b, Brownscombe et al. 2022), including to identify migration barriers (Verhelst et al. 2018b), to evaluate marine protected areas design (Lea et al. 2016, Kendall et al. 2017) and to delineate stock structure (Brodie et al. 2018).

Table 1.1. Glossary of terms used throughout the dissertation.

Movement reflects the change in the spatial location of an organism in time. Movement can be regarded as a dynamic interplay of an individual's internal state, motion capacity and navigation capacity, in addition to the external (a)biotic factors influencing that movement (Nathan et al. 2008).

Migration is a directional movement of individuals and groups between separate habitats, generally along a seasonal cycle (Dingle & Drake 2007, Secor 2015).

Homing behaviour reflects an animal performing directed movements to a previous habitat (Secor 2015).

Natal homing consists of the return of an individual to the area where it was born for the purpose of reproduction (Secor 2015).

Residency reflects an individual occupying a specific area for a period of time largely uninterruptedly (Reubens et al. 2013b, Doyle et al. 2017).

Site fidelity is defined as the return of an individual to a location where it previously resided after having left it for some defined period of time (Doyle et al. 2017).

A **population** is defined as a group of individuals of the same species that breed with each other, but that are reproductively isolated from other groups of the same species (Secor 2015).

Connectivity can have different definitions, depending on the context and research field (Calabrese & Fagan 2004). Population connectivity is defined as the degree of demographic exchange between and within populations. Connectivity consists of a structural component, relating to the environment, and a functional component, relating to the organism (e.g. movement behaviour) (Drake et al. 2022). Whereas genetic connectivity quantifies the degree of gene flow within and among populations, ecological connectivity evaluates the exchange of individuals through recruitment (larval dispersal) and migration (Singleton & McRae 2013, Hawkins et al. 2016, Marandel et al. 2017). Low ecological connectivity can still maintain high genetic connectivity (e.g. interchange of few individuals can maintain panmixia) (Hawkins et al. 2016). When we use the term connectivity in this dissertation, we refer to ecological connectivity.

Table 1.1. (continued) Glossary of terms used throughout the dissertation.

Population structure refers to the spatial structure of populations. In genetics, this entails separations between or within populations based on differences in allele frequencies. In movement ecology, population structure is investigated from the viewpoint of ecological connectivity, thus investigating the spatial interchange of individuals. Individuals exhibiting highly localized behaviour, such as residency and site fidelity, demonstrate the complex, fine-scaled structuring of a population (Hawkins et al. 2016, O'Donnell et al. 2022).

Stock is defined in EU policy as 'a marine biological resource that occurs in a given management area' (EU 2013). The word 'stock' has been contested for the implied bias whereby living organisms are considered as exploitable resources by default (Telesca 2017). Nonetheless, we chose to use the word throughout the dissertation to be consistent with existing literature. European seabass in the southern North Sea is part of the stock in the central and southern North Sea, Irish Sea, English Channel, Bristol Channel, and Celtic Sea (ICES divisions 4b-c, 7a,d-h), which is also referred to as the "northern stock" (ICES 2020b).
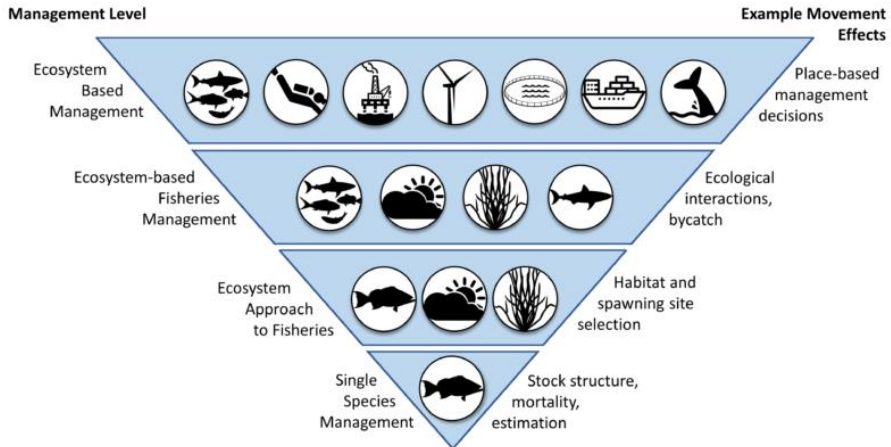

Figure 1.2. Visualisation of how movement ecology data can be taken into account on different levels of the management of fisheries and other human activities. Adopted from iTag (https://itagscience.com/movement-management/).
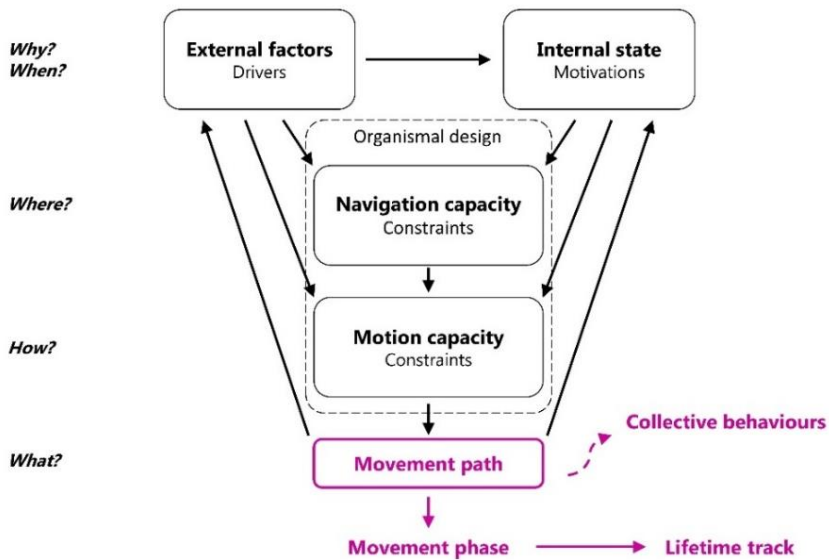
Figure 1.3. Schematic of the movement ecology paradigm of Nathan et al. (2008) with mechanisms acting as drivers, constraints, motivations and feedbacks on the movement of individual animals. External factors (e.g. environmental conditions or food availability) drive an individual's motivation and ability to move (why and when). An individual's internal state (e.g. stored energy or physiology) determine the motivation to move. Navigation and motion capacities constrain an individual's ability engage in a directed movement (where and how). The actual movement path (what) can then influence the individual's environment and internal state. The functioning of these mechanisms can differ among life-history stages. In this dissertation we only investigate the movements of adult individuals. Adapted from Secor (2015).

Range of technologies, range of scales

A range of technologies enables researchers to investigate animal movement behaviour in different aquatic environments (Fig. 1.4) (Thorstad et al. 2013). In marine waters, the main technologies involve the tag logging or transmitting data. In acoustic telemetry, a tag transmits an acoustic signal that can be picked up by an acoustic receiver when the tagged animal is within the detection range of that receiver (Hussey et al. 2015). The transmitted signal contains the information of the unique ID of the tag, potentially supplemented with a sensor measurement (e.g. pressure, temperature, acceleration) (Brownscombe et al. 2019). Data loggers store sensor information in the tag memory. Access to the archival data requires the physical recovery of the tag

(Metcalfe & Arnold 1997) or the transmission of the information through satellites (Coyne & Godley 2005). Providing highly complementary information, acoustic and archival technologies were combined in one physical tag, the acoustic data storage tag (ADST) (Goossens et al. 2023).

The different tagging technologies provide movement data at distinct spatiotemporal scales. Archival data series provide high resolution, continuous information on vertical space use (pressure sensor) (Heerah et al. 2017) and sensory experience (e.g. temperature sensor) (Righton et al. 2010). Using these data, trajectories can be reconstructed with geolocation modelling (Pedersen et al. 2008, Thygesen et al. 2009, Woillez et al. 2016), thus allowing to estimate horizontal position at a lower resolution (in relation to model error). Acoustic telemetry informs on presence when a tagged animal is in the vicinity of a receiver, but leaves you clueless on its position when it is outside of the receiver's detection range. The detection range itself varies with environmental factors (Huveneers et al. 2016, Reubens et al. 2019a), as well as transmitter and receiver settings and technologies (Clements et al. 2005, Kessel et al. 2014, Kessel et al. 2015). The spatial resolution of acoustic detection data can be further optimized using position systems based on triangulation (Baktoft et al. 2019). Spatial scale depends on the scope of the acoustic receiver array, which is enhanced by data sharing over (international) receiver networks (Abecasis et al. 2018, Ellis et al. 2019). Through the data management platform of the European Tracking Network (ETN; https://lifewatch.be/etn) (Fig. 1.5), a researcher can directly access the detections of their own tagged animals on other arrays (Reubens et al. 2019b). For both acoustic and archival tags, the temporal range and resolution depends on battery lifetime, which is limited by the size requirements for the tag in relation to the size of the studied animal (Hussey et al. 2015).

Impact on the animal

An important condition in tagging research is that the attachment or presence of a tag doesn't impede the animal's behaviour, physiology and survival (Alfonso et al. 2020). Tags can be attached externally (Verhelst et al. 2022) or injected (Walker et al. 2016), but here we focus on surgically implanting a tag into the coelomic cavity (Fig. 1.6) (Cooke et al. 2011b, Georgopoulou et al. 2022). Different steps of the procedure - capture, anaesthesia, surgery and

release - can cause severe stress for the animal (Jepsen et al. 2002, Georgopoulou et al. 2022). The impact of the procedure on the animal and its survival varies with a number of factors, including species, sex, season, tag type and tagging procedure (Cooke et al. 2011b, Huusko et al. 2016, Winter et al. 2020). A common rule is that the tag's weight should not exceed 2 % of the animal's biomass (Jepsen et al. 2002), although heavier tags have been shown to innocuous in species-specific studies (Brown et al. 1999, Childs et al. 2011, Smircich & Kelly 2014). Therefore, we should always consider that the effect of tagging is non-trivial and can affect our understanding of wild behaviour (Cooke et al. 2011b, Georgopoulou et al. 2022).

Innovations

Tagging research has vastly progressed by virtue of technological advancements, such as battery miniaturization, new tag types, receiver deployment methods and the incorporation of different sensors (Lennox et al. 2017, Crook et al. 2018, Weinz et al. 2020, Brownscombe et al. 2022). These innovations have enabled scientists to investigate animal behaviour and physiology across a wider scope in terms of geography, taxonomy and life-history (Edwards et al. 2019, Matley et al. 2022a). In line with the evolution of acoustic telemetry research from project-specific receiver arrays to (international) cooperative networks (Abecasis et al. 2018, Ellis et al. 2019, Reubens et al. 2019b), the 'open protocol' providing the interoperability between different manufacturers of acoustic tags and receivers, promises to further enhance tagging research and potentially map unprecedented movements (Reubens et al. 2021). In the age of ecoinformatics (Michener & Jones 2012), movement ecologists now have access to analytical tools ranging from open software for the calculation of common movement metrics (Udyawer et al. 2018) to highly complex modelling approaches (Braun et al. 2018, Whoriskey et al. 2019). Venturing into the world of 'big data', new challenges arise in terms of data storage needs and computational speed and power (Liu et al. 2019, Verhelst et al. 2023). Increasingly, tagging is used in combination with other methods (e.g. passive acoustic monitoring of cetaceans, Chapter 5) to maximize the information potential (Lowerre-Barbieri et al. 2019a, Matley et al. 2022b, Verhelst et al. 2023).
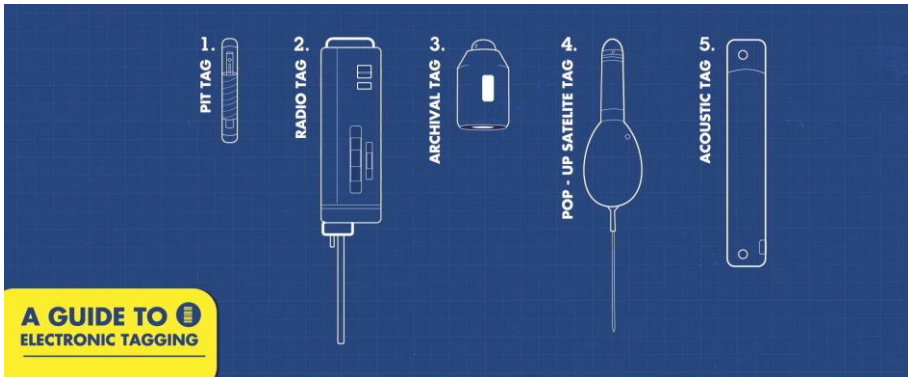
Figure 1.4. Different types of electronic tags. Still image adopted from European Tracking Network, 'Telemetry – A window into the aquatic world' (https://www.youtube.com/@europeantrackingnetwork).
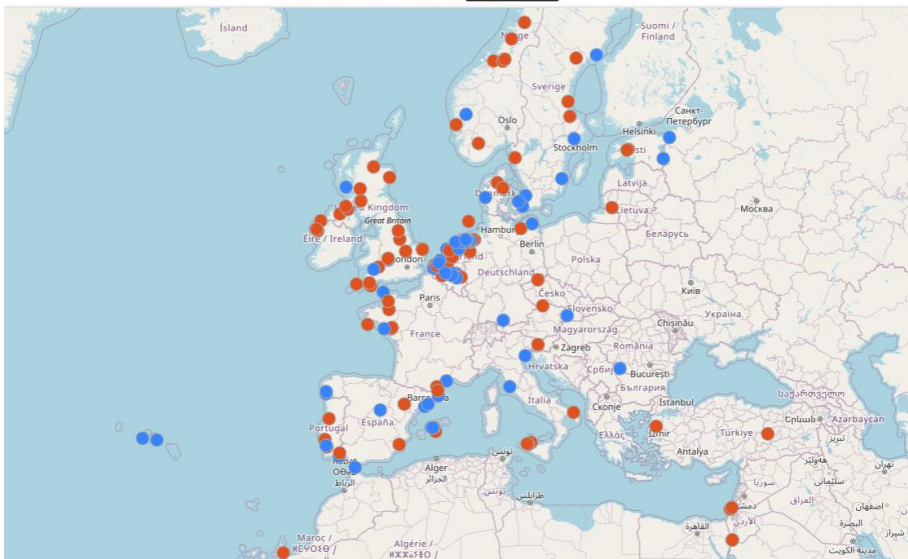
Figure 1.5. Data platform of European Tracking Network (ETN) with map of currently active (blue) and inactive (red) acoustic receiver arrays. Adopted from ETN: https://lifewatch.be/etn/.

Figure 1.6. Surgical implantation of a tag into the coelomic cavity of a European seabass. Source images: Verhaeghe (2020) (top) and Johan Reubens (bottom).

SEABASS BIOLOGY

The main study species of this research is the European seabass, *Dicentrarchus labrax* L. 1758. In this section, we introduce the species and provide an overview of its general biology and movement patterns, as well as a brief introduction to the fisheries exploiting seabass as a resource.

Figure 1.7. European seabass. Source image: Verhaeghe (2020).

Phylogeny and morphology

European seabass is one of the six species in the Moronidae family or temperate basses of the order Perciformes (Pickett & Pawson 1994). European seabass are fast-moving predators with a physical appearance to show for it (Fig. 1.7). These hunters have a streamlined body with spines in the anterior dorsal fin, the anal fin and on the operculum. The scaled skin varies in colour depending on the individual's origin, but generally has shades from silver-white or yellow on the ventral side to dark grey or blue on the dorsal side to blend in in its aquatic surroundings (Pickett & Pawson 1994). Sex is defined by genotype-environment interactions, whereby high temperatures during early development produces more males (Vandeputte et al. 2012). The maximum morphometric records reach a total length of 103 cm, a weight of 12 kg and an age of 30 years (Pickett & Pawson 1994, López et al. 2015, Froese & Pauly 2022). In the Northeast Atlantic, first maturity occurs at a size ranging from 32 to 36 cm total length (4 – 5 years old) for males, and from 40 to 45 cm total

length (5 – 8 years old) for females. Seabass mature earlier in the Mediterranean, at total lengths of 20 – 25 cm and 29 to 34.5 cm total length for males (2 years old) and females (3-4 years old) respectively (Pawson & Pickett 1996, López et al. 2015).
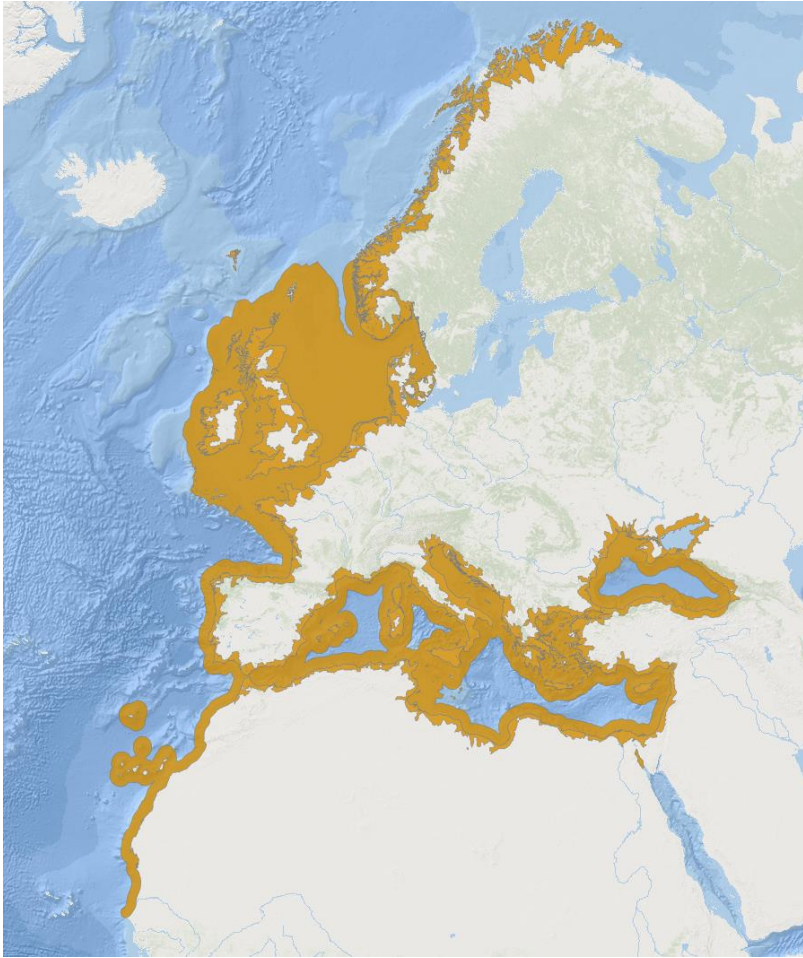

Figure 1.8. Distribution of European seabass across the Mediterranean Sea and Northeast Atlantic Ocean. Source image: IUCN (https://www.iucnredlist.org/).

Distribution and population genetics

European seabass are found in coastal waters, lagoons, estuaries and rivers from the Black and Mediterranean Sea to the Northeast Atlantic, tolerating a range of temperatures (2-32°C) and salinities (0-40 ppt) (López et al. 2015, Vandeputte et al. 2019). Their distribution ranges from the Black Sea to the Atlantic water of Morocco and Canary islands all the way north up to the coasts of Scotland and Scandinavia (Fig. 1.8) (Vázquez & Muñoz-Cueto 2014, López et al. 2015). Genetic studies show a clear distinction between the Atlantic and Mediterranean seabass populations. The Mediterranean lineage further differentiated in three groups in the Adriatic, the Eastern and Western Mediterranean (Souche et al. 2015). The Northeast Atlantic population is considered genetically homogenous, except for a subtle latitudinal gradient (Robinet et al. 2020), and some local differentiation found for seabass in Irish waters (Fritsch et al. 2007). In this dissertation, we focus on the population in the Northeast Atlantic.
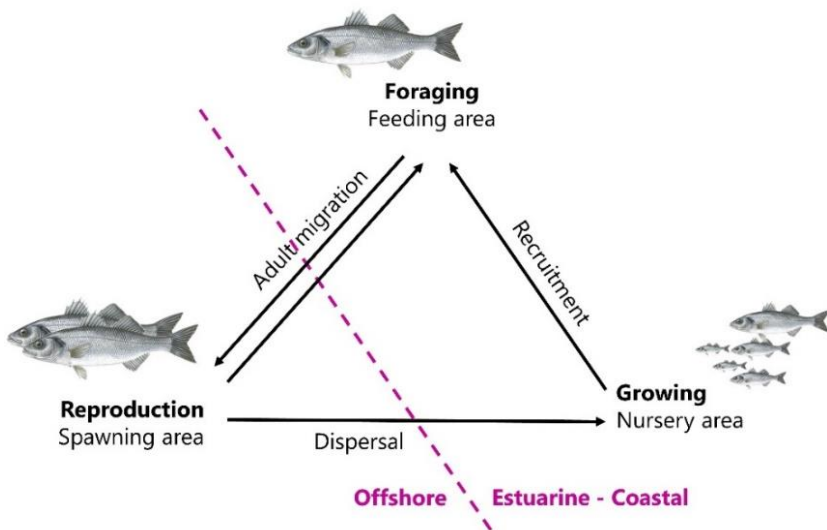

Figure 1.9. The migration triangle (Harden Jones, 1968), adapted to European seabass. Seabass have estuarine and coastal nursery and feeding areas, but head offshore to spawn. Adapted from Dambrine (2020); seabass image © Scandinavian Fishing Year Book.

Life cycle

Along its life-history stages, seabass occupies different habitats, undertaking seasonal migrations as an adult (Fig. 1.9) (Vázquez & Muñoz-Cueto 2014, López et al. 2015). Eggs are assumed to be deposited in offshore spawning grounds in midwater (20 m depth to surface) (López et al. 2015). Three main spawning areas are in the Bay of Biscay (Rochebonne Plateau), the western and the eastern English Channel (Dambrine et al. 2021). Observations of eggs and ripe seabass indicate spawning also takes place in the southern North Sea (Schnitzler et al. 2011, Tulp et al. 2016, ICES 2020b). The distribution of eggs and hatched larvae is determined by spawning location and hydrodynamics. Strong westerly winds and resulting currents increase the potential to drift further, whereas warmer temperatures reduce the duration of the pelagic phase (Beraud et al. 2018). During these early life phases, seabass can cope well with food deprivation, but abundant food in nursery areas is required for individual survival and population recruitment (Dambrine et al. 2020).

In the metamorphosis from post-larvae to juveniles (> 11 mm), seabass undertake active horizontal movements towards inshore waters (López et al. 2015). Shallow areas in coastal lagoons and estuaries serve as nurseries for young seabass (Vázquez & Muñoz-Cueto 2014, Beraud et al. 2018). In the Northeast Atlantic, males mature earlier (32 - 36 cm, 4 – 5 years old) than females (40 – 45 cm, 5 – 8 years old) (Kennedy & Fitzmaurice 1972, Pawson & Pickett 1996, López et al. 2015). Adult seabass feed on the abundance of food in coastal and inshore waters, as well as around sand banks and ship wrecks, in the warmer time of the year from March – June to September – November (Cambiè et al. 2016). Seabass consume various prey species of crustaceans, polychaetes, bivalves, gastropods, cephalopods and fish (pelagic, demersal and benthic), with diet composition varying with age, season and location (Kennedy & Fitzmaurice 1972, Pickett & Pawson 1994, Rogdakis et al. 2010, Spitz et al. 2013, Cobain et al. 2019).

For spawning, seabass turn to deeper, offshore waters where reproduction takes place between December and June, depending on the area (López et al. 2015, Dambrine et al. 2021). These spawning migrations are related to temperature, as growth and gonad development are reduced in colder waters (minimum 9 °C for females) and the spawning period starts earlier in southern

waters (Jennings & Pawson 1992, Pickett & Pawson 1994, Pawson et al. 2007, López et al. 2015). Coastal and estuarine areas are abundant in food but are more variable in terms of temperature and salinity. Coping with this environmental variability is thought to be too energy-demanding during reproduction, causing seabass to move offshore for spawning (Dambrine et al. 2021). However, environmental variables serve poorly to predict distribution across spawning areas, suggesting another mechanism related to the individual movement ecology is at play (de Pontual et al. 2019, Dambrine et al. 2021).

Movement behaviour & tagging research

Aside from laboratory experiments, individual seabass movements have been investigated with conventional tags in mark-recapture studies (Pawson et al. 1987, Fritsch et al. 2007, Pawson et al. 2007), as well as electronic tagging using acoustic telemetry (Pita & Freire 2011, Doyle et al. 2017, Stamp et al. 2021), data storage tags (Quayle et al. 2009, de Pontual et al. 2019) and pop-off satellite tags (O'Neill et al. 2018). Some studies have evaluated the impact of tagging on European seabass. Based on the results of an experiment examining juvenile growth, tags should not exceed 2.2 – 2.5 % of body mass (Bégout Anras et al. 2003). In experimental set-ups in aquaculture settings, physiological stress indicators (cortisol, glucose and lactate levels in blood samples) were not significantly different between tagged and untagged individuals after 14 and 95 days (Alfonso et al. 2020, Georgopoulou et al. 2022). Although mid-term (95 days) growth rate seemed unaffected, tagged fish did not eat for 2 to 4 days post-operatively due to acute surgery-induced stress (Alfonso et al. 2020). Significant differences were found in group-level swimming performance (group cohesion, polarization and exploratory tendency) 14 days after tagging (Georgopoulou et al. 2022), although this is not unusual in collective motion research in laboratory environments and have been attributed to collective personality variation (MacGregor & Ioannou 2021).

Seabass are fast swimmers capable of migrating hundreds of kilometres (López et al. 2015, de Pontual et al. 2019). The maximum depth has been observed to exceed 225 m (de Pontual et al. 2019). Different activity regimes have been drawn from patterns in vertical movement behaviour, including diel

and tidal cycles (Quayle et al. 2009, Heerah et al. 2017). Activity rhythms can be higher diurnally and nocturnally and can switch, depending on the individual and the season (Reebs 2002, Heerah et al. 2017). Seabass can be solitary, but they are also known to form shoals (Anras et al. 1997, Quayle et al. 2009). By swimming in a group, seabass adapt their swimming activity and patterns, whereby they can shift in diel activity rhythm (Anras et al. 1997, Bégout Anras et al. 2004).

Individual seabass have been shown to be associated to specific locations through the behaviours of long-term residency and interannual fidelity. Residency reflects an animal staying or 'residing' in a limited area for a longer period of time (Reubens et al. 2013b). When an animal returns to a specific area, for example on a yearly basis, it exhibits site fidelity (Doyle et al. 2017). Tagging studies have revealed seabass residency and site fidelity to feeding (Pawson et al. 1987, Pawson et al. 2007, Pawson et al. 2008, Doyle et al. 2017, O'Neill et al. 2018, de Pontual et al. 2019, Stamp et al. 2021, de Pontual et al. 2023) and spawning areas (de Pontual et al. 2019, Le Luherne et al. 2022, de Pontual et al. 2023). Environmental factors (e.g. temperature) are defining for habitat suitability – and thus the potential geographic distribution – of seabass as a species. However, environmental covariates serve poorly to explain the actual space use of individual seabass, indicating other factors are at play for seabass habitat selection (Dambrine et al. 2021).

Seabass stock delineation and fisheries

Northeast Atlantic seabass faced severe declines in the past decades due to intense fishing pressures. Slow growth, late reproductive maturity, aggregation at spawning areas and high residency add to seabass's vulnerability for overexploitation and local depletion (i.e. when fisheries deplete or exhaust animals residing at a given location) (López et al. 2015, Doyle et al. 2017). The International Council for the Exploration of the Sea (ICES) delineates four stocks in the Northeast Atlantic: North Spain and Portugal (southern Bay of Biscay and Atlantic Iberian waters; ICES divisions 8c,9b), Biscay (northern and central Bay of Biscay; 8ab), West coast Scotland and Ireland (West of Scotland, West of Ireland and eastern part of southwest of Ireland; 6a,7b,j) and the Northern stock (central and southern North Sea, Irish Sea, English Channel, Bristol Cannel and Celtic Sea ; 4b,c, 7a,d-h) (Fig.

1.10) (ICES 2012a). Spawning stock biomass estimates for 2022 are 17,174 tonnes for the Bay of Biscay stock and 12,384 tonnes for the Northern stock (ICES 2022b, c). Biomass estimates are not available for the stocks in North Spain and Portugal, and West coast Scotland and Ireland, which ICES considers data limited (ICES 2020a, 2021).

European seabass is a prized target species for both commercial and recreational fisheries. Seabass can be caught using different gears: demersal, midwater or pelagic trawls, fixed and drift nets, seines, and hook and line for angling (ICES 2022b, c). Recreational removals of seabass are estimated to be high (up to one quarter of the total catch of the Northern and Biscay stocks) (ICES 2022b, c). Estimation of recreational catches remains difficult due to the data poverty and diversity of recreational fisheries, but are set to improve with increasing research efforts and voluntary monitoring schemes (Hyder et al. 2020, Verleye et al. 2022). At the time of writing, commercial landings of the Northern stock are mainly attributed the UK, followed by France, the Netherlands and Belgium (ICES 2022b). France is almost entirely responsible for catches of the Biscay stock (ICES 2022c), whereas the stock in North Spain and Portugal is targeted by Spanish and Portuguese fishers (ICES 2021). Fisheries targeting the West coast Scotland and Ireland stock are almost entirely recreational (ICES 2020a). The seasonal differences of seabass habitat use are also reflected in the seasonality of the fisheries. In the warmer months, seabass are targeted by inshore and coastal fisheries. Offshore spawning aggregations (December to May) in the English Channel, Bristol Channel and Bay of Biscay were increasingly targeted by pelagic trawlers from the 1980s onwards (Colman et al. 2008), but pelagic trawling on the Northern stock was banned from 2017 onwards (EU 2017b). Seabass fisheries measures on the EU level include commercial catch limitations, recreational bag limits and a seasonal closure (EU 2023). Additional national measures were taken, such as spatial closures in the assigned Bass Nursery Areas in the UK (Ministry of Agriculture Fisheries and Food & Welsh Office Agriculture Department 1990) and in the Port of Zeebrugge in Belgium (Flemish Government 2017). Evolutions of seabass stock status and fisheries policy were further detailed in chapter 9.
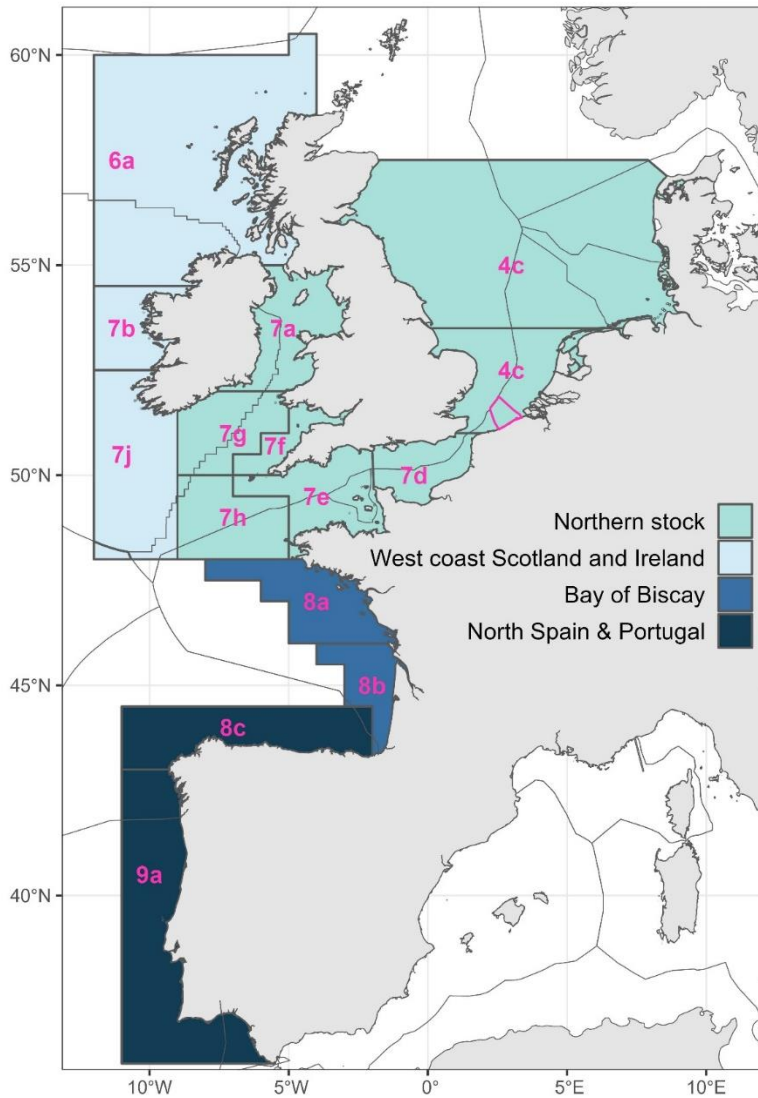
Figure 1.10. ICES stock divisions for European seabass in the Northeast Atlantic: southern Bay of Biscay and Atlantic Iberian waters (North Spain and Portugal; ICES divisions 8c,9b), northern and central Bay of Biscay (Biscay; 8ab), West of Scotland, West of Ireland and eastern part of southwest of Ireland (West coast Scotland and Ireland; 6a,7b,j) and the central and southern North Sea, Irish Sea, English Channel, Bristol Cannel and Celtic Sea (Northern stock; 4b,c, 7a,d-h). The map shows the exclusive economic zones (EEZ), with the Belgian EEZ highlighted in pink. Shape files originated from ICES (https://gis.ices.dk) and Marine Regions (https://www.marineregions.org).

Seabass in the southern North Sea

Not much is known about seabass in the North Sea. Over the past decades, seabass has expanded northwards, occurring as far north as Norwegian waters and the Baltic Sea (Hind 2006, Bagdonas et al. 2011). In the southern North Sea, seabass can be found in estuarine and inshore areas, such as the Thames Estuary, Scheldt Estuary, Eastern Scheldt and Wadden Sea, which are thought to be nursery and feeding grounds (Pawson et al. 1987, Schnitzler et al. 2011, Cardoso et al. 2015, Tulp et al. 2016). Applying mark-recapture, individual seabass tagged in summer feeding areas along the English coast in the North Sea were shown to migrate southward into the English Channel during spawning season (Pawson et al. 1987, Pawson et al. 2007). Information on potential seabass spawning within the North Sea is scarce, as there is no targeted spawning survey in the area. However, stage 1 eggs (lasting 24 hours) were observed in April and May 2011 along the English coast, around the Dogger bank and west of the Voordelta (area stretching 3 to 15 km seaward along the Dutch coast from Walcheren to the Maasvlakte) (Tulp et al. 2016). Spawning in the North Sea is hypothesized to be likely later in the spawning season (April – May) during warmer years, with higher settlement rates in North Sea coastal and estuarine areas (e.g. Wadden Sea and Thames) during warmer years with strong westerly winds (López et al. 2015, Beraud et al. 2018).

Within Belgian waters, patterns of seabass presence are mainly known through fisheries practices. Anglers target seabass from vessels, as well as from the beach, where they are also caught by passive gears (Verleye et al. 2022). The periods of April – May and September – November are considered good to catch seabass offshore at sand banks and artificial structures (mainly shipwrecks), whereas seabass is more often caught from the beach during the summer months (Bral pers. comm.). Anglers report high catches of seabass along water inlets of sluices, where seabass is thought to predate on prey fish gushed with the incoming water (Deputter pers. comm.). This phenomenon was used by poachers, causing a restriction of seabass fishing in the ports of Oostende and Zeebrugge (Flemish Government 2017). A mark-recapture experiment in the port of Zeebrugge showed some seabass exhibit interannual fidelity to the port area (Delbare 2012). Monitoring of estuarine and riverine areas has shown seabass occurring as far inland as Hamme and Mechelen (Brosens et al. 2015).

OUTLINE OF THIS THESIS

In this PhD thesis dissertation, we investigated the movement ecology of European seabass occurring in the southern North Sea, using electronic tags. To that extent, we first take a detour to the methodological technicalities of electronic tagging (Part I). The elaborated methodologies contribute to electronic tagging research as a whole, but were also required to investigate seabass movements at multiple spatiotemporal scales. We examine seabass movement behaviour and habitat use in specific areas in Belgian waters, but also their migration patterns in the southern North Sea and surrounding waters (Part II). Next to seabass ecology, we evaluate seabass fisheries policy to understand the lack of recovery of the Northeast Atlantic seabass population (Part III).

Part I – ELECTRONIC TAGGING

The main technique used for this research consisted of electronic tagging. In this part, we explain the concept and the applied technologies, where we elaborate how we contributed novel practical and analytical methodologies in chapters 2 to 5.

Chapter 2: Acoustic and archival technologies join forces: A combination tag

The acoustic data storage tag (ADST) combines the features of acoustic telemetry and archival tagging. Being the first to use this novel tag type, we describe the new technology and how we applied it to three species: European seabass, Atlantic cod and starry smooth-hound. A geolocation modelling approach was adapted to include the information of the tag's acoustic detections.

Chapter 3: Mooring scientific instruments on the seabed—Design, deployment protocol and performance of a recoverable frame for acoustic receivers

Using acoustic telemetry in challenging marine environments requires practical deployment mechanisms. A tripod frame was developed for deploying acoustic receivers on the seabed. We tested the deployment and

recovery protocol in a field trial and compared the performance in terms of detection range with a commonly used cabled design.

Chapter 4: Taking the time for range testing: an approach to account for temporal resolution in acoustic telemetry detection range assessments

Understanding variability in detection range is crucial to adequately interpret acoustic telemetry data. A novel method for estimating detection probability was elaborated, whereby the temporal aspect of the presence of a tagged animal within a specific time bin is taken into account.

Chapter 5: The importance of multi-sensor observations to advance species co-occurrence knowledge: a demonstrator application of acoustic technologies

The technique of passive acoustic monitoring, enabling the observation of the presence of echolocating cetaceans, was combined with acoustic telemetry in one physical deployment set-up. We applied different analysis techniques to explore how the resulting long term data series could benefit research on species co-occurrence.

Part II – MOVEMENTS OF EUROPEAN SEABASS FROM THE SOUTHERN NORTH SEA

Using electronic tagging, the movement behaviour and migration patterns of European seabass were investigated at different spatiotemporal scales.

Chapter 6: Elucidating the migrations of European seabass from the southern North Sea, using mark-recapture data, acoustic telemetry and data storage tags.

To understand migration patterns of European seabass residing in the southern North Sea, we combined conventional and electronic tagging data from different projects (from Belgium, France, the UK and The Netherlands). We investigated large-scale migrations using seabass recapture positions, acoustic detections across international receiver networks and migration trajectories that were reconstructed with geolocation modelling.

Chapter 7: Using acoustic telemetry to investigate habitat use of European seabass in the southern North Sea

We investigated patterns in space use over time and connectivity in the study area the Belgian part of the North Sea (BPNS) and the Scheldt Estuary. Seabass habitat use was further examined at four sites with artificial substrates (port infrastructure, offshore wind farm, radar tower and offshore wreck).

Chapter 8: Not all are equal before the law – fisheries measures protect European seabass groups with distinct habitat use differently

In a case study in a Belgian port area, seabass movements were investigated to understand habitat use and connectivity in the study area. The patterns in movement were directly linked to the prevailing spatiotemporal fisheries restrictions to estimate how individual seabass are protected from capture by fisheries policy measures.

Part III – SEABASS FISHERIES POLICY

Chapter 9: Lessons (still not) learned from a decade of European seabass fisheries policy

In this chapter we investigate seabass fisheries policy. An overview of EU-level measures since emergency measures of 2015 was made, but we also zoomed in on the Belgian situation. We identify key issues that have contributed to the lack of a full recovery of the Northeast Atlantic seabass population.

Part IIII – DISCUSSION

Chapter 10: General discussion

The lessons learned from this PhD research are summarized and contextualized in the broader framework of tagging research and seabass ecology, for which we provide future research recommendations. We translate the findings on seabass ecology and policy into management recommendations, and add some personal reflections on the positionality of scientists.

Part ⅢⅢ – EPILOGUE

Sexism and its intersections in (marine) science

In a final essay, I discuss how I experienced and witnessed sexism and its intersections throughout the PhD project. This chapter serves as a personal testimony and a plea for change.

I

ELECTRONIC TAGGING

CHAPTER 2

ACOUSTIC AND ARCHIVAL TECHNOLOGIES JOIN FORCES: A COMBINATION TAG

AUTHORS Jolien Goossens, Mathieu Woillez, Arnault LeBris, Pieterjan Verhelst, Tom Moens, Els Torreele, Jan Reubens

ABSTRACT

1. Technological advances are key to maximize the information potential in electronic tagging studies. Acoustic tags inform on the location of tagged animals when they are in range of an acoustic receiver, whereas archival tags render continuous time series of logged sensor measurements, from which trajectories can be inferred.

2. We applied a newly developed acoustic data storage tag (ADST) on 154 animals of three fish species to investigate the potential of this combination tag. Fish trajectories were reconstructed from logged depth and temperature histories using an existing geolocation modelling approach, adapted to include a likelihood for acoustic detections.

3. Out of 126 detected fish (accounting for over 700,000 detections) and 25 tag recoveries, eight ADSTs rendered both acoustic and archival data. These combined data could validate that the original geolocation model performed

adequately in locating the fish trajectories in space. The acoustic data improved the timing of the daily position estimates.

4. Acoustic and archival tagging technologies provided highly complementary information on fish movement patterns and could partly overcome the limitations of either technique. Furthermore, the ongoing developments to acoustically transmit summary statistics of logged data would further increase the information potential of combination tags when tracking aquatic species.

INTRODUCTION

Electronic tagging enables the spatiotemporal analysis of aquatic animal movements and vastly contributes to our understanding of these animals' behavioural and spatial ecology (Hussey et al. 2015, Lennox et al. 2017, Brownscombe et al. 2022). Over the past decade, technological advances have led to tag miniaturization and longer battery life, diverse attachment methods and increased data resolution (Hussey et al. 2015). Tags have been fitted with sensors (measuring e.g. pressure, acceleration, temperature and predation) to log or transmit information on behaviour, physiology and the physical environment (Brownscombe et al. 2019). These technological advances have allowed to address a wider range of questions on a greater diversity of species (Brownscombe et al. 2022).

Two common electronic tagging technologies for aquatic animals are acoustic telemetry and archival tags. In acoustic telemetry, a tag transmits an acoustic signal, coded with a unique ID and optionally a sensor measurement. An acoustic receiver can detect this transmitted signal when the tagged individual is within the receiver's detection range. Detection data are accessed through the receiver. Archival tags, on the other hand, store sensor measurements at a predefined time interval in the tag memory. These tags must therefore be recovered or send their information through satellites to access the logged data. The resulting time series can provide fine-scale information on vertical movement behaviour (Heerah et al. 2017), environmental preferences (Righton et al. 2010), and can be used to reconstruct migration trajectories with geolocation modelling (Pedersen et al. 2008, Woillez et al. 2016).

Double-tagging, i.e. tagging an animal with two tags, has been used to benefit from specificities and complementarity of different tag types (Strøm et al.

2017, Gatti et al. 2021). Aside from providing complementary information on ecology and/or physiology, the combined use of distinct technologies allows to evaluate the interpretation of one technology's results and ground-truth modelled outcomes (e.g. geolocation models, as reviewed by Gatti et al. (2021)). In addition, double-tagging enables to assess tag retention and effect (Brownscombe et al. 2019, Verhelst et al. 2022). Although limitedly studied (Verhelst et al. 2022), double-tagging comes with reasonable concern over an increased impact of the tagged fish' welfare and movement behaviour. Combining technologies in one physical tag allows to avoid the longer handling time in a more complex procedure and the added effect of the second tag. In this study, we report on the first utilization of a novel type of electronic tag that combines the technologies of acoustic telemetry and archival tagging.

MATERIALS AND METHODS

Tag specifications

We used the acoustic data storage tag (ADST) (Fig. 2.1), developed by Innovasea Ltd. (USA), in two sizes: ADST-V9TP (diameter 13 mm, length 65 mm, weight in air 8.5 g, transmitting power output 151 dB) and ADST-V13TP (diameter 16 mm, length 75 mm, weight in air 14.2 g, transmitting power output 154 dB). The ADST was equipped with a pressure sensor (maximum depth 68 m, accuracy ± 1.0 m, resolution 0.3 m) and a temperature sensor (range -5 to 35 °C, accuracy ± 0.5 °C, resolution 0.15 °C). Tags were coloured brightly red and fitted with a sticker with contact details of the principal investigator and the mentioning of a reward (€25 or a T-shirt), to increase the probability of tag recoveries. The built-in floatation enabled tags to drift ashore when they got separated from the fish (e.g. due to predation, fishing or natural death).

Sensor data were stored as continuous time series on the tag itself. Sensor information at the time of transmission was also transmitted acoustically (69 kHz, MAP114, protocol A69-9006). When selecting the transmit ratio of temperature versus pressure measurements, we favoured depth use for its information potential on vertical movement behaviour. The transmitting and logging interval were selected in consideration of the study species, the study

objectives and the trade-off with battery lifetime (Table 2.1, more details in Supporting information). Tag settings had to be selected at the time of ordering the tags, as the programming of settings had to be performed by the manufacturer. Because the ADST lacked an internal clock, the time of activation of the tag (i.e. by removing a magnet) had to be registered to the second. Upon retrieval of an ADST, the physical tag was mailed to the manufacturer to download the data.

Figure 2.1. Acoustic data storage tag (ADST), developed by Innovasea Ltd. (USA).

Table 2.1. Tag settings applied for different species. Temperature (T) and pressure (P) sensor measurements were logged continuously at a fixed interval and were transmitted at a fixed ratio (more details in Supporting information).

Species	N	Type	Battery life (days)	Logging interval T - P (s)	Transmit ratio T:P
European seabass	27	ADST-V9TP	354	180 - 90	1:3
	40	ADST-V9TP	339	180 - 90	1:3
	19	ADST-V9TP	400	180 - 90	1:9
	23	ADST-V9TP	425	300 -90	1:9
Atlantic cod	3	ADST-V9TP	339	180 - 90	1:3
	12	ADST-V9TP	350	180 - 90	1:3
Starry smooth-hound	30	ADST-V13TP	518	240 - 120	1:3

Tagging procedure

From 2018 to 2021, we tagged three different fish species in the Belgian Part of the North Sea (BPNS), the Western Scheldt Estuary and the Eastern Scheldt in the Netherlands. We used the ADST-V13TP for 30 starry smooth-hound (*Mustelus asterias* Cloquet 1821) and the ADST-V9TP for 109 European seabass (*Dicentrarchus labrax* L. 1758), and 15 Atlantic cod (*Gadus morhua* L. 1758). All fish were caught with rod and line. Immediately after capture, fish were unhooked and placed in a holding tank. Prior to the surgery, seabass and cod were anaesthetised with clove oil (0.05 mL per L of seawater), whereas starry smooth-hounds were held with the ventral side up to induce tonic immobility. The tag was surgically inserted in the abdominal cavity through an incision across the midventral line, which was closed by three stitches using non-absorbable mono-filament. A Pederson disc (9.5 mm diameter; Floy Tag & Mfg., Inc., USA) stating 'REWARD: TAG INSIDE' and individual reference number, was attached between the dorsal and caudal fin for the majority of seabass and cod. Before release, the tagged fish was placed in a tank for 5 – 15 minutes to recover from the surgery. The animal tagging procedure was approved under the ethical certificates EC2017-080 (Belgium), 2016.D-0041.004 and 2016.D-0041.008 (The Netherlands).

Data management

Acoustic detections could be registered on the permanent Belgian acoustic receiver network (Reubens et al. 2019b), with the detection range distance (where the probability of detecting a tagged animal within a day exceeded 0.5) averaging from 500 to 700 m (Goossens et al. 2022). The data management was facilitated through the European Tracking Network (ETN) database (https://lifewatch.be/etn) (Reubens et al. 2019b), archiving the data and metadata for both the acoustic and logged data.

Analysis

For the recovered tags, trajectories were reconstructed with geolocation modelling, using a hidden Markov model (HMM). The hidden state (daily fish position) was estimated with an observation model, relating sensor measurements to environmental reference fields, and a movement model, describing the time dynamics of the state sequence as a Brownian random walk model (Pedersen et al. 2008). Full details on the geolocation approach

were outlined in previous publications (Woillez et al. 2016, de Pontual et al. 2023), but we describe below how this HMM was adapted for the application on ADST data in our study area.

The reference fields of bathymetry and temperature at depth for the observation model were drawn from the 3D Dutch continental shelf model in flexible mesh, 3D DCSM-FM (Zijl et al. 2021). Building on an existing HMM, we decided to maintain an approach with a regular grid, rather than using the original irregular grid of the 3D DCSM-FM output (Liu et al. 2017). The depth and temperature irregular grids were rasterized to a regular grid (48.8°N – 53.0°N, 3.2° W - 5.0° E) with the field's finest resolution of 0.5' x 0.75' (latitude x longitude). The original 3D DCSM-FM output for the English Channel offshore area was at a coarser resolution of 1' x 1.5'. Pixels in this area were resampled to the values of the nearest neighbouring cell to retain the highest resolution in the main area of interest (southern North Sea). The raster fields were transformed to a metric grid of a resolution of 1 km x 1 km. The temperature likelihood was estimated using a multivariate normal probability density function at the different depth layers (0, 5, 10, 15, 20, 25, 30, 50 and 100 m). This temperature likelihood was then multiplied by the depth likelihood (de Pontual et al. 2023).

Using the acoustic detection data, we implemented a detection likelihood. This likelihood layer was calculated differently for days with and without acoustic detections. If a fish was detected, the likelihood was set to 1 for the grid cell with the receiver location and to 0 for the rest of the area. For days without detections, the grid cells with active receivers were assigned a detection likelihood of zero, with the rest of the field having an equal non-null value.

For European seabass a behavioural switch was implemented (de Pontual et al. 2023) to discern two (daily) behavioural states: low versus high activity. As the behavioural pattern segmentation used here (Heerah et al. 2017) was developed specifically for seabass, we did not apply the behavioural switch for Atlantic cod and starry smooth-hound. Hence, the diffusion coefficient D (the mean daily distance covered by a fish, in km2/day) of the movement model was estimated with a maximum likelihood estimation for two behavioural states for seabass and for one state for the other species. From the daily posterior probability distributions of the observation and movement model

combined, we calculated the most probable sequence of positions (Viterbi track).

Model performance was evaluated using the information on acoustic detections. We defined positional accuracy as the distance between the known receiver location and the trajectory as estimated by the geolocation model without including the acoustic detections (detailed explanation in Supporting information). Track sensitivity was defined as the distance between the entire trajectories reconstructed with and without implementing the detection likelihood. To account for potential errors in the timing of the estimated track, both metrics were calculated as timed (distance to the estimated position at the exact day) and non-timed (minimum distance to the estimated positions at all days).

RESULTS

Up until June 2022, 25 tags were retrieved (16.2%): four tagged seabass were caught with rods and 21 tags were found washed ashore. Plotting the depth and temperature histories of the tags, we could visually determine that two seabass and one cod died in the week after tagging; these datasets were omitted from the analysis. Two of the recovered tags experienced technical failures: an issue with the temperature sensor and another with the tag's hardware. At the time of writing, three of the recovered tags still had to be processed by the manufacturer. The acoustic data storage tags (ADST) resulted in over 700,000 acoustic detections from 126 out of 154 tagged animals.

Eight ADSTs provided both acoustic and archival data (Table 2.2). The complementarity of the two electronic tagging data types was visualized in figure 2.2. The cod remained in an offshore receiver array until it died, as verified by the 87 detected days, which was accurately estimated with the geolocation model (median timed positional accuracy 4.1 km). For the European seabass, the archived depth history showed a very shallow depth use (mostly the upper 5 m of the water column) during summer and a deeper occupancy during colder months, which would likely be interpreted as inshore feeding behaviour during summer and offshore excursions during winter (de Pontual et al. 2023). The acoustic data, however, showed that the seabass was

detected inside a port area (Zeebrugge) for 124 days throughout the year. For the example of the starry smooth-hound, the information of solely acoustic detections would have only indicated that the shark passed by the offshore wind farms nine months after release before returning to its area of release (Scheldt Estuary). The geolocation model unravelled the shark's winter migration to the English Channel. Supplemented with the acoustic telemetry data (55 days detected), the trajectory was shown to be more offshore. The archival depth series showed the shark went deeper than 75.5 m, the factual maximum depth. The evaluation of the model with the information of acoustic detections produced median values of 21.4 km (maximum 134.7 km) for timed and 5.9 km (maximum 46.9 km) for non-timed positional accuracy, and 6.9 km (maximum 133.9 km) for timed and 1.5 km (maximum 59.3 km) for non-timed track sensitivity. The contrast between the timed and non-timed metrics indicated the inclusion of the information on acoustic detections vastly improved the timing of the reconstructed tracks.

DISCUSSION

The unique value of combination tags consisted of the possibility to understand residency and habitat use in a specific area with a receiver array, in addition to studying migration behaviour and trajectories during the period animals were not detected. As illustrated by the seabass in the port area, the bathymetry and temperature variability of (secluded) inshore areas might not reliably be accounted for in environmental reference fields. Acoustic data were vital to recognize fish presence in this specific habitat. The inclusion of acoustic data could thus overcome the limited performance of geolocation models in coastal areas (due to an insufficient resolution of environmental reference fields), where the deployment of acoustic arrays would be relatively convenient. The vast contribution of the archival component was illustrated in the starry smooth-hound example. A solely acoustic tag would have only informed on site fidelity and some residency in the estuary, whereas with the archival data we were able to reconstruct its southward migration trajectory. Acoustic detections informed on presence at specific locations, whereas the archival data contributed large-scale modelled trajectories on a low resolution and fine-scale information on behaviour and temperature experience on a high resolution.
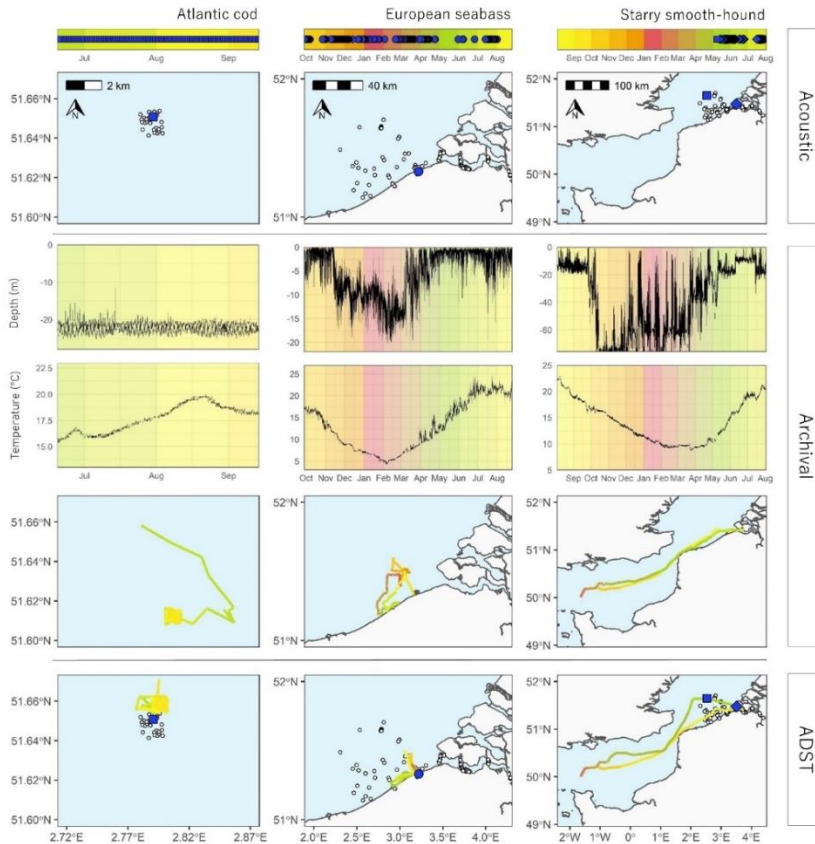
Figure 2.2. Examples of tagging results for an Atlantic cod (left), European seabass (middle) and starry smooth-hound (right), shown with only the acoustic detection data (top), only the archival data (middle) and the combination of both in the ADST (bottom). White dots represent the locations of the active receivers with the locations of detections in blue (square: offshore wind farm; diamond: estuarine station; circle: harbour station). Archival depth and temperature histories were plotted over time and the modelled trajectories were visualized on the map in the timeline's colouring. Combining acoustic and archival data, trajectories were estimated with the inclusion of acoustic detection data in the geolocation model.

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Table 2.2. Overview of tags resulting in both acoustic and archival data with the number of days of archived data and days detected per fish, in addition to the archived depth (m) and temperature (°C) measurements. Performance metrics were computed in km: timed (TPA) and non-timed positional accuracy (NPA), timed (TTS) and non-timed track sensitivity (NTS). Values were shown as median [range].

Species	Trajectories	Days detected	Archived days	Depth (m)	Temperature (°C)
European seabass	3	18 [1 – 124]	235 [38 – 331]	2.4 [0.0 – 20.2]	2.4 [4.3 – 25.8]
Atlantic cod	2	46 [2 – 89]	178 [88 – 268]	22.0 [0.0 – 25.3]	17.7 [14.5 – 19.9]
Starry smooth-hound	3	2 [1 – 55]	38 [23 – 367]	34.3 [0.0 – 75.5]	13.5 [8.6 – 29.2]

Table 2.2. **(continued)**

Species	TPA	NPA	TTS	NTS
European seabass	25.3 [2.5 - 37.2]	7.7 [0.3 - 7.5]	23.0 [0.1 - 37.6]	4.8 [0.1 - 29.6]
Atlantic cod	4.1 [0.5 - 27.6]	0.5 [0.5 - 19.7]	0.7 [0 - 27.3]	0.6 [0 - 20.0]
Starry smooth-hound	48.6 [9.1 - 134.7]	5.9 [4.3 - 46.9]	0.7 [0 - 133.9]	0.5 [0 - 59.3]

The acoustic detections enabled the validation of the geolocation model, which was shown to perform in line with expectations for demersal and pelagic fish (Gatti et al. 2021). As illustrated by the smaller distances of the non-timed performance metrics, the geolocation model would adequately position the trajectory in space, but would often err in the timing of the daily position estimates along the track. Building on an assumption of Brownian motion (Pedersen et al. 2008), the movement model of the geolocation assumed a fish to move to an area of high likelihood rather gradually. The acoustic detections however, showed that fish movement could be abrupt in distinct periods of time.

To fully benefit from this information potential, combination tags should be highly modular. We regarded the floatability option as an important asset, as we retrieved the majority of recovered tags after washing ashore. Depending on the study species, researchers might opt for pressure and temperature sensors with a different range and resolution. Since the fish' temperature experience could have been drawn from existing temperature data series in the study area, the acoustic transmission of depth use information was preferred. The ability to (re-)program transmitting and logging settings and performing the data offload of recovered tags yourself, as well as the inclusion of an internal clock, would highly increase user-friendliness. Other acoustic and archival tags on the market do entail these features, as well as a wider range of options regarding tag size, battery time and storage memory, sensor range and resolution, pop-off mechanisms, etc. Although using one tag instead of two may be less invasive and reduces fish handling time, the flexibility of a more diverse set of options remains a crucial advantage of double-tagging.

With regard to future developments, however, combining technologies in one physical tag entails the possibility of transmitting information collected before the time of transmission. Like satellite tags (pop-up satellite archival tags and smart position and temperature transmitting tags), acoustic data storage tags could transmit summary metrics of the archived data, but through an acoustic receiver rather than through satellite transmission. Currently, an acoustic signal can only transmit a very small amount of data (8 bites at time of study) in addition to the tag ID. The limited computing power within tags prevents

the use of advanced algorithms. Considering the present technological challenges, the transmitted information will likely consist of simple summary statistics. To maximize this potential future utility, combination tags should be customizable, enabling users to prioritize the transmission of information on individual location (e.g. time stamped maximum depths), behaviour (e.g. seasonal depth range), or habitat (e.g. seasonal temperature range), depending on their research objectives.

AUTHOR CONTRIBUTIONS

JG led the analysis and writing. JR, PV, TM, ET and JG designed the study. JG, JR and PV carried out the field work. MW and JG performed the geolocation analysis. ALB and JR contributed to the writing. All authors read and reviewed the drafts and approved the final manuscript.

ACKNOWLEDGEMENTS

CHAPTER 3

MOORING SCIENTIFIC INSTRUMENTS ON THE SEABED: DESIGN, DEPLOYMENT PROTOCOL AND PERFORMANCE OF A RECOVERABLE FRAME FOR ACOUSTIC RECEIVERS

AUTHORS Jolien Goossens, Michiel T'Jampens, Klaas Deneudt, Jan Reubens

ABSTRACT

1. Acoustic telemetry is increasingly used to observe and monitor animal movements in aquatic environments. Practical deployment mechanisms are needed to sustain consistent data flows in challenging environments.

2. A tripod frame was developed to facilitate the deployment of acoustic receivers on the seabed, allowing for the recovery of all equipment with an acoustic release system.

3. The procedures of deployment and recovery proved to be practical and efficient during a field trial in the North Sea. Compared to a common cabled design, the tripod frame realized a significantly higher detection probability and performed consistently better at greater distance and louder ambient noise.

4. In the context of ocean observation in challenging environments, the tripod frame is a useful tool for temporary and continuous monitoring of tagged fish presence, potentially fitted with additional instruments.

INTRODUCTION

Acoustic telemetry enables the observation of animal movements in aquatic environments. Individual animals are provided with a transmitter, relaying a signal that can be picked up by acoustic receivers (Hussey et al. 2015). Receivers are physically set-up in temporary deployments or permanent networks in a range of habitats (Reubens et al. 2019b). A lot of practical issues remain with the deployment of receivers, especially in challenging environments and weather conditions.

For deployment on the seabed, receivers are commonly fixed to a line that is attached to a float and anchored to a weight (Gazit et al. 2013, Cowley et al. 2017, Hoenner et al. 2018, Ellis et al. 2019). Two concerns regarding this design are the retrieval of equipment and the variability in receiver orientation. Recovery by diving is limited by depth and weather conditions, as well as budget and person hours. Acoustic releases allow for receiver retrieval without the need to access the instrument at depth. To facilitate this recovery, alternative designs (e.g. products of RS Aqua Ltd and Kintama Research Services) incorporate these acoustic releases with mechanisms for the retrieval of mooring anchor and release pins (Titzler et al. 2010, Crook et al. 2018). However, the use of anchor lines in these systems entails a fluctuation of the receiver's orientation and therefore, its performance (Clements et al. 2005). In this study, we developed and tested a new design for the installation of acoustic receivers in the field, aiming to facilitate a convenient, cost-effective deployment, with minimal disposal or loss of equipment and an assurance of a high data quality.

DESIGN

The frame consists of a galvanized-steel tripod (*c.* 80 kg), mounted with a custom-made collar (Deepwater Buoyancy Inc.) with a floating capacity of 11.5 kg (Figure 3.1). A tether line, correctly coiled in the rope canister in the central beam, connects the tripod to an eye bolt on the bottom of the collar. The rope

(8 mm diameter with Dyneema core, 1,000 kg traction) is 1.5–2 times larger than the bottom to surface distance. A Vemco VR2AR receiver with built-in acoustic release is fixed into the collar with stainless-steel screws using the float attachment bracket on the receiver. The collar is then placed on the platform on top of the tripod, with the eye bolt and tether line inside the rope canister. The receiver's release pin, which protrudes through the hole in the top platform of the frame, is connected to the tripod's eye nut with turnbuckles.
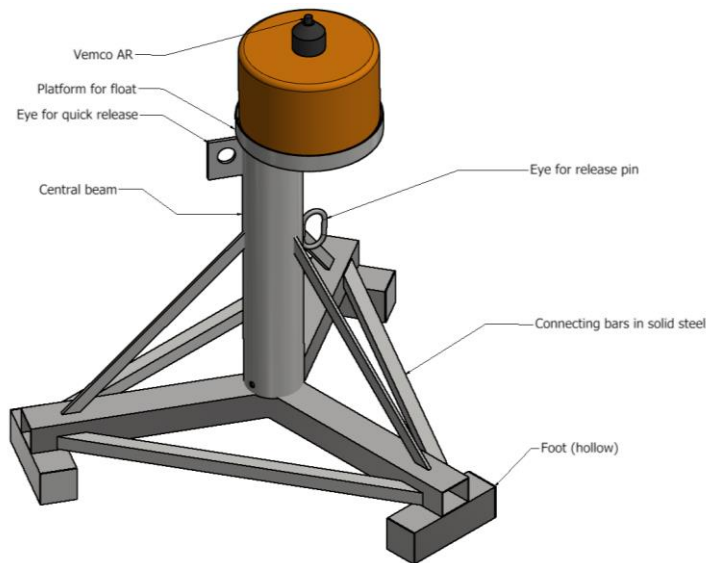
Figure 3.1. Technical drawing of the tripod frame design. The Vemco VR2AR acoustic receiver is mounted on a floatable collar, with the receiver's acoustic release pin attached to the galvanized steel tripod at the designated eye. A tether line inside the rope canister connects the float with the frame, allowing for retrieval of the tripod after release of receiver and float.

Protocol

For deployment, the eye on the frame is used to place a quick release clamp, connected to the cable of a winch and to a rope. The tripod is then hauled into the water and lowered to 2 m above the seabed. A forceful tug of the rope disconnects the release clamp, and therefore the cable, from the frame. For the recovery of the tripod, a VR100 transceiver aboard a smaller manoeuvrable boat is used to activate the acoustic release (see videos supporting

information). This mechanism separates the release pin (fixed to the frame) from the receiver (attached to the buoyant collar).

After release activation, the collar and receiver will surface, and can be retrieved using the smaller boat. The tether line, of which the length exceeds the bottom to surface distance, is then disconnected from the collar and passed onto the ship. After fixing the tether line on the ship's winch, the tripod frame is hauled on board. The execution of this protocol requires access to a vessel, equipped with an A-frame (minimal lifting capacity of 1,000 kg). Recovery procedure should be performed during slack tide, to reduce the tension on the tether line.

Protocol field trial

The practical operability of the tripod in North Sea conditions was assessed in a field trial. In the framework of the PCAD4Cod project (Slabbekoorn 2019), 40 tripods were placed in the offshore wind farms Belwind I and Gemini from June to October 2018 (106–119 days; Figure 3.2). The depth of deployment ranged between 19 and 36 m. Out of 40 deployments, recovery failed twice. In one instance, the release mechanism could not be activated due to a technological error in the receiver firmware that could have occurred in any design, where the depletion of the battery lead to the corruption of the internal circuitry and to the inability to initiate the release. The other frame was not recovered due to strong currents during retrieval. Tension on the tether line caused the rope to be cut as a result of friction with the edge of the frame. This resulted in adapting the recovery procedure to include tides and weather conditions for deployment and recovery. Ideally, recovery should be performed during slack tide and significant wave height below 1 m.

The tripod was developed for deployment in sandy habitat in the southern North Sea, but could be adapted to meet the specific needs of other areas. The depth limit for the current design was 40 m. Increasing the diameter of the central beam, thus fitting more rope in the canister, would facilitate deployment at greater depth. Likewise, a larger collar with greater floatation would ensure the recovery of equipment in areas with more or harder biofouling growth. Finally, sediment type and displacement should be carefully taken into account. For example, frame recovery in silty habitat has proven complicated, as the suction force endured by the equipment might

exceed the rope's traction in some cases. For hard substrates on the other hand, deployment would be restricted to areas with sufficiently low rugosity and slope. Considering the challenging conditions in the North Sea, the tripod frame significantly eased the deployment and recovery of the acoustic receivers on the seabed.
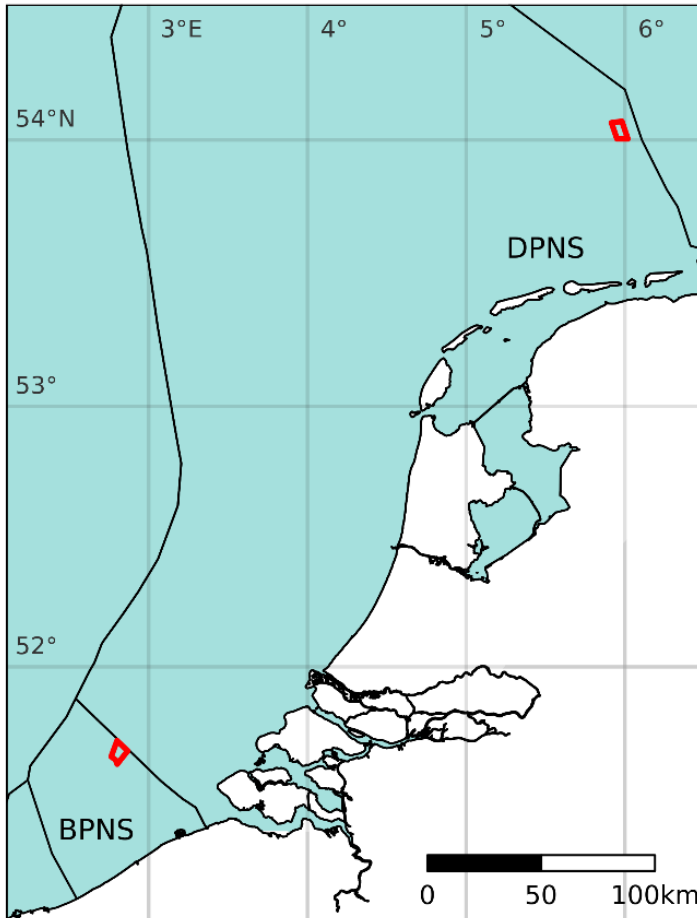
Figure 3.2. Map of study area with offshore wind farms (red) Belwind I and Gemini in the Belgian (BPNS) and Dutch part of the North Sea (DPNS) respectively. Shape files originate from MarineRegions.org.

PERFORMANCE TEST

The performance of the tripod frame was compared to a stone mooring with an anchor line as previously applied by Reubens et al. (2019a). In two subsequent years, receivers were deployed in a circular set-up around the offshore wind turbines of Belwind I, with the distance between receivers varying from 120 to 310 m (Figure 3.3). The cabled design was used around turbine F05 in 2017 and the tripod frame around turbines B08, B10 and C09 in 2018. Tilt angle and noise (mV) were measured at a sampling interval of 10 min by the built-in sensors of the VR2AR receivers and built-in sync tags were programmed to transmit at a delay between 540 and 660 s. For every individual broadcasted signal, it was investigated whether it was picked up by the other receivers over different distance ranges. All analyses were performed in R software (R Core Team 2022), with full details provided in the Supporting information.
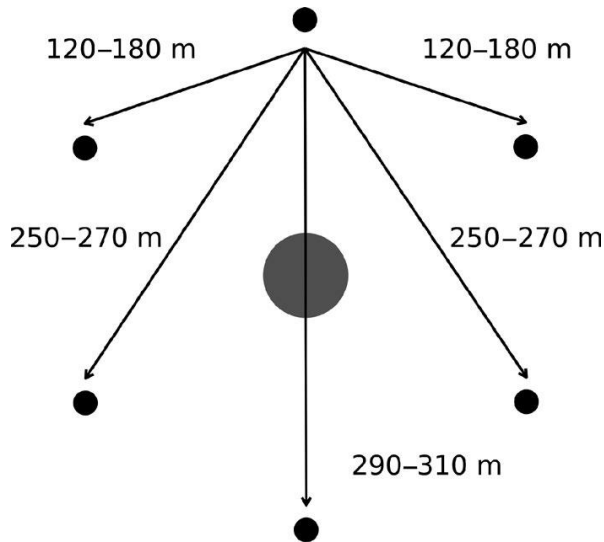
Figure 3.3. Positions of VR2AR acoustic receivers (black dots) around each turbine (large grey dot in the centre).

Design performance: Tilt

The stability of the fixed receiver position in the tripod frame resulted in lower and more consistent tilt values. For every 10 min, the median tilt value was calculated over all receivers of the two mooring types (Figure 3.4A). The tripods maintained a more constant and smaller tilt angle, whereas the considerably higher variation in tilt allowed to visually distinguish spring and neap tides for the cabled design. Strikingly, every receiver with the stone mooring reached a maximum tilt angle of 90°, indicating the receivers would hit the seabed (Table 3.1). Tilt autocorrelation was calculated for 10 min lags up to 25 hr. The resulting peaks at 6.2–6.5 and 12.3–12.5 hr indicated that the inclination of the cabled design was influenced by tides (Figure 3.4B). No cyclical patterns could be identified for the tripod frame. Running SD of tilt was calculated for each receiver to assess variability in orientation, i.e. how much the receiver moved. The window size was set at 3.5 hr, considering the first drop in the autocorrelation at 180–200 min (for the stone mooring). For the stone mooring, running SD tilt values varied up to 19.5°, whereas the values for the tripod mooring did not exceed 1.5° (Table 3.1). No temporal pattern was seen in the latter, whereas apparent spring and neap tides were discernible for the stone mooring (Figure 3.4C).
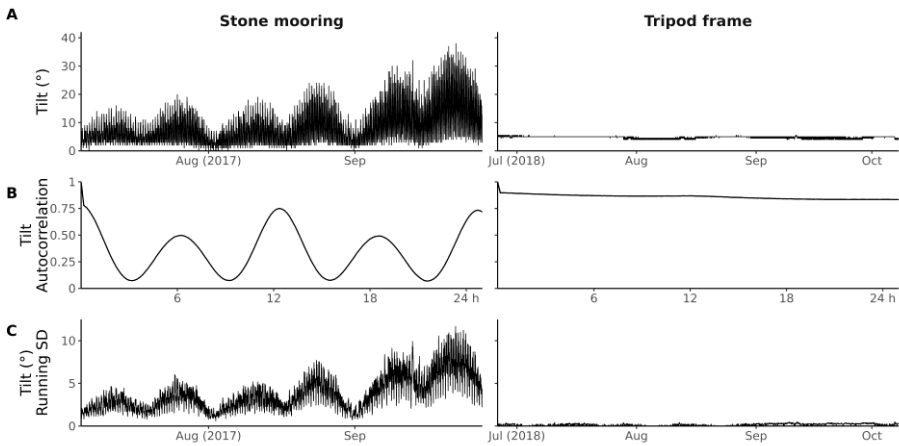
Figure 3.4. Median values of tilt (a), tilt autocorrelation (b) and running standard deviation of tilt (c) for the receivers deployed on the stone mooring (left) and on the tripod frame (right).

The acoustic receivers in the tripod design therefore better maintained a vertical position and remained more stable. As both tilt angle and oscillation of the receiver would negatively influence a receiver's ability to detect transmitted signals (D. Webber, pers. comm.), the acoustic receivers in the tripod frame would better capture biologically driven patterns in the presence of tagged animals, rather than variation in receiver performance.

Table 3.1. Tilt measurements of each VR2AR receiver deployed at different depths around turbines F05 (stone mooring) and B08, B10 and C09 (tripod frame): minimum, median and maximum values of tilt and tilt running standard deviation (*SD*).

Turbine	Receiver	Depth (m)	Tilt (°)			Running SD Tilt (°)		
			Min	Median	Max	Min	Median	Max
F05	546622	30.3	0	7	90	0.5	3.6	19.3
	546891	24.4	0	10	90	1.0	5.5	19.4
	546892	25.7	0	7	90	0.0	1.0	19.5
	546893	26.8	0	4	90	0.3	2.2	19.1
	546894	28.9	0	7	90	0.7	3.3	19.2
	546895	31.6	0	6	90	0.4	2.5	19.3
B08	545718	23.3	0	3	5	0.0	0.2	0.7
	545720	20.8	5	7	11	0.0	0.0	0.9
	546043	20.7	0	6	8	0.0	0.4	0.9
	546044	22.3	0	3	6	0.0	0.2	0.8
	546045	23.8	4	7	9	0.0	0.0	0.8
	546047	24.0	0	4	5	0.0	0.2	0.5
B10	546052	27.6	3	5	9	0.0	0.3	0.5
	546130	25.7	7	9	10	0.0	0.2	0.5
	546620	24.4	2	3	5	0.0	0.4	0.6
	546621	25.8	0	3	12	0.0	0.0	0.9
	546622	27.4	2	4	5	0.0	0.0	0.7
	546893	28.1	3	5	6	0.0	0.0	0.5
C09	546891	22.0	2	6	9	0.0	0.0	1.3
	546895	21.2	2	6	8	0.0	0.0	1.0
	546897	19.9	2	4	6	0.0	0.3	0.9
	546898	19.9	3	5	7	0.0	0.2	0.8
	546899	20.9	0	5	9	0.0	0.4	1.5
	546900	21.6	2	6	8	0.0	0.0	0.5

Design performance: Detection efficiency

To compare detection efficiency between designs, periods of time when nearby fish-borne transmitters were transmitting at an extremely low delay of 30–60 s were excluded from the data. In the remaining subset, the hourly number of fish present around each turbine was maximum 5, which was considered low enough not to impact detection probability. Mean hourly detection percentages decreased at greater distance for every turbine, but this decline was markedly stronger for the stone set-up than for the tripod (Figure 3.5A). On average, receivers mounted on a tripod would still register 65% of signals transmitted at larger distance, whereas detections by the stone set-up were limited to 26%. Hourly median noise values at each turbine allowed to visually distinguish spring and neap tides (Figure 3.5B), whereby comparable noise peaks seemed to reduce the detections more drastically for the stone mooring than for the tripod, especially at greater distance.

Detection probability was then compared between designs at various distances and noise levels in a generalized linear model with the Bernoulli distribution (Zuur et al. 2009). Tilt was not considered in the model, as the effect would be strongly dependent on, yet not distinguishable from, the effect of the deployment set-up. Detection probability was estimated as a three-way interaction between deployment set-up, distance and noise. The tripod coped significantly better with distance and ambient noise than the stone mooring (Figure 3.6). The detection range of the receivers in the tripod frame was only severely reduced at extremely high noise. The stability of the frame therefore produced a better and more consistent receiver performance.
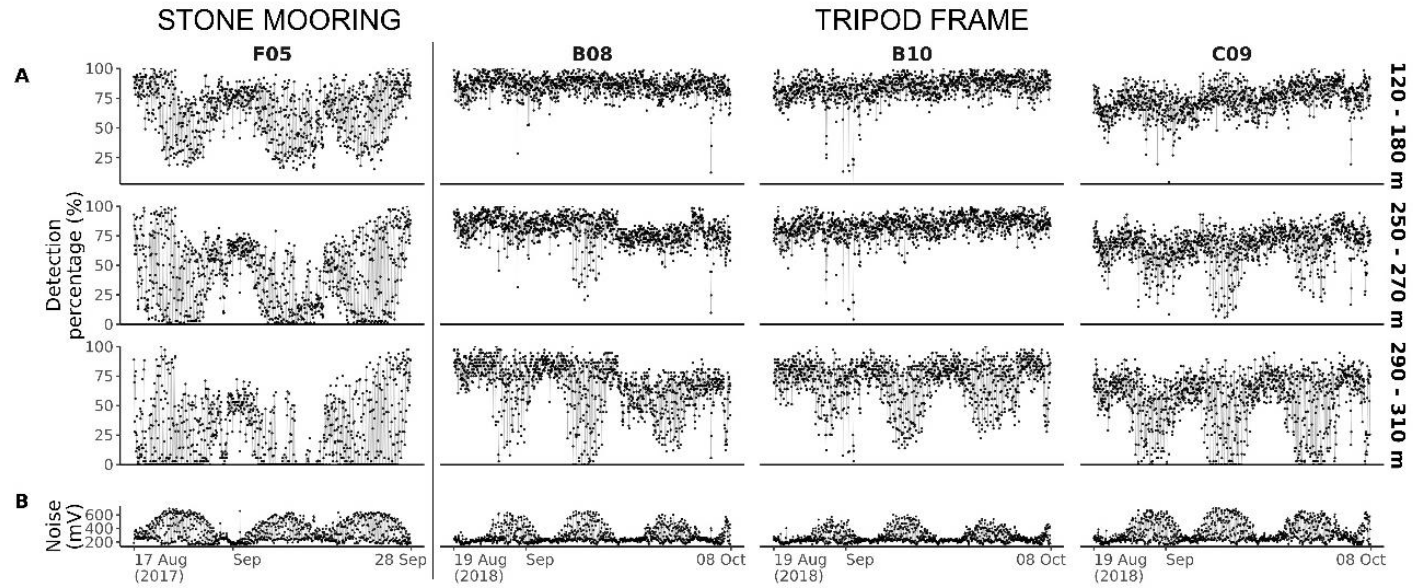
Figure 3.5. Mean hourly detection percentage of built-in transmitter signals at each turbine (a), averaged (mean) over receivers placed next to each other (120–180 m), diagonal of each other (250–270 m) and opposite to each other (290–310 m). Median hourly noise measurements by the built-in sensor of the receivers, averaged (median) over each turbine (b).
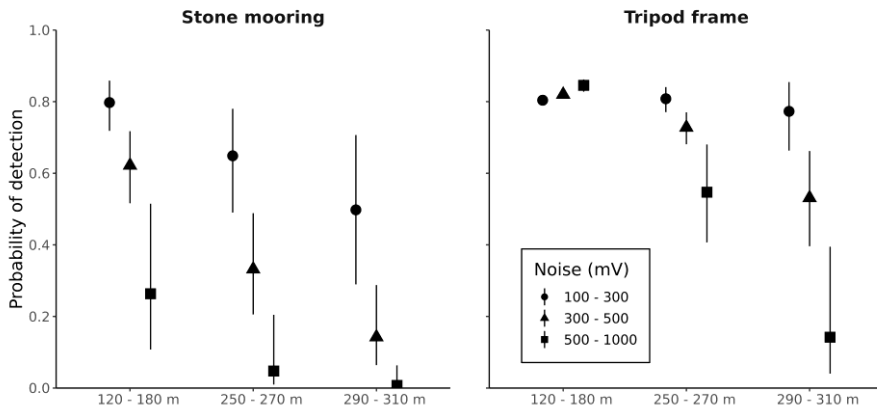
Figure 3.6. Predicted detection probability of the logistic regression model.

CONCLUSIONS

The tripod frame facilitates the gathering of tracking data in challenging environments. In this study we demonstrated that the design of the tripod allows for efficient deployment and recovery of acoustic receivers. The rigid design of the frame resulted in stability of the receiver, providing more continuity in data quality and detection range than a commonly used cabled design. The majority of deployment set-ups in scientific publications however, consisted of anchored buoy lines, implying considerable variation in detection probability. Apart from retroactively accounting for this performance variability (Payne et al. 2010, Brownscombe et al. 2020), the application of the frame could help avoid drawing erroneous conclusions on movement patterns based on (rhythmic) changes in detection probability. The acoustic release system and principle of the tripod frame can serve other instruments as well, alongside the acoustic receiver. Since the described field trial, the frame has been modulated to hold a C-POD (Chelonia Ltd.), a SoundTrap hydrophone (Ocean Instruments NZ) and an acoustic Doppler current profiler (ADCP; Teledyne Marine). It has also been used in the framework of the autonomous reef monitoring structures (ARMS) program. Such a multidisciplinary scientific equipment entity can be deployed as an ambulatory mooring, answering a diverse range of integrated research questions. The continuous development and modification of operable field systems such as the tripod are vital to

provide the high quality observation data necessary for the understanding and conservation of aquatic ecosystems.

AUTHOR CONTRIBUTIONS

JG analysed the data and wrote the manuscript. MT and JR developed the design and deployment protocol. KD coordinated the work and managed the LifeWatch project. JR contributed to the data analysis and the writing. All authors critically revised the paper and approved the final manuscript.

DATA AVAILABILITY STATEMENT

Technical details of the frame can be shared upon request, on the condition that the design is correctly acknowledged. All data are available through DOI https://doi.org/10.14284/404. In addition, detection data are available on the data platform of the European Tracking Network (http://lifewatch.be/etn/). R scripts are made available on GitHub (repository https://github.com/lifewatch/Tripod-frame_Performance-test).

ACKNOWLEDGEMENTS

CHAPTER 4

TAKING THE TIME FOR RANGE TESTING: AN APPROACH TO ACCOUNT FOR TEMPORAL RESOLUTION IN ACOUSTIC TELEMETRY DETECTION RANGE ASSESSMENTS

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ABSTRACT

Background

In acoustic telemetry studies, detection range is usually evaluated as the relationship between the probability of detecting an individual transmission and the distance between the transmitter and receiver. When investigating animal presence, however, few detections will suffice to establish an animal's presence within a certain time frame. In this study, we assess detection range and its impacting factors with a novel approach aimed towards studies making use of binary presence/absence metrics. The probability of determining presence of an acoustic transmitter within a certain time frame is calculated as the probability of detecting a set minimum number of transmissions within that time frame. We illustrate this method for hourly and daily time bins with

an extensive empirical dataset of sentinel transmissions and detections in a receiver array in a Belgian offshore wind farm.

Results

The accuracy and specificity of over 84% for both temporal resolutions showed the developed approach performs adequately. Using this approach, we found important differences in the predictive performance of distinct hypothetical range testing scenarios. Finally, our results demonstrated that the probability of determining presence over distance to a receiver did not solely depend on environmental and technical conditions, but would also relate to the temporal resolution of the analysis, the programmed transmitting interval and the movement behaviour of the tagged animal. The probability of determining presence differed distinctly from a single transmission's detectability, with an increase of up to 266 m for the estimated distance at 50% detection probability (D_{50}).

Conclusion

When few detections of multiple transmissions suffice to ascertain presence within a time bin, predicted range differs distinctly from the probability of detecting a single transmission within that time bin. We recommend the use of more rigorous range testing methodologies for acoustic telemetry applications where the assessment of detection range is an integral part of the study design, the data analysis and the interpretation of results.

BACKGROUND

Understanding performance variability of scientific equipment is crucial to correctly interpret patterns in its measurements. In acoustic telemetry, this entails the assessment of the detectability of animal-borne transmitter signals by an acoustic receiver set-up (Kessel et al. 2014). This relationship is subject to the transmitter – receiver distance, environmental conditions and technical features, in addition to the behaviour of the tagged animal itself. Environmental impacts include static features, such as habitat type and bottom depth (Selby et al. 2016, Scherrer et al. 2018) , as well as system dynamics that vary over time, such as wind, water currents, precipitation, biogenic and anthropogenic noise, temperature and stratification (Huveneers et al. 2016, Reubens et al. 2019a, Winter et al. 2021b). The detection range can also be

dependent on the specifications of the equipment used, including transmitter type, transmitting power output and transmitter placement (Kessel et al. 2015, Dance et al. 2016, Stott et al. 2021), as well as receiver depth, orientation and deployment method (Welsh et al. 2012, Huveneers et al. 2016, Goossens et al. 2020). Biofouling on the receiver can significantly decrease receiver performance over time (Heupel et al. 2008). The tagged animal's behaviour can influence the detectability, e.g. through the occupancy of a specific depth or a propensity to hide or burrow (Grothues et al. 2012, Swadling et al. 2020). Spatiotemporal variability in detection range is commonly investigated with a range test (Kessel et al. 2014, Huveneers et al. 2016, Reubens et al. 2019a), where these patterns are evaluated against a relevant subset of factors of potential interference to transmissions.

Whether to optimize the design of a receiver array or to account for variability in detection probability during a study, a range test must be tailored to a study's specific application (Heupel et al. 2006, Kessel et al. 2014, Whoriskey et al. 2019). Before and/or during a telemetry study, the detection range is generally evaluated by means of sentinel transmitters at a known, generally fixed, position. Detection range is then typically assessed as the probability of detecting a single transmission at the known distance between receiver and transmitter. This individual detection probability is estimated either for every single transmission (Selby et al. 2016, Cimino et al. 2018, Goossens et al. 2020), or as the probability of detecting a single transmission within a period of time (e.g. for a daily resolution, this represents the probability of detecting a transmission given that day's conditions) (Huveneers et al. 2016, O'Brien & Secor 2021, Winter et al. 2021b). However, many telemetry analyses do not build on single detections as a response variable, but rely on a binary presence/absence metric within a specified time bin (e.g. residency) (Doyle et al. 2017, Ramsden et al. 2017, Novak et al. 2020). For these studies, one detection (or at most a few) within a period of time, generally one hour or day, will suffice to classify the animal as present in that time bin. The probability of determining presence, i.e. detecting at least one or a few transmitted signals within a period of time, thus differs distinctly from the probability of detecting a single transmission (Melnychuk 2012).

For studies investigating presence of a tagged animal within a specified time bin, the assessment of range has to take into account the temporal resolution of interest. Environmental variables may impact detection range differently on distinct temporal scales (Mathies et al. 2014). The effect of tidal currents for example, can differ between hourly and daily resolutions. Moreover, the probability of determining presence of a tagged animal will increase if multiple transmissions can be detected. The number of potentially detectable transmissions is related to the chosen time bin and the transmitting interval settings, as well as the behaviour of the animal itself. A larger time bin and shorter transmitting interval result in a higher number of transmissions that can be detected by a receiver and thus in a higher probability that a fish is effectively observed as present within the specified time bin. Fish movement behaviour will also influence the probability of determining presence. An animal passing by a receiver location is expected to spend less time within range of a receiver than an animal that resides at that location. Telemetry researchers already adapt transmitter settings in line with the expectations of residency and movement behaviour to increase the detection probability (e.g. a shorter transmitting interval during the expected migration along a receiver curtain) (Heupel et al. 2006) or reduce the risk of collisions (Brownscombe et al. 2019). However, assumptions on movement behaviour are rarely taken into account explicitly in detection range assessments.

In this study, we propose an approach to assess factors that impact the detection range, suitable for studies making use of binary presence/absence metrics. Our conceptual approach builds on the detection probability of a single transmission within a certain time frame to calculate the probability of detecting a given minimum number of transmissions within that time frame. The method can be applied to any receiver array equipped with sentinel transmitters. When investigating the probability of determining the presence of a tagged animal, the number of potentially detectable transmissions is estimated as a function of the chosen time bin, the transmitting interval settings and the behaviour of the animal itself. By applying the method to an extensive data set, the objectives of the current study are to 1) evaluate the predictive performance of the new approach, 2) compare different hypothetical range testing scenarios using this method and 3) investigate the

implications for detection range in study designs with different transmitter settings and animal species.

METHODS

All analyses were performed in R software (R Core Team 2022). R scripts are made available on GitHub (https://github.com/JolienGoossens/RangeTestingTime).

Analytical protocol

Firstly, data are prepared to model the detection probability of individual transmissions π at a given temporal scale (e.g. hourly or daily). For every receiver – sentinel transmitter combination, the number of transmissions and detections are calculated for the relevant time bin and fitted in a binomial generalized linear model (using a frequentist or Bayesian approach) to predict π in relation to ambient and technical variables. The probability P of discerning k or more detections out of n transmissions throughout that time bin is then calculated as the cumulative distribution function:

$$P = P(X \geq k) = 1 - P(X \leq [k-1]) = 1 - \sum_{i=0}^{k-1} \binom{n}{i} p^i (1-p)^{n-i} \qquad \text{(Eq. 4.1)}$$

with p representing the individual detection probability, obtained as the predicted π from the logistic model. In equation 4.1, X denotes the number of detections and n the number of transmissions within the considered time frame. The detection threshold k is the minimum number of detections (X) for a transmitter to be ascertained as present. Therefore, P amounts to the probability of detecting a transmitter at least k times out of the n transmitted signals within a period of time, given the probability π of detecting a single transmission under the prevailing circumstances within that time frame (Fig. 4.1).
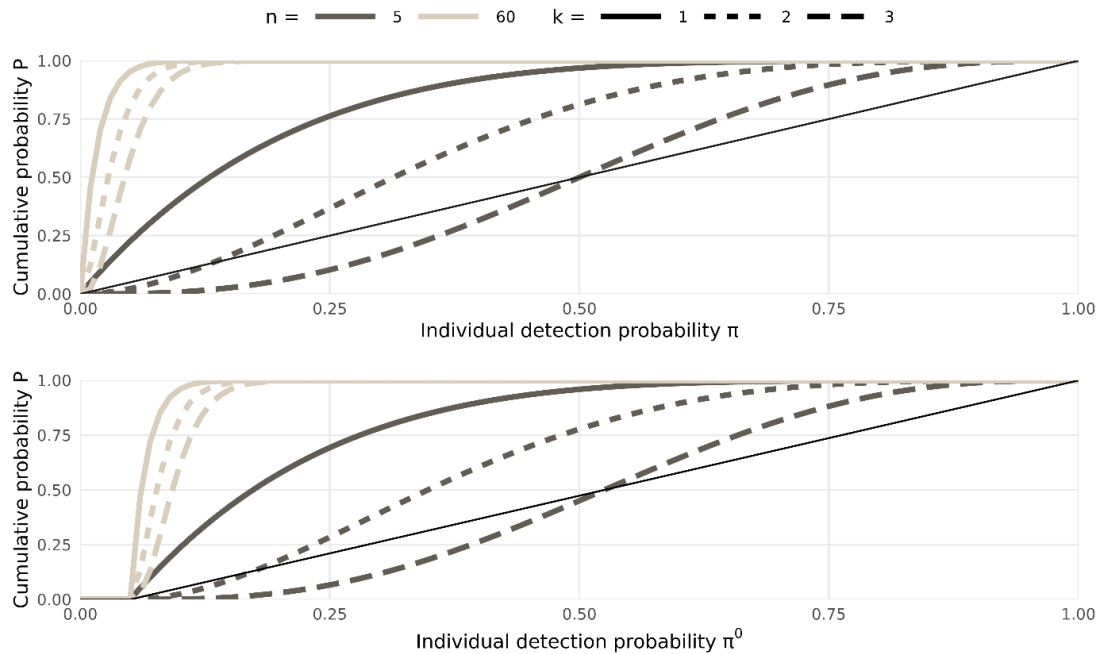
Figure 4.1. Graphical illustration of the relationship between the individual and cumulative detection probability as calculated with equation 4.1. P represents the probability of observing a minimum of 1, 2 or 3 detections (k) out of 5 (grey) or 60 (beige) transmissions (n) as calculated with the probability π of detecting an individual transmission (upper) and for π^0 with zero threshold of 0.05 (lower).

Zero threshold

To address the risk of overestimating P, we propose to set a zero threshold for the modelled probability π. The 'zero-corrected' individual probability π^0 is defined as 0 below a set threshold value for π and rescaled to values between 0 and 1 for the remaining range of the predicted π. Even an extremely low individual probability π can generate a high cumulative probability P if n is high (Fig. 4.1). The zero threshold deals with the concern of cumulating low predicted probabilities. A logistic model can never render a predicted probability of zero, as the logarithm of zero is not defined. The predicted probability π is also associated with uncertainty, which will propagate with the summing and multiplication operations in equation 4.1 (Ku 1966). Setting the zero threshold should be a study-specific consideration, where one evaluates the confidence in the logistic model on the one hand and weights the risk of overestimating versus underestimating π on the other.

Defining n

In equation 4.1, n represents the number of transmissions that can be detected by a receiver. For a fixed sentinel transmitter, n is defined as the number of executed transmissions within the considered time bin. For a non-stationary animal-borne transmitter, however, n needs to reflect the number of transmissions broadcasted while the tagged animal is within a certain range around a receiver. Therefore, the value of n will depend on the programmed transmitting interval and the time bin, in addition to the movement behaviour of the tagged animal. Here, we calculate the integer n as

$$n = \left\lfloor \frac{t_{min}}{\bar{T}} \right\rfloor \qquad \text{(Eq. 4.2)}$$

where $\bar{T}$ is the mean transmitting interval and t_{min} is the minimum time an animal is hypothesized to spend within range of the receiver. When defining t_{min}, we make assumptions based on the expected movement behaviour (e.g. speed or residency) of the species of interest. For example, high residency or low activity would result in a higher estimate for t_{min} than for migrating behaviour. The less is known about a study species and/or area, the more conservatively low t_{min} should be set.

Empirical data set

Between 13 May and 12 October 2020, an array of 27 VR2AR receivers (InnovaSea Systems Inc., USA) was set up in the Belwind offshore wind farm in the Belgian part of the North Sea. Receivers were deployed with tripod moorings (Goossens et al. 2020), with distance between receivers ranging from 125 to 1628 m (Fig. 4.2). The array design was purposed to investigate presence and fine-scale movement patterns of plaice (*Pleuronectes platessa*), Atlantic cod (*Gadus morhua*) and European seabass (*Dicentrarchus labrax*) in the framework of ongoing studies, for which the VR2AR receivers' built-in transmitters (mean transmitting interval of 10 minutes) served as synchronisation tags for a fine-scale positioning application. Transmitting power output was set as high (154 dB) for the entire study period for all built-in transmitters, except for three (Fig. 4.2) that were programmed as low (142 dB) before 16 June 2020 in the interest of assessing the effect of power output on detection range. Detections on the dates of receiver installation, receiver recovery and power setting changes were excluded from the analysis, making for a total of 150 days of detection data.

Ambient and technical conditions taken into account consisted of wind and current speed and azimuth, noise, receiver tilt angle, temperature and days since deployment (Table 4.1). Wind measurements were obtained from 'Meetnet Vlaamse Banken' from station Westhinder (51.38°N, 2.44°E). Modelled current data originated from a forecast model (Legrand & Baetens 2021). From the hourly wind and current velocities, daily median current and direction were calculated using trigonometry principles. For both wind and current, the azimuth was calculated as the angle between the transmitter – receiver bearing and the direction. Noise (mV), tilt angle (°) and temperature (°C) were drawn from the VR2AR built-in sensors. The hourly measurements were linearly interpolated to the stroke of every hour, from which daily medians were calculated. Before inclusion in the model, all continuous variables were standardized.
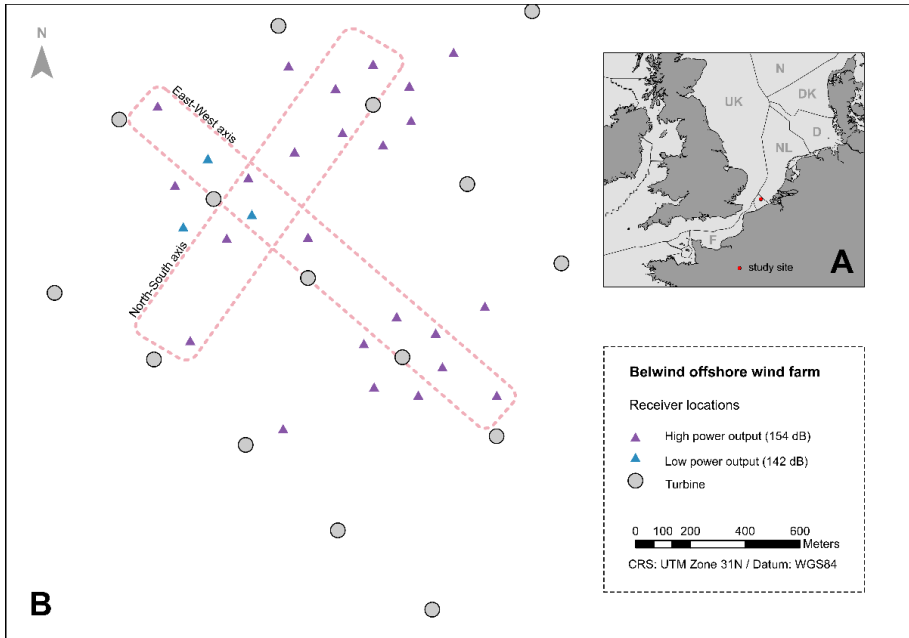
Figure 4.2. Map (A) with the location of the study area (B) in the Belwind offshore wind farm with locations of VR2AR receivers. The built-in transmitters were either set to transmit at high power output for the entire study period (purple) or at low power output before 16 June 2020 and high power output afterwards (blue). Hypothetical range testing scenarios included either all receivers and built-in transmitters or those within a North-South or East-West axis (pink dotted lines).

Table 4.1. Overview of ambient and technical conditions during the study (14 May – 11 October 2020).

Variable	Range	Median	Method
Distance (m)	125 - 1628	743	
Transmitting power output	142 dB (Low) / 154 dB (High)		
Wind speed (m/s)	0.4 - 24.9	7.1	Measured (Westhinder)
Wind azimuth (°)	0 - 180	90	Measured (Westhinder)
Current speed (m/s)	0.09 - 0.69	0.36	Modelled
Current azimuth (°)	0 - 180	90	Modelled
Temperature (°C)	10.7 - 20.6	17	Measured (VR2AR)
Tilt (°)	0 - 17	4	Measured (VR2AR)
Noise (mV)	150 - 917	287	Measured (VR2AR)
Days since deployment	1 - 158		

Application of the approach

The described protocol was applied to the empirical data set to assess the detection range for determining presence in hourly and daily time bins.

Logistic model

We evaluated for every sentinel transmission whether it was detected by the receivers in the study set-up. To account for internal clock drift of the acoustic receivers, the recorded time of detection had to be within 100 seconds before or after the registration of the successful transmission on the built-in transmitter's receiver (D. Webber, pers. comm.), after applying a linear time correction on the offloaded receiver data (VUE software, InnovaSea Systems Inc., USA). For every transmitter – receiver combination, the hourly and daily numbers of transmissions and detections were calculated. Transmitter – receiver combinations spaced more than 1,100 m were excluded from the analysis. Generalized linear models with a binomial distribution were applied to predict π_{hour} and π_{day}. Response variables were the hourly and daily number of transmissions successfully detected versus those undetected. The inclusion of different explanatory variables was evaluated for 1) relevance by data exploration (Zuur et al. 2010), 2) statistical significance by backwards model selection using the Akaike Information Criterion (AIC) and Likelihood Ratio Test (LRT) (Zuur et al. 2009), and 3) practical significance on the basis of effect size (Ellis & Steyn 2003, Sullivan & Feinn 2012), whereby factors were excluded from the model if the effect estimate was below |0.2|.

Cumulative detection probability

Cumulative detection probabilities P_{hour} and P_{day} were then calculated (Eq. 4.1) and validated for the entire study period. The detection threshold k was set at 2, as applied by many studies (Doyle et al. 2017, Ramsden et al. 2017, Novak et al. 2020). The number of tries n was set as the registered number of sentinel transmissions within the hour or day. Individual detection probabilities π_{hour} and π_{day} were obtained using the logistic model formulae. P_{hour} and P_{day} were then calculated with individual detection probabilities π^{0}_{hour} and π^{0}_{day} at a zero threshold of 0.05. If $P \geq 0.5$, sentinel transmitters were classified as present versus not present for $P < 0.5$ (Peng et al. 2002). These binary predictions were compared with the determined presence throughout every day and hour (0/1, with 1 meaning at least 2 (k) transmissions were detected). To assess the

predictive performance, a confusion matrix was inspected from which the performance metrics sensitivity, specificity and accuracy were calculated, in addition to the computation of area under the curve (AUC) (Hanley & McNeil 1982). High values for accuracy and AUC suggested a good overall performance, whereas sensitivity and specificity depicted the model's ability to correctly predict positive and negative values, respectively. For range testing, we favoured high scores for specificity over sensitivity, as a high number of false positives would indicate an overestimation of range.

Scenarios for detection range assessment

Using our empirical data set, we evaluated different scenarios for detection range assessment with a cross-validation approach. Therefore, we split the full data set of sentinel transmissions and detections into different training and test subsets (Table 4.2), as if we were assessing detection range (training set) for an actual telemetry study (test set). For each of the test subsets, we considered 16 June 2020 as the start of the hypothesized study. Training sets either contained 'range test' data from before this date, 'reference tag' data from during this study, or both. 'Range test' training data considered the data of 8, 16, 24 or 32 days before the start of the hypothetical study. Spatially, these training sets consisted either of all 27 receiver – sentinel transmitter combinations, a North-South axis (8 receivers) or East-West axis (9 receivers), approximately parallel and perpendicular to the dominant current direction, respectively (Fig. 4.2). The 'reference tag' training data on the other hand consisted of detections on all 27 receivers of 1, 2 or 3 sentinel transmitters during the hypothesized study. When the model was trained on both 'range test' and 'reference tag' data, training data consisted of 32 days of all 27 receiver- transmitter combinations before the start date, in addition to the detections of 1, 2 or 3 sentinel transmitters during the study. Test data subsets consisted of detection data from after the start of the study (118 days), excluding transmitter detections included in the training subset, if any. The cross-validation was performed for both hourly and daily probabilities.

For the cross-validation, logistic models were trained on each of the specified training sets. The included variables were drawn from the model selection based on the full hourly and daily data sets. As sentinel transmitters were all set to transmit at high power output after 16 June 2020, power output was not

included in the logistic models for the 'reference tag' training data. Using the logistic model formulae from the training model, π_{hour} and π_{day} were predicted for the test data. Cumulative probabilities P_{hour} and P_{day} were calculated with equation 4.1, with k set as 2 and n as the number of registered sentinel transmissions in each specific hour or day. Transmitters were thus predicted as detected in that hour or day if $P \geq 0.5$ and as not detected (0) if $P < 0.5$. The predictive capacity of these models was assessed by calculating root mean square error (RMSE) of the true detection percentage and the predicted π and by calculating specificity, AUC and the Brier skill score (BSS) for the binary predictions based on the cumulative probability P (Table 4.2). For the calculation of BSS, the Brier score of the full model was used as the reference value Brier score (Brier 1950).

Assessing range for different study species

Detection range in our study area was estimated in the context of ongoing telemetry studies investigating hourly or daily presence of different species. The expected minimum time t_{min} was hypothesized to be 15 minutes per hour and 30 per day for very mobile species (e.g. European seabass), 30 and 60 minutes for less active species (e.g. Atlantic cod) and 1 and 3 hours for species that would mostly stay put (e.g. plaice). Using these t_{min} estimates in equation 4.2, n was calculated for the different species at mean transmitting intervals $\bar{T}$ of 90, 180 and 360 seconds. P_{hour} and P_{day} were calculated (Eq. 4.1) for distances from 100 to 1100 meters with $k = 2$ and the predicted π^0_{hour} and π^0_{day} at median hourly and daily conditions, respectively. The distance at which detection probability was predicted to be 50% (= D_{50}) was calculated using one-dimensional root-finding.

Table 4.2. Overview of training and test data subsets to test different range assessment scenarios, with the number of days, built-in transmitters (T) and receivers (R) included in the subsets.

	Training set		Test set	# Models
	Before study 32 days	**During study** 118 days	**During study** 118 days	**# Models** (per time bin)
Range test	*8 / 16 / 24 / 32 days* 27 T – 27 R 9 T – 9 R (East-West) 8 T – 8 R (North-South)		27 T – 27 R 27 T – 27 R 27 T – 27 R	4 4 4
Reference tag		1 T – 27 R 2 T – 27 R 3 T – 27 R	26 T – 27 R 25 T – 27 R 24 T – 27 R	27 351 2925
Range test + reference tag	*32 days* 27 T – 27 R 27 T – 27 R 27 T – 27 R	1 T – 27 R 2 T – 27 R 3 T – 27 R	26 T – 27 R 25 T – 27 R 24 T – 27 R	27 351 2925

RESULTS

Logistic model

After variable selection, the final logistic regression models for both hourly and daily response variables included the explanatory variables distance, noise, power output, the interactions of distance – noise and distance – power output (Table 4.3). Visual inspection of the relationship with distance lead us to include distance transformed to the second power (Rönkkö et al. 2021), which contributed to an improved model fit. In summary, high levels of ambient noise and low transmitting output power significantly reduced the probability of a transmission being detected, whereby these negative effects were exacerbated at greater distance (Fig. 4.3). At shorter distance (< 300 m) of a receiver, the detection probability of a low power output transmitter exceeded that of one with high power output, which was likely due to close proximity detection interference (Scherrer et al. 2018, Klinard et al. 2019). Details of the model selection were fully described in Supplementary material.

Cumulative detection probability

Performance metrics were compared for calculations of P_{hour} and P_{day} ($k = 2$, n: median 143 per day, 6 per hour) using π and π^0 (Table 4.4). While the predictive performance differed only slightly for P_{hour}, it markedly improved with the zero threshold for P_{day}. Aside from a higher overall performance (accuracy and AUC), specificity increased by 30.3% for the daily model (2.2% for the hourly model). Whereas P_{hour} was overestimated at short distance (< 600 m), the accuracy of the daily predictions was more consistent over distance (Fig. 4.3).

Scenarios for detection range assessment

The performance of distinct scenarios for the assessment of detection range varied considerably (Fig. 4.4). When models were trained exclusively with 'range test' data before the hypothesized start of the study, the performance of the scenarios using the full receiver set-up and the East-West axis were comparable. Training sets with receivers located parallel to the dominant current direction along the North-South axis, resulted in a lower performance (higher RMSE and lower specificity and AUC). The variation in performance between different study durations was considered to be minor for the 'range

testing' set-ups. For the 'reference tag' training data, the logistic models were trained on the detections of 1, 2 or 3 sentinel transmitters during the study period. The overall median performance persisted or improved (i.e. lower RMSE, higher specificity, AUC and BSS) as more sentinel transmitters were included. Still, variation was very large, indicating the representativeness of the 'reference tag' training set varied strongly with the sentinel transmitter locations. Finally, including both 'range test' and 'reference tag' data yielded much more consistency in the performance metrics. Yet, specificity for 'reference tag' training sets excluding the 'range test' data was often higher than for those where it was included, therefore seemingly resulting in improved predictions.

Table 4.3. Summary of the GLM with binomial distribution for individual detection probability π_{hour} (top) and π_{day} (bottom). Hourly noise measurements were linearly interpolated to the stroke of every hour (left), from which daily medians were calculated (right).

Coefficients	Estimate	Std. Error	*p*-value
Intercept	-2.299	0.0018	<0.001
Distance	-3.425	0.0037	<0.001
Distance^2	-0.963	0.0025	<0.001
Noise	-1.056	0.0021	<0.001
Power (Low)	-3.203	0.0197	<0.001
Distance:Noise	-0.448	0.0020	<0.001
Distance:Power (Low)	-2.732	0.0184	<0.001

Coefficients	Estimate	Std. Error	*p*-value
Intercept	-2.320	0.0018	<0.001
Distance	-3.327	0.0037	<0.001
Distance^2	-0.866	0.0025	<0.001
Noise (median)	-1.012	0.0020	<0.001
Power (Low)	-3.187	0.0198	<0.001
Distance:Noise (median)	-0.388	0.0019	<0.001
Distance:Power (Low)	-2.561	0.0185	<0.001

Table 4.4. Performance metrics for binary predictions calculated with and without zero thresholds for P_{hour} and P_{day}.

Individual detection probability	Sensitivity	Specificity	Accuracy	AUC
π_{hour}	84.9	83.6	84.1	84.3
π^0_{hour}	81.9	85.8	84.4	83.8
π_{day}	96.3	56.2	82.0	76.3
π^0_{day}	86.5	86.5	86.5	86.5
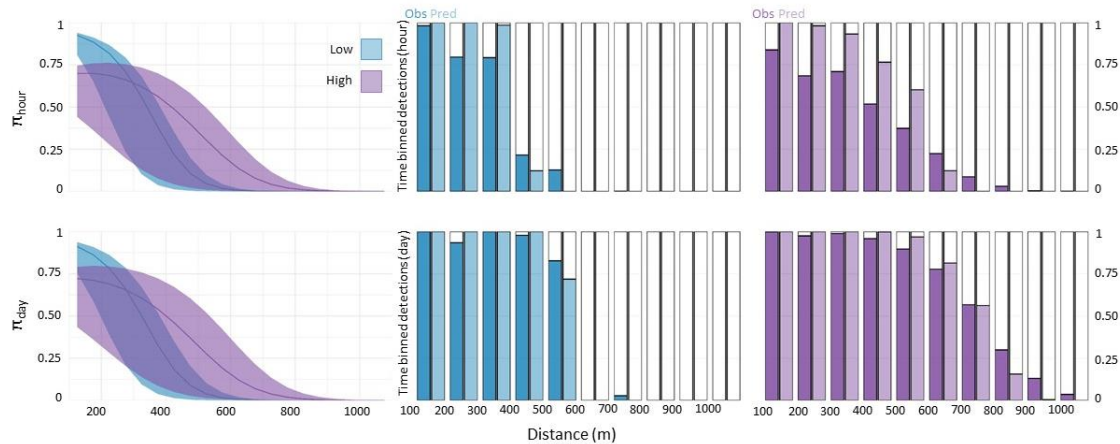
Figure 4.3. Estimated probabilities of detection over distance for high (purple) and low (blue) transmitting power output at an hourly (upper) and daily (lower) resolution. Left: Range and median (line) logistic model predictions. Middle and right: Bar plots of observed (left bar, darker colouration) and predicted (right bar, lighter colouration) binary detection metric (at least $k = 2$ detections out of n transmissions) per distance bin of 100 m.
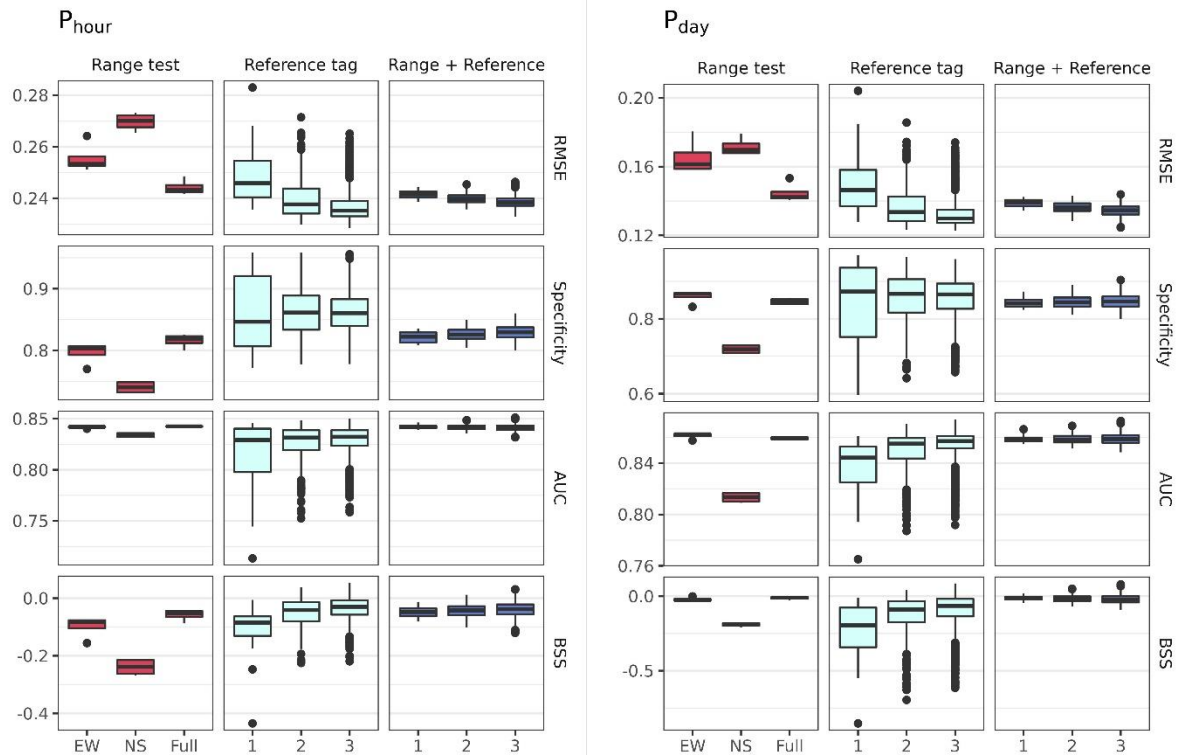
Figure 4.4. Performance metrics root mean square error (RMSE), specificity, area under the curve (AUC) and Brier skill score (BSS) for hourly (left) and daily (right) models trained on range test data (red), reference tag data (light blue) or both (dark blue).

To understand the variation in the performance metrics, AUC and BSS were plotted against specificity and RMSE (Fig. 4.5). AUC and BSS displayed a parabolic relationship with specificity, meaning higher specificity came at the cost of lower overall prediction performance. An optimal approach for range assessment should be found at the trade-off between specificity and general performance, i.e. at the top of the parabola. Importantly, the training models combining 'range test' and 'reference tag' data were all found to be comparable in this relationship. Finally, low RMSE values for individual detection probability π produced more accurate cumulative probability predictions, as could be expected.

Assessing range for different study species

Using hypothesized t_{min} values for species with distinct movement patterns, we calculated n at different mean transmitting intervals (Table 4.5). For a fast moving species, thought to spend at least 30 minutes throughout a day around a receiver if present that day, and equipped with a tag transmitting on average once every 180 seconds, n would result in minimum 10 transmissions that could be detected by that receiver throughout the day. Notice that different values for t_{min} can result in a similar n, depending on the transmitting interval.

Table 4.5. Calculation of detectable transmissions n for different values of the expected minimum time t_{min} and mean transmitting interval $\overline{T}$.

|	t_{min} = 15 min	t_{min} = 30 min	t_{min} = 60 min	t_{min} = 180 min
$\overline{T}$ = 90 s	10	20	40	120
$\overline{T}$ = 180 s	5	10	20	60
$\overline{T}$ = 360 s	2	5	10	30
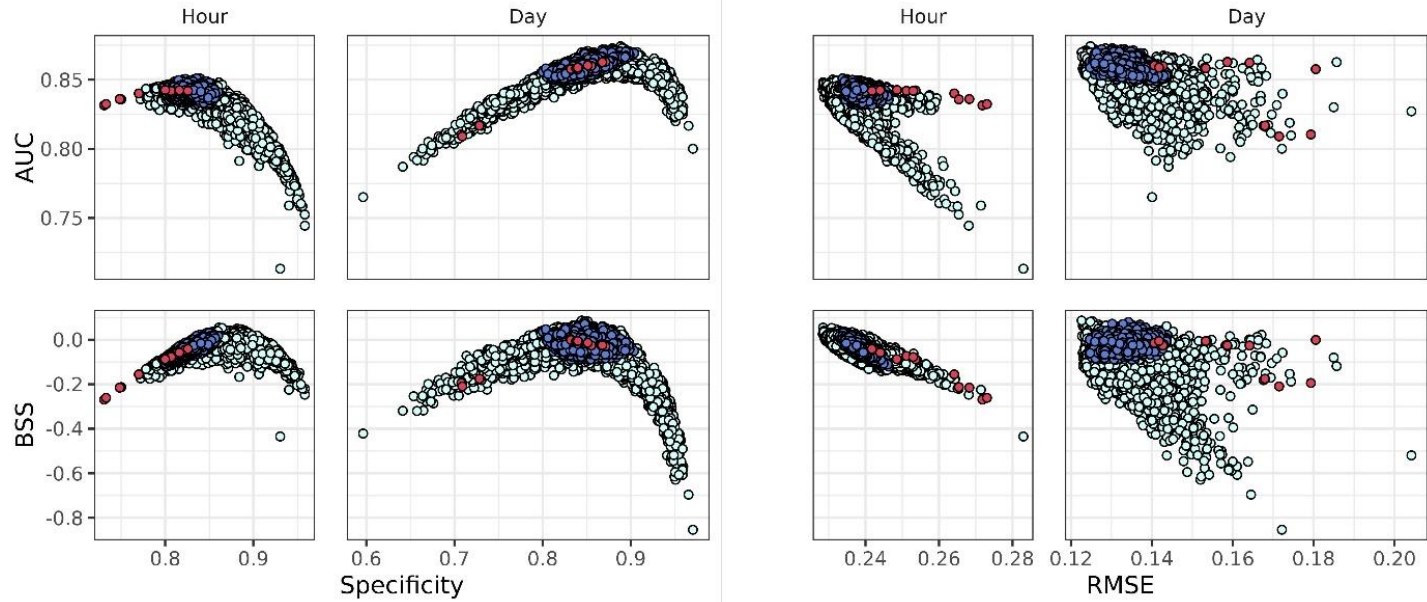
Figure 4.5. Relationship between performance metrics root mean square error (RMSE), specificity, area under the curve (AUC) and Brier skill score (BSS) for hourly and daily models trained on range test data (red), reference tag data (light blue) or both (dark blue).

Using these values for n, detection probabilities P_{hour} and P_{day} were calculated (Eq. 4.1; $k = 2$) using the logistic model predictions of π over distance for median noise conditions and high transmitting power output. The visualizations in figures 4.6 and 4.7 illustrate the impact of temporal resolution, transmitter interval settings and (expected) movement behaviour on detection range. Detection range as predicted by P_{hour} and P_{day} markedly exceeded π_{hour} and π_{day}. The estimated D_{50} increased by 84 to 266 m, depending on n. These results illustrate the distinction between the probability π of detecting an individual transmission in a given time frame versus the probability P of determining presence during that time frame.

DISCUSSION AND CONCLUSION

Importance of considering time

Our results stress the importance of explicitly accounting for time when assessing detection range. When few detections of multiple transmissions suffice to ascertain presence within a time bin, predicted range differs distinctly from the probability of detecting a single transmission within that time bin. Our results showed that detection range might be severely underestimated when applying the individual detection probability for studies making use of binary presence/absence metrics. Moreover, a single receiver station can result in different detection ranges for animals occupying the space at that location differently. High values of t_{min}, e.g. for animals known to move slowly and/or to exhibit high residency (or for transmitters set at short transmitting intervals), were demonstrated to result in a higher estimated range.

Figure 4.6. Predicted detection probabilities over distance for high transmitting power at median noise conditions for an hourly (upper) and daily (lower) resolution, as calculated with different numbers of detectable transmissions n (Table 4.5). The intersection of the curves with a probability of 0.5 (white line) indicates the D_{50}. The intersection of the curves of π and P was a result of setting the detection threshold k at 2, whereas π and P at k = 1 would never intersect (Fig. 4.1).

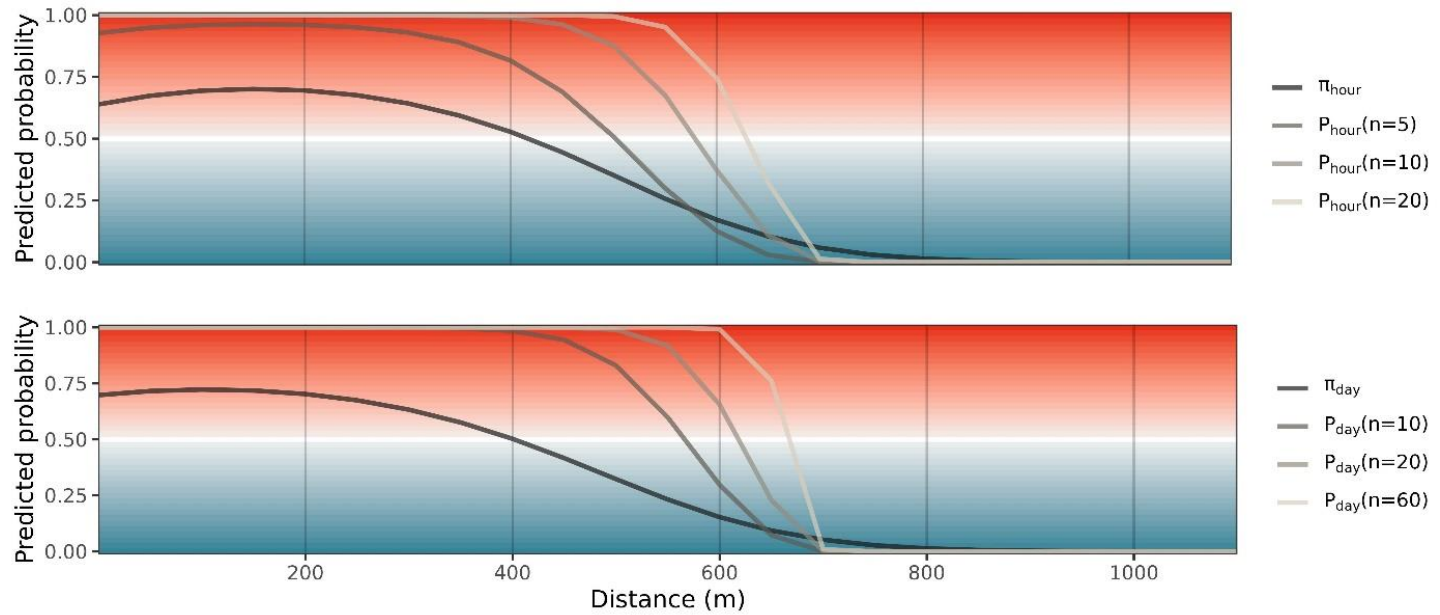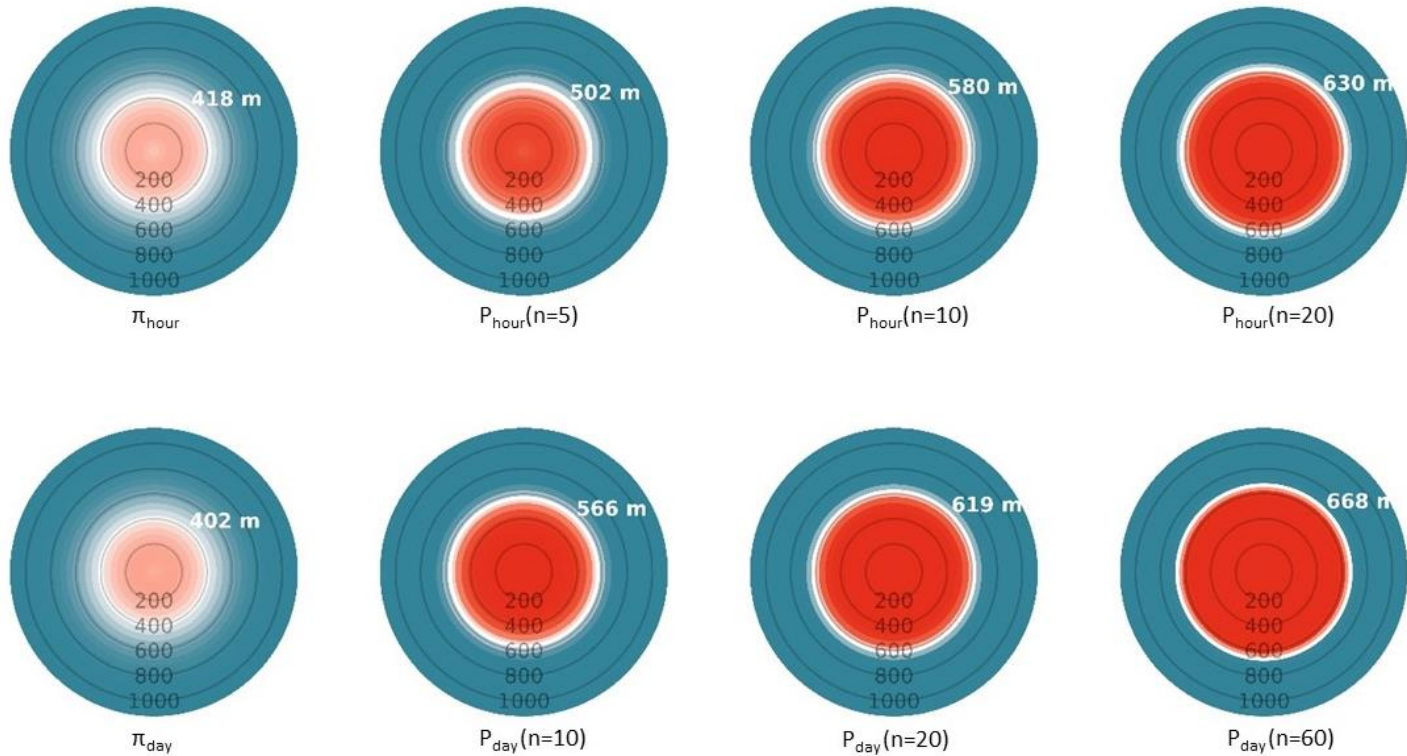**Figure 4.7.** Predicted detection probabilities over distance around a receiver for high transmitting power at median noise conditions for an hourly (upper) and daily (lower) resolution, as calculated with different numbers of detectable transmissions n (Table 4.5). The D_{50} distance is marked for each probability (white line and text) with probabilities over and under 0.5 coloured in red and blue, respectively.

Evaluation of the proposed method

To our knowledge, this study offers the first framework to quantify the detection range for presence/absence metrics within a given time frame. The proposed formula (Eq. 4.1) provides a mathematically straightforward tool that builds on the commonly estimated probability of detecting a single transmission π. The accuracy and specificity of over 84% shows the developed approach performs adequately. However, the performance of the hourly model varied with distance, whereas the accuracy of the daily predictions were more consistent. The formula's parameters zero threshold, detection threshold k and number of tries n should therefore be set and evaluated according to the specific needs of a study.

The zero threshold can explicitly deal with the risk of cumulating low logistic probabilities. The selected value for this threshold depends on the confidence in the binomial model predictions and the trade-off of the risks of over- and underestimating detection range. We believe that the relatively simple concept of a zero threshold – "below what threshold value do I not trust my logistic model outcome to exceed zero" – is to be preferred over a more sophisticated, yet mathematically exceedingly complex alternative of calculating the logistic error propagation (Ku 1966). For the purpose of understanding hourly and daily presence within the study area, we explicitly wanted to limit the amount of false positives as to not overestimate detection range. In contrast, telemetry studies that build on a smaller detection range (Mourier et al. 2017) need to favour higher sensitivity. Applying the zero threshold in our study improved the daily predictions more dramatically than it did for the hourly model. This was in part attributed to a larger n, which made for a steeper curve than P_{hour} (Fig. 4.1). When setting a zero threshold therefore, the number of transmissions n, as well as the detection threshold k, should always be taken into consideration.

In addition to the estimated π_0, the proposed approach requires values for n and k that are tailored to the telemetry study. Firstly, although a minimum of (generally 2) detections is often applied to qualify a time bin with fish presence (Doyle et al. 2017, Ramsden et al. 2017, Novak et al. 2020), this detection threshold k has never been considered in range assessments. Secondly, the formula obliges a researcher to contemplate on the presumed number of

detectable transmissions n in an animal study. Reflecting the hypothesized minimum time an animal would be in range of a receiver, t_{min} depends on the animal's behaviour in a certain habitat (e.g. proneness to residency or a tendency to burrowing) and the considered time bin. Depending on the species, t_{min} may even be assumed to vary over time, for example if an animal is only seasonally resident (Doyle et al. 2017) or exhibits diel variation in movement behaviour (Reubens et al. 2014). If little is known about the animals, researchers can opt to set precautionary low values for t_{min} and therefore n. Likewise, if a study requires to pick up nearly every transmission of a tagged animal in a certain area (e.g. during migration), researchers have to program the transmitting interval settings and/or space between receivers in the array accordingly (Heupel et al. 2006). The predicted cumulative probability P would then reach values similar to or even lower than the individual detection probability π (Fig. 4.1). In many cases, however, information is available on the expected movement behaviour (e.g. if the species was tagged before), which can be used for a more adequate assessment of range. Intuitively, one may resist the idea of seemingly imposing a bias on the analysis. In practice, however, the formula for calculating n (Eq. 4.2) builds on parameters that are otherwise presumed implicit when designing a telemetry study (e.g. for the choice of transmitting interval settings) (Heupel et al. 2006, How & de Lestang 2012, Ellis et al. 2019). By specifying how these parameters relate (Eq. 4.1 & 4.2), they can explicitly be taken into account in the assessment of detection range and in the design of a telemetry study.

Accounting for range

Despite an increasing recognition in the telemetry community for the need of range testing, only few range test studies (Baktoft et al. 2015, Mourier et al. 2017) evaluate their own design or the applicability to the telemetry study and analytical application. As a standard practice, receivers and sentinel transmitters are placed on a line to investigate range (Huveneers et al. 2016, Loher et al. 2017, Reubens et al. 2019a). In this study, we show that the orientation of that line can influence the estimation of detection range, likely in relation to the direction of the dominant currents (Mathies et al. 2014). Likewise, detections of sentinel transmitters used during this study weren't necessarily representative of the performance of the entire array. In our case, the optimal strategy to obtain reliable detection errors was to assess range

before the study using the entire receiver array, in addition to sentinel transmitter data during the study.

Aside from the range test itself, the method to account for detection error must be tailored to the analytical application and its temporal resolution. From the method elaborated in this study, the cumulative probability P enables the calculation of detection error at the same temporal resolution of the presence metric of interest. When analysing patterns in presence, this measurement error can be directly included either as a Bayesian error structure in a generalized model (Zuur et al. 2017) or in a state-space modelling framework (Pedersen & Weng 2013, Alós et al. 2016, Auger-Méthé et al. 2021). For telemetry analyses that do not build on presence/absence as a response variable, different methods have been developed to account for range or detection efficiency (Whoriskey et al. 2019). Detection counts for example can be directly recalibrated using a correction factor (Brownscombe et al. 2020), whereas error can also be included in the calculation of centres of activity based on detection counts (Simpfendorfer et al. 2008, Winton et al. 2018). When investigating the sequence of detections in space, range can be assessed specifically for migratory routes (Melnychuk & Walters 2010) or network analysis (Mourier et al. 2017). For fine-scale positioning, horizontal position errors would be quantified within an entire receiver array (Stott et al. 2021), potentially accounting for individual receiver's contributions (van der Knaap et al. 2021) and system settings (Vergeynst et al. 2020a).

Implications for study design

We strongly argue to consider the assessment of range as a fundamental aspect of the study design, the data analysis and the interpretation of results. Aside from factors beyond a researcher's control, such as environmental conditions and movement behaviour (Heupel et al. 2006), range is an interplay of distance to a receiver (Kessel et al. 2014), the deployment set-up (Goossens et al. 2020) and receiver type (Mourier et al. 2017), tag attachment (Dance et al. 2016), transmitting power output (Kessel et al. 2015, Scherrer et al. 2018) and depending on the application: transmitting interval and temporal resolution of the analysis. Therefore, researchers can fine-tune more aspects in the design of a telemetry study than simply the lay-out of a receiver array. Understanding the effect of these factors on detection range, is also

advantageous for budget management of expensive telemetry equipment. Adequate range assessments may optimize transmitter battery life times, e.g. by carefully deciding on transmitting interval and power output (Scherrer et al. 2018), or reduce the number of receivers required in an array (Pedersen et al. 2014, Kraus et al. 2018, Kendall et al. 2021). Building on the multitude of detection range studies, this study can serve as a plea to rethink detection range as a spatiotemporal interplay of many factors.

AUTHOR CONTRIBUTIONS

JG analysed the data and wrote the manuscript. JR, JB and JG designed the study and collected the data. JR, JB, PV and SB contributed to the data analysis. JB created the map. All authors critically contributed to the drafts and gave final approval for publication. All the authors read and approved the final manuscript.

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CHAPTER 5

THE IMPORTANCE OF MULTI-SENSOR OBSERVATIONS TO ADVANCE SPECIES CO-OCCURRENCE KNOWLEDGE: A DEMONSTRATOR APPLICATION OF ACOUSTIC TECHNOLOGIES

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ABSTRACT

Multi-sensor observations, integrated across time and space, may bridge knowledge gaps in ecosystem dynamics, one aspect of which is species co-occurrence. In the present work, we combined data streams from two acoustic technologies—passive acoustic monitoring (PAM) and acoustic telemetry (AT) jointly installed under the LifeWatch project. We made use of existing long-term data series from studies on single-species dynamics, to investigate the co-occurrence of marine predators: European seabass and Atlantic cod, and cetaceans, harbour porpoise and dolphins, in the Belgian part of the North Sea (BPNS). Common co-occurrence analyses were applied to a combined PAM and AT hourly presence-absence matrix at different spatial and temporal resolutions. The fish species were in the presence of porpoise at least one third (seabass) to nearly half (cod) of the time they were detected. At a seasonal resolution, we did not observe probabilities of occupancy to be higher or lower than what is expected by chance, while we could discern patterns of co-

occurrence when using an hourly resolution. Analyses done at an hourly resolution showed that porpoises have a significantly higher probability of co-occurring with the cod or seabass during autumn and winter nights. Developing these large-scale networks of integrated acoustic instruments while considering species co-occurrences would further expand the data potential. Considering co-occurrence in ecological research is a step towards an ecosystem-based management of our oceans.

INTRODUCTION

Ecological research has flourished from investigating single-species distributions to the interactions of various species across space and time in community and ecosystem research (Carmel et al. 2013). Different species having similar habitat requirements, are drawn to the same environments. Over time, they may avoid or actively seek each other's presence for interactions such as competition, predation or collaboration (Blanchet et al. 2020). Anthropogenic impacts ranging from global climate change to local habitat loss, affect species differently, making the disturbance of species' interactions part of the poorly understood cumulative effects (Tulloch et al. 2018, Hodgson & Halpern 2019). Understanding how species co-occur within communities is therefore a vital step towards an ecosystem-based management (EBM) (Howell et al. 2021), wherein cumulative impacts are considered, and management is geared towards protecting the ecosystem as a whole (Rosenberg 2005).

A key aspect of well-functioning marine ecosystems are the relationships and interactions of higher trophic levels (Hazen et al. 2019), including various species of cetaceans and fish. Consuming significant amounts of prey biomass, marine predators can impact food webs through top-down forcing (Ballance 2018). In addition, as migratory species make their way from one habitat to another, they are key transportation elements on nutrient cycles (McInturf et al. 2019). Marine predators face a range of anthropogenic stressors, including fisheries, shipping, chemical, noise and waste pollution (Maxwell et al. 2013). As a result of interactions between marine predator species (competition, predation, collaboration), a threat to one species can impact co-occurring species. Fisheries bycatch in particular is one of the primary causes of the decline of marine megafauna (Lewison et al. 2004). For example, bycatch of

common dolphins (*Delphinus delphis*) in the pelagic trawl fishery in the Bay of Biscay has been attributed to the dietary overlap with the fisheries' target on European seabass (*Dicentrarchus labrax*) (Spitz et al. 2013). Understanding patterns of co-occurrence of marine predators is therefore key to establish better conservation and management plans that consider species ecology.

Some acoustic technologies allow to gather long-term data series on the presence and behaviour of aquatic animals. Passive acoustic monitoring (PAM) can be used to detect sounds produced by aquatic animals, such as whistles and echolocation clicks of cetaceans (Schaffeld et al. 2016, Nuuttila et al. 2017, Williamson et al. 2022). In acoustic telemetry (from here on referred to as AT), an animal is fitted (externally or internally) with an electronic tag that transmits an acoustic signal which can be detected by an acoustic receiver (Hussey et al. 2015). Each of the technologies has some (dis)advantages in observing these animals in the wild: in PAM, detecting the presence of a species relies on the animal effectively producing sounds, with its presence remaining undetected during silent periods. In contrast, an acoustic receiver can detect a tagged animal (when the individual is within its detection range), but it is oblivious to untagged animals (Brownscombe et al. 2022). AT provides information on individual movement behaviour, whereas PAM does not distinguish individuals. Both acoustic technologies have greatly advanced marine ecological research.

In the present work, we combined the technologies of PAM and AT, making use of long-term data series from studies on single-species dynamics, to investigate co-occurrence of marine predators. We therefore 1) described the jointly installed technologies and data management flow, 2) applied different analysis methods that are commonly used to investigate species co-occurrence, to the long-term data series at high temporal resolution from PAM and AT, and 3) evaluated how the combined technologies can contribute to community and ecosystem ecology research.

Figure 5.1. Multi-use platform of the Belgian passive acoustic network (BPAN) equipped with a C-POD and receiver.

MATERIALS AND METHODS

Study area

The Belgian passive acoustic network (BPAN) has been providing long-term data series on the presence of porpoises and dolphins in the Belgian Part of the North Sea (BPNS) since 2016, as part of the LifeWatch observatory (https://lifewatch.be/en/cetacean-passive-acoustic-network). Echolocation signals of odontocete cetaceans (with the exception of sperm whales) can be detected using C-PODs (Chelonia Ltd., UK). A C-POD is a passive acoustic monitoring (PAM) logger programmed to autonomously log echolocation clicks over long periods of time (up to four months) (Roberts & Read 2015). C-PODs listen continuously for high frequency clicks (20 – 160 kHz) and store the parameters of these clicks (e.g., frequency, bandwidth, sound pressure level, duration), and not the raw recording itself. Each BPAN station is

equipped with a multi-use platform moored on the seabed (Fig. 5.1): a tripod frame originally designed for acoustic telemetry (AT) studies. The adapted frame fits a C-POD in the floatable collar in a fixed vertical position, together with VR2AR acoustic receivers from InnovaSea Systems Inc., USA. These receivers detect acoustic signals at 69 kHz transmitted by electronic tags implanted in/attached to individual organisms. These tags allow to detect the presence of the individual when it is within the detection range of the acoustic receiver (namely a detection). The receivers are equipped with an acoustic release system, enabling the retrieval of all equipment (design and deployment protocol were detailed in (Goossens et al. 2020). This multi-use platform provides in tandem PAM data to the BPAN, and AT data to the permanent Belgian acoustic receiver network (PBARN) (Reubens et al. 2019b), both part of the LifeWatch observatory.

In the BPAN, ten stations were installed across the BPNS, which reaches up to 83 km out to sea (45 sea miles) from a coast with a length of approximately 65 km (Fig. 5.2). The BPNS has a mean depth range of 20 m with a maximum depth of 45 m, and is characterized by a variety of sandbanks enriching the region's biodiversity (Belgian Federal Public Service Health 2015). Anthropogenic activities in the BPNS are ubiquitous, including fishery activities, offshore wind energy production and shipping. Eight stations are located near shipwrecks and two stations are installed next to biodiversity-increasing artificial reefs in two offshore wind energy production (Fig. 5.2). Two stations (G-88 and Nauticaena) were discontinued over time due to external problems. G-88 was only operational for less than a year, from November 2018 to August 2019. Nauticaena was operational until January 2021.

Data management and access

The data management of PAM and AT data was facilitated through the European Tracking Network (ETN) database (https://lifewatch.be/etn). The C-POD data were first processed with the cpod.exe software (Chelonia Ltd., UK) with an automatic click train detection classifier, KERNO. The clicks from the raw data (.CP1 file) were identified as originating from click trains of harbour porpoises (narrowband high frequency clicks) or dolphins with a quality label (high, moderate or low). As the KERNO classifier could not make a distinction between dolphin species, these are grouped together under the label 'Other

cetaceans.' The click train classifications (.CP3 file) were manually validated by visual inspection with the cpod.exe software. For this study, we only considered click trains with high and moderate quality labels. The data with a temporal resolution of one minute were then exported per quality label. For every C-POD deployment, the data (TrainDuration.txt and Detenv.txt files) and metadata were stored on the underwater acoustics component of the ETN database. PAM data can be visualized online and downloaded by registered users via the LifeWatch Data Explorer R Shiny app (https://lifewatch.be/en/lifewatch-data-explorer). The AT data and metadata were archived and accessed as described in detail by Reubens et al. (2019b).

PAM and AT data from all deployments of all stations were accessed via the *lwdataexplorer* (Hernández et al. 2023), and *etn* (Desmet et al. 2022) packages, respectively. PAM data were downloaded in units of detection positive hours (DPH), defined as the observed odontocete presence (at least one echolocation click train) within a given hour. The acoustic detection data consisted of the times of detection of individual transmitters at each receiver. The ETN download of the AT data originated from transmitters of different telemetry projects. We contacted the principal investigators of each of these projects to get permission to use the data. Our dataset was therefore limited to detections that we had permission to use during the period of analysis. Detections that were time stamped at dates outside of the receiver and/or tag battery lifetimes were considered false detections and were excluded from the analyses.
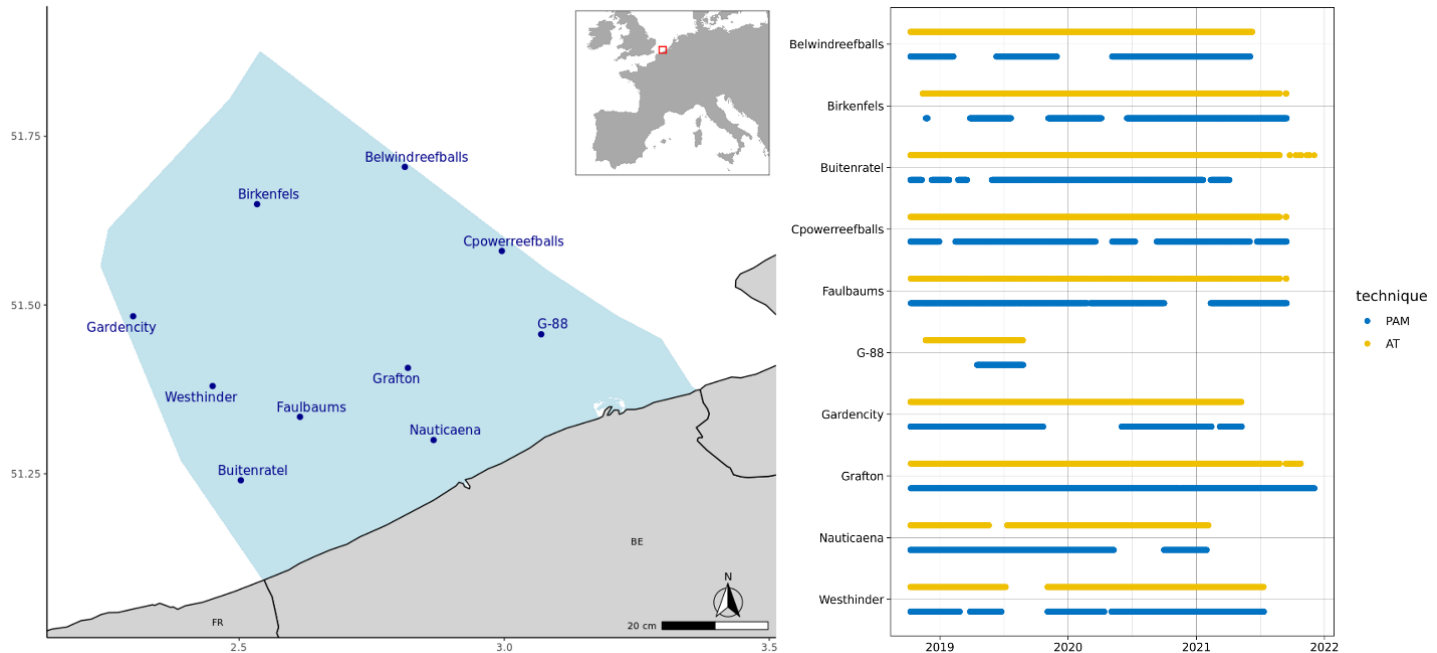
Figure 5.2. The ten stations of the Belgian passive acoustic network (BPAN; left) and each station's data availability based on Passive acoustic monitoring (PAM) and Acoustic telemetry (AT) techniques (right). Polygon shaded blue corresponds to the area of the Belgian part of the North Sea (BPNS). Nauticaena and G-88 were discontinued in 2019 and 2021 respectively, due to external problems.

Data analysis

All data processing and analyses were performed in R (R Core Team 2022), with scripts made available on the GitHub repository https://github.com/lifewatch/lifewatch_speciescooccurrence. For each species, the data was organized in an hourly presence-absence matrix at every station (Table 5.1). For the PAM data, the detection of at least one echolocation click train sufficed to regard the species as present within the hour (DPH = 1). For the AT data, at least one tagged individual had to have been detected at least once to label the species as present within the hour (DPH = 1). Absence of a species was defined for both techniques as the lack of detecting the species in an hour (DPH = 0). If the C-POD or acoustic receiver were inactive, or if there were no animals of that species with active acoustic transmitters (i.e., with active batteries) then the value for that hour was regarded as not applicable (DPH = NA). The hours of detections, regardless of the exact minute, were classified as day or night using the local sunrise and sunset timings from the *StreamMetabolism* package based on the NOAA sunrise and sunset calculator.

Using these hourly presence-absence matrices, we investigated spatiotemporal patterns in occupancy and co-occurrence. Presence of different species within the same stations, expressed by occupancy, indicated similar patterns in habitat use, while animals of different species had to be present at the same time (hour) to indicate co-occurrence. We defined co-occurrence as the detection of two or more species at a station within a given hour on the same date. An overlap in occupancy indicated two or more species detections at a station in the same season. Five different analyses were performed to investigate occupancy and co-occurrence at different temporal scales, summarised in Table 5.2.

Table 5.1. Definition of values of detection positive hour (DPH) in the presence-absence matrix for species of fish (acoustic telemetry; AT) and odontocete cetaceans (passive acoustic monitoring; PAM).

DPH	PAM (C-POD)	AT (VR2AR)
1	Detection of at least one echolocation click train	Detection of at least one acoustic transmitter
0	No detection of an echolocation click train	No detection of an acoustic transmitter
NA	Inactive C-POD	Inactive acoustic receiver or no acoustic transmitters with active batteries

Pairwise species monthly occupancy

A probabilistic pairwise species monthly occupancy analysis was performed using the R package *co-occur* (Griffith et al. 2016). This package computed the probability that species *A* was present at a station, given the presence of species *B* (at least one DPH) for a particular month. A simplified data frame was used, solely considering the presence-absence of the species for each station monthly. The probability P_j of two species both occurring at j number of stations in the same month is:

$$P_j = \frac{\binom{N_A}{j} x \binom{N - N_A}{N_B - j}}{\binom{N}{N_B}}$$
(Eq. 5.1)

where N_A and N_B are the number of sites where species A and species B occur respectively, and N as the total number of sites of the network. This equation results to the proportion of N_B sites where species A is occurring, given that both species occupy j sites (Griffith et al. 2016).

If a species pair did not share any site for certain months, this would result to low probabilities of occupancy (threshold explained by Veech (2013)). Results therefore only showed species pairs whose expected shared occupancy ≥ 1 site.

Table 5.2. Overview of analyses in hourly, monthly or seasonal temporal resolutions, with spatial resolutions of either the BPAN (Belgian passive acoustic network) as a whole or per station. Publications listed serve as examples, but this list is not exhaustive.

Analysis	Occupancy / Co-occurrence	Temporal Resolution	Spatial Resolution	Description	Application in other publications
Pairwise species monthly occupancy	Occupancy	Monthly	BPAN	Probability of two species both occurring in the same month based on the number of stations they occupied within that month	Pulver et al. (2016) Noor et al. (2017)
Co-occurrence percentage	Co-occurrence	Hourly	Station	Percentage of solitary hours (or no other species detected) and hours of co-occurrence with other species	Bauer et al. (2015)
C-score	Co-occurrence	Hourly	BPAN (stations with at least 10 DPH of both species)	A measurement of aggregation of two species based on the number of stations of co-occurrence per hour	Kamilar and Ledogar (2011) Ramos et al. (2019)
Diel overlap	Occupancy	Seasonal	BPAN (stations with at least 10 DPH of both species)	Extent of overlap of the species' seasonal diel patterns	Noor et al. (2017) Gracanin and Mikac (2022)
Co-occurrence modelling: Logistic Regression	Co-occurrence	Hourly	Station (with at least 10 DPH of both species)	Probability of a species, if present at a certain station, co-occurring with another species	MacKenzie et al. (2004) Sebastián-González et al. (2010)

Co-occurrence percentage

For each species, we calculated the co-occurrence percentage as the amount of time (number of DPH) one species co-occurred with each of the other species out of its total DPH. In the case of detecting only one species for a given hour at a particular station, we made the distinction between the cases where (1) the detection of another species was not possible because of inactivity of the C-POD, receiver or transmitters (DPH = NA), and (2) no other species were detected within that station's detection range (DPH = 0). In the latter case, a true absence of other species could not be distinguished from the presence of untagged fish of that species.

C-score

Using the *EcoSimR* package (Gotelli et al. 2015), the C-score (Stone & Roberts 1990) was calculated to quantify the association between species pairs based on the number of shared stations. The C-score for species *A* and *B* is:

$$C_{AB} = (R_A - SS)(R_B - SS) \hspace{3cm} \text{(Eq. 5.2)}$$

where R_A and R_B are the number of stations where species *A* and *B* occur, respectively, and SS is the number of stations where the species pair co-occurs. The C-score would therefore range from 0 (maximally aggregated) to a maximum of $R_A R_B$ (maximally segregated with no shared sites). C-scores were calculated for every hour of the dataset, excluding stations where the species occurred for less than 10 hours. The non-parametric Kruskal-Wallis test (Kruskal & Wallis 1952) was used to test for significant differences in C-scores between seasons and between day and night. As a post-hoc test, we performed pairwise comparisons using a Wilcoxon rank-sum test (Wilcoxon 1945).

Diel overlap pattern

Similarity between species' diel occupancy during different seasons was estimated with the R package *overlap* (Meredith & Ridout 2021). For this analysis, kernel density functions were fitted to estimate a coefficient (Δ), which calculates the overlap in 24-hour diel pattern per season. We used a type 4 overlap estimator (Δ_4), which compares densities at the actual times of observation of species, and it is only recommended if both samples are larger

than 50 (Meredith & Ridout 2021). Only stations where the species occurred for at least 10 hours were included in this analysis.

Co-occurrence modelling: logistic regression

Finally, spatiotemporal patterns in co-occurrence of different pairs of species were analyzed with generalized linear mixed effects models (GLMM) (Zuur et al. 2009), using the *lme4* package (Bates et al. 2015). Separate models were used to investigate co-occurrence from the point of view of one species: when species *A* is present, what is the probability of it co-occurring with species *B*? The data subset for each model was therefore limited to the hours where species *A* was present (DPH = 1). Hours when the detection of species *B* was technically not possible (i.e., DPH = NA) were removed. Locations where the species were detected for less than 10 hours were excluded from the analysis. The co-occurrence of species *A* and *B* was modelled with a GLMM with a Bernoulli distribution, a type of binomial distribution, wherein the value of co-occurrence is only either 0 or 1 for every DPH. The GLMM estimated the probability of co-occurrence as a function of the fixed effects season, day-night and their interaction, with the interaction of station and season as random effect:

$$Co\text{-}occurrence \sim Diel * Season + (1| \ Station/Season) \qquad (Eq. 5.3)$$

Models were evaluated by backwards model selection, using the Akaike Information Criterion (AIC) (Akaike 1974), and Chi-square test. If the GLMM model resulted in a singular fit (Barr et al. 2013, Matuschek et al. 2017), the random effect was simplified by removing the interaction effect. The random effect was then assessed by computing the intra-class correlation coefficient (ICC) of its variance (Snijders & Bosker 1999). Low or zero ICC indicated independence of groups, implying that the random effects should be dropped from the analysis (Solorio-Rivera et al. 2007). In this case, a generalized linear model (GLM) with a Bernoulli distribution was used instead. The model's assumptions of the distribution from an exponential family and independence of cases were satisfied.

RESULTS

The BPAN recorded the presence of harbour porpoise (*Phocoena phocoena* L. 1758), dolphins (Delphinidae Gray 1821), and 11 species of fish carrying acoustic transmitters (Fig. 5.3). The detections of acoustic transmitters originated from fish tagged in the framework of different projects (Supporting information Fig. S5.1, Table S5.1). Considering the limited number of DPH for some species, we applied the analyses on harbour porpoise (PAM), dolphins (PAM), European seabass (*Dicentrarchus labrax* L. 1758; AT), and Atlantic cod (*Gadus morhua* L. 1758; AT). Therefore, the dataset was limited to the period when data of all four species were available, i.e., from 9 October 2018 to 3 December 2021.

Within this study period, harbour porpoises were registered for 84,431 DPH (almost half of the time the C-PODs were active). Porpoise click trains were observed year-round at all stations. Dolphins only accounted for 160 DPH, mainly at the stations Westhinder and Birkenfels. Both species were observed slightly more frequently during the night (64.4% of dolphin DPH, 56.7 % of porpoise DPH).
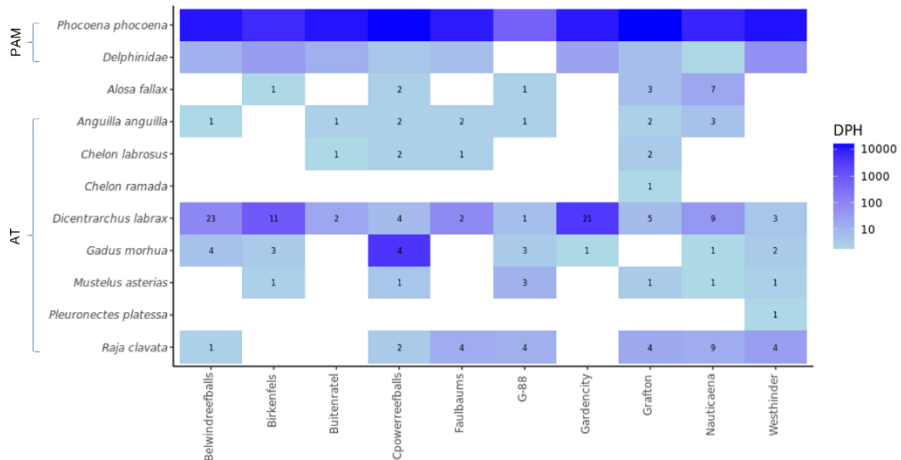

Figure 5.3. Detections of various species from the Belgian passive acoustic network (BPAN). Numbers indicate count of tagged animals detected.
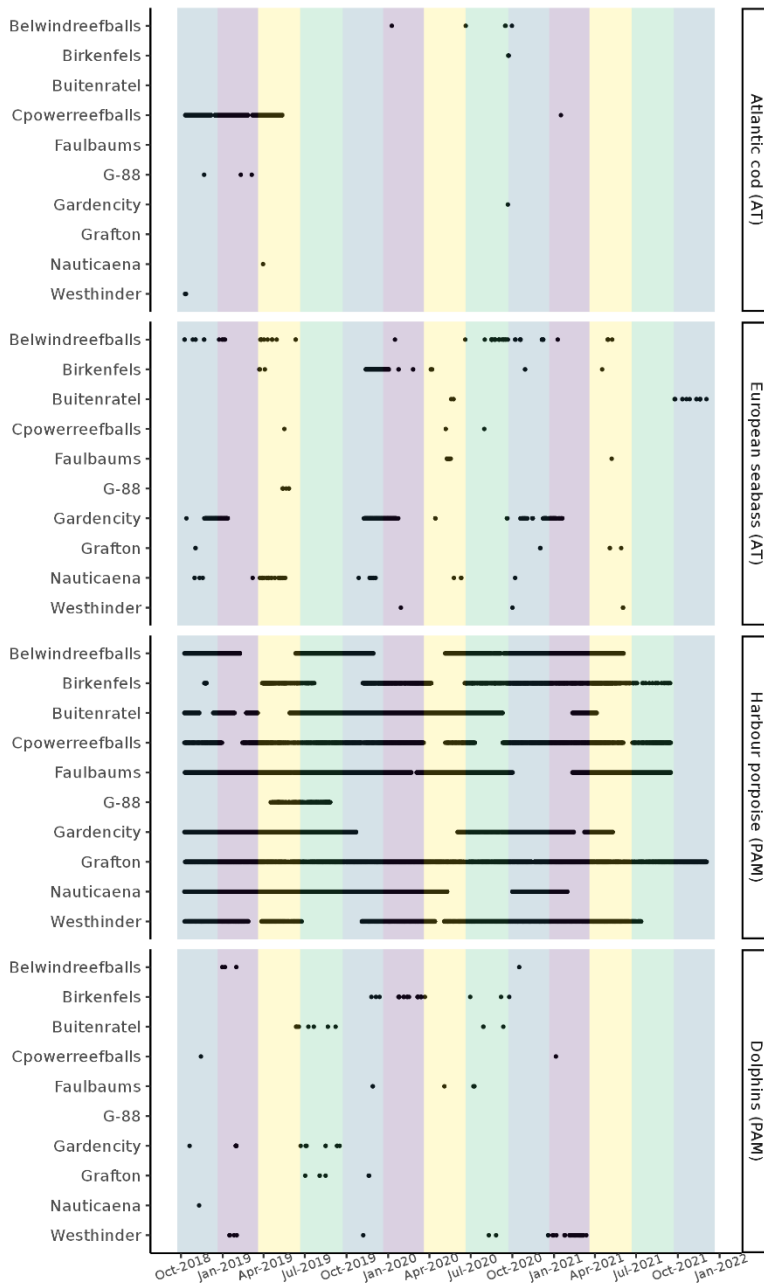
Figure 5.4. Detections per station throughout the study period. Seasons are distinguished by the colour of the rectangle.

The acoustic receivers registered a total of 4,704 DPH (out of 215,374 possible detection hours) for seabass and 4,538 DPH (out of 69,607 possible detection hours) for cod. The majority of detected cod (13 individuals, 39 – 42.5 cm) was caught and tagged near the offshore wind farms, while seabass (47 individuals, 33 – 66 cm) were tagged along the coast and near shipwrecks (Supporting information Fig. S5.1). The majority of DPH for seabass was found at the stations Garden City (76%) and Birkenfels (19%), mainly in the period from November to January (Fig. 5.4). During spring, seabass was detected at all stations, albeit in very low numbers of DPH, whereas seabass detections during summer were limited to offshore wind farm stations. Almost all (99.6%) of the cod DPH were observed at the station Cpowerreefballs. Here, cod was detected in fall, winter and spring, but not in summer. Like the cetaceans, the fish were observed more frequently during the night (64.0% of seabass DPH and 55.0% for cod DPH).

These detections, however, do not thoroughly reflect the spatiotemporal pattern of habitat use of these fish species, mainly due to the spatial dispersion of receivers, and the residency/site fidelity of tagged fish within the vicinities of artificial reefs (Reubens et al. 2013a). In contrast to targeted telemetry studies where information of undetected fish normally holds value, our study only considered available fish detection data, therefore it should not be used to interpret the spatiotemporal pattern of habitat use for each fish species.

Pairwise species monthly occupancy

Due to very low probabilities of occupancy, not all pairs of species were expected to share at least one site (Fig. 5.5). However, where suitable data was available, monthly co-occurrence was observed for most of the pairs of species. Dolphins and harbour porpoises consistently had the highest probability of occupying the same stations (at least three) throughout autumn, winter and summer among the three species pairs. Seabass and harbour porpoises were predicted to occupy all stations around spring (probability = 1 in May), while the probability for cod and harbour porpoises to occupy the same stations was highest around autumn (probability = 0.45 in September). Based on the probabilistic analysis of monthly occupancy of the stations, none of the species pairs were significantly associated, neither positively nor negatively.
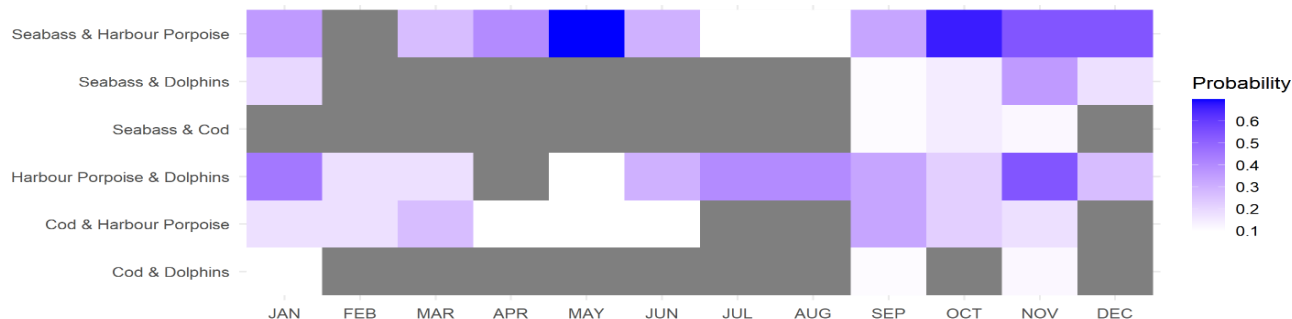
Figure 5.5. Pairwise monthly occupancy of all species pairs. Grey zones indicate species pairs which were not expected to share any site because not enough data was available for the analysis.

Table 5.3. Co-occurrence of species as a percentage of each species' total detection positive hours (DPH). Total DPH is categorized into percentages of 'Alone,' where DPH of other species was 0, 'Inactivity' (of the C-POD, receiver or transmitters), where DPH of other species was NA (thus, detecting other animals was not possible) and co-occurring with the other species, where DPH of the other species was 1.

Species	Total DPH (DPH =1)	Alone (%)	Inactivity (%)	With cod (%)	With seabass (%)	With harbour porpoise (%)	With dolphins (%)
Atlantic cod	4538	16.7	39.3	-	0.0	44.0	0.0
European seabass	4704	7.8	59.3	0.0	-	32.9	0.0
Harbour Porpoise	82431	26.3	69.3	2.4	1.9	-	0.1
Dolphins	160	18.1	32.5	1.3	0.0	48.1	-

Co-occurrence percentage

Dolphins, European seabass, and Atlantic cod were frequently observed to co-occur with harbour porpoise (Table 5.3). Out of the total hours these species were observed, porpoises were present during 48.1% of the DPH of dolphins, 44.0% of the DPH of Atlantic cod, and 32.9% of the DPH of European seabass. For the highly prevalent harbour porpoise on the other hand, the other species were only detected during 4.4% of its DPH. Atlantic cod and harbour porpoise were detected at the same station for one hour and were never found to co-occur with seabass. In the following analyses, we investigated the co-occurrence of harbour porpoise with each of the other species.

C-scores

The European seabass and harbour porpoise were maximally aggregated (C-score = 0), co-occurring in the greatest number of stations, during winter and autumn nights (Wilcoxon rank-sum test, p < 0.01) (Fig. 5.6). Similar distributions of C-scores of the seabass and porpoise can be observed during these seasons. During the summer, the European seabass and harbour porpoise had higher C-scores indicating segregation—species were rarely detected in the same stations and thus had lower probabilities of co-occurrences within BPAN. The dolphins and harbour porpoise were maximally aggregated during autumn and winter nights and summer days (Fig. 5.6). During spring, for every hour that both a dolphin and a porpoise were detected, the two species were maximally aggregated, sharing the same sites. However, differences between seasons and diel variation were statistically insignificant for this species pair (Kruskal-Wallis test, p > 0.05). The C-scores of Atlantic cod and harbour porpoise were not assessed since the DPH of Atlantic cod were only at least 10 in one station (Cpowerreefballs).
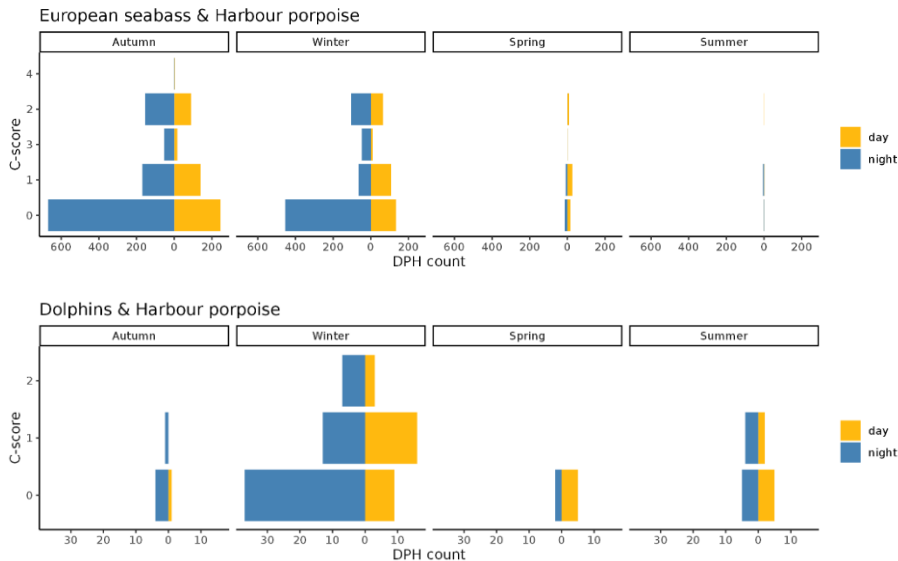
Figure 5.6. Bar plots of C-scores per day and night for each season for the species pairs of harbour porpoise with seabass (top) and dolphins (bottom).

Diel overlap pattern

Diel patterns of detected presence were analysed for the three pairs of species (namely, harbour porpoise with cod, seabass, and dolphins, Table 5.4). Higher diel overlap coefficients of cod and seabass with the porpoise during autumn (Δ_4 = 0.94) and winter (Δ_4 = 0.93) show similar diel occupancy during these seasons. In these seasons, cod and seabass seemed to be continuously detected regardless of the hour of the day, while the presence of porpoises dropped during the day (Fig. 5.7). Cod had very few DPH during the summer (DPH = 4) and was thus excluded from this analysis. Dolphins and harbour porpoises had lower diel overlap coefficients compared to the other two species pairs as the diurnal presence of dolphins varied for each season. The dolphins and the harbour porpoise had the highest diel overlap during winter (Δ_4 = 0.86).

Since presence/detection densities varied per station, it is expected that these diel overlap patterns per species pair were not representative of the diel overlap pattern for each station in the BPAN. Large ranges of diel overlap coefficients across the BPAN were observed especially for the seabass and porpoise.

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Table 5.4. Diel overlap coefficients of the three species pairs calculated for all stations mentioned, and diel overlap coefficients calculated per station indicated as the median [range] in the last column. A value of NA indicates insufficient data.

Species	Stations	Season	Diel overlap coefficient for all stations mentioned	Diel overlap coefficients calculated per station
Atlantic cod & Harbour Porpoise	Cpowerreefballs	Autumn	0.94	0.94
		Winter	0.93	0.93
		Spring	0.97	0.97
		Summer	*NA*	*NA*
European seabass & Harbour Porpoise	Belwindreefballs, Birkenfels, Faulbaums, Garden City, Nauticaena	Autumn	0.94	0.83 [0.64-0.96]
		Winter	0.93	0.92 [0.49-0.92]
		Spring	0.90	0.71 [0.33-0.88]
		Summer	0.71	0.46 [0.24-0.68]
Dolphins & Harbour Porpoise	Birkenfels, Buitenratel, Garden City, Westhinder	Autumn	0.74	0.5
		Winter	0.86	0.72 [0.69-0.74]
		Spring	0.62	*NA*
		Summer	0.76	0.51 [0.40-0.62]
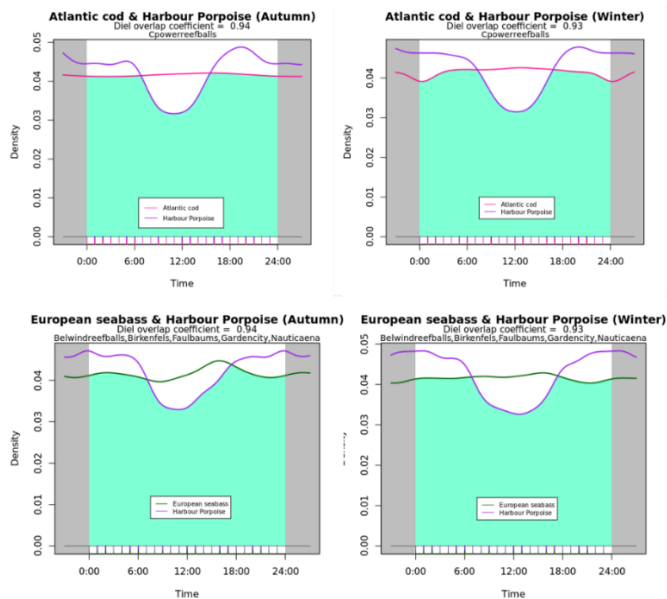
Figure 5.7. Diel overlap patterns of two co-occurring species pairs during autumn and winter.

Model probabilities of co-occurrence

For the 3 pairs of species selected, a GLMM was fitted (fixed factors season, day-night, and their interaction, and random factors station and season interaction). AIC model selection resulted in season and diel as significant factors for the three pairs of species (Table 5.5, Fig. 5.8, Supporting information Tables S5.2-4). When a European seabass was present, it had the highest probability of co-occurring with a harbour porpoise during autumn and winter nights, and the lowest during summer days. Co-occurrence of the European seabass and harbour porpoise during autumn and winter were significantly different from spring and summer ($p < 0.05$), as well as between day and night ($p < 0.05$). Meanwhile, when an Atlantic cod was present, it had a higher probability of co-occurring with a harbour porpoise during winter nights and least during autumn days ($p < 0.01$). The probability of co-occurrence of cod and porpoise during winter nights was significantly different from both autumn and spring days. The dolphins were predicted to have a higher probability of co-occurring with a harbour porpoise during spring than during winter ($p < 0.05$). Throughout all four seasons, there is a higher probability of dolphins co-occurring with harbour porpoises during the night.

Table 5.5. Final model selected for each species pair. Indicated are the stations included in the model with detection positive hours (DPH) >= 10 hours.

Species pair (with harbour porpoise)	Model selected (AIC)	Stations with DPH >= 10 hours	AIC
European seabass	Co-occurrence ~ Diel + Season	Belwindreefballs, Birkenfels, Faulbaums, Garden City, Nauticaena	3872.5
Atlantic cod	Co-occurrence ~ Diel * Season	Cpowerreefballs	4591.8
Dolphins	Co-occurrence ~ Diel + Season	Birkenfels, Buitenratel, Garden City, Westhinder	192.6

Figure 5.8. Generalized linear model (GLM) results of the 3 species pairs. Numbers indicate the number of detection positive hours (DPH) taken into account. Points indicate the predicted value of probability while errors bars show the lower and upper confidence interval. Significance codes: '***' 0.001 '**' 0.01 '*' 0.05.

DISCUSSION

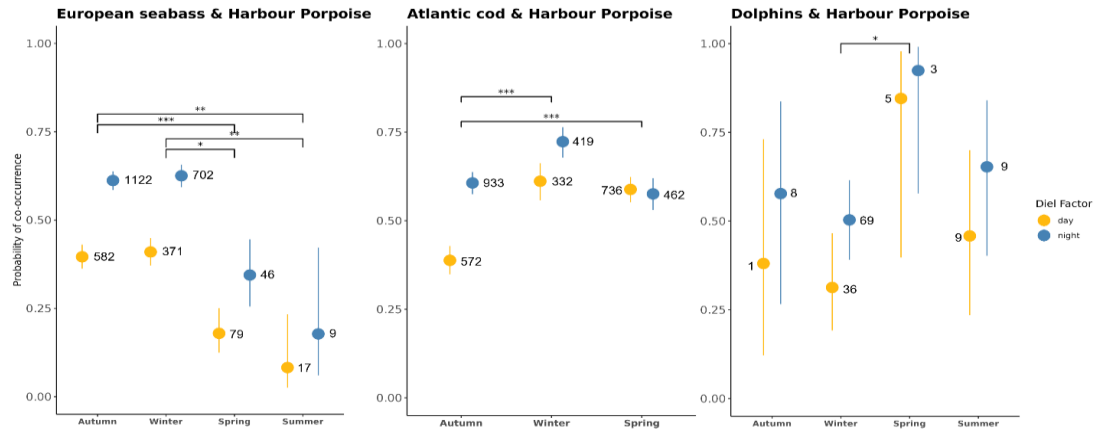Our study serves as a demonstrator use case of how integrating multi-sensor observations can maximize the data potential of long-term data series, which can be of use to EBM. One challenging aspect of EBM is the consideration of cumulative impacts and the interdependent nature of ecosystems (Rosenberg 2005, Curtin & Prellezo 2010). Defined as a strategy to address this challenge, an integrated approach is central to EBM in achieving conservation and sustainability (UN Convention for Biological Diversity 2000). Integration, however, is not only profitable in management but also in developing large-scale observation networks. Previous research that integrated sensors proved to increase survey accuracy (Giordano et al. 2016) and allowed for uniform data acquisition (El Mahrad et al. 2020), crucial in sustaining data usability for various types of studies. Multi-sensor observations integrated across time and space may bridge knowledge gaps in ecosystem dynamics, one aspect of which is species co-occurrence. In this study, we demonstrated how a new layer of knowledge at a broader ecological level can be obtained when relevant techniques are combined on one platform.

To our knowledge, we were the first to report on the combined use of PAM and AT, two separate techniques that have provided continuous, long-term data series beneficial for ecological studies. The combination of PAM and AT was first driven by practical considerations: the tripod proved to be an efficient mooring design which can fit both a C-POD and a VR2AR acoustic receiver equipped with an acoustic release system (Goossens et al. 2020). Through this opportunistic application of the technologies, we gathered a dataset of 3 years with a median of 23,898 and 17,868 hours of AT and PAM data respectively at 10 stations. This type of continuous long-term datasets at such high temporal resolution are rare for co-occurrence studies, which require large datasets but generally rely on data from sparse/discontinuous sampling periods (MacKenzie et al. 2004, Lamothe et al. 2019, Blanchet et al. 2020). In this manuscript, we showed how common analyses from co-occurrence studies could be applied to integrated PAM and AT data.

When combining the two data types, it was important to recognize the quintessential difference in the information acquired by PAM – observations of any vocalizing dolphins and porpoises, and AT – detections of a limited

number of tagged individuals. Although we opted to adapt the format of the AT (detections of individuals) to PAM data (DPH of species), we still had to account for the individual aspect of AT data. Since individual cod and seabass were known to exhibit residency and site fidelity (e.g., the stations near their release site) (Reubens et al. 2013b, Doyle et al. 2017), we reduced the dataset to stations with a minimum set number of detections of species of interest (DPH >= 10). In addition, absence information had to be regarded differently: PAM would be limited to registering vocalizing cetaceans, but AT was limited by the number of tagged fish. This was illustrated by cod co-occurring with porpoise for 44.0% out of its total DPH, whereas the porpoise co-occurred with cod for only 2.4% of its total DPH. Porpoise observations were approximately twenty times larger than fish detections, which had to be interpreted from a technical perspective rather than an ecological one.

Applying different co-occurrence analyses, we obtained different results depending on the spatial and temporal resolution of the analysis. At a seasonal resolution, we did not observe probabilities of occupancy to be higher or lower than what is expected by chance (pairwise species occupancy), while we could discern patterns of co-occurrence when using an hourly resolution (C-score and GL(M)M). The hourly resolution matrix showed greater variation in co-occurrence over time, resulting in statistically significant patterns. The methods of pairwise species occupancy (Griffith et al. 2016) and C-score (Stone & Roberts 1990, Gotelli et al. 2015) were originally designed to investigate co-occurrence through a species-by-site matrix and therefore lacked the temporal aspect that our hourly presence-absence matrix had. However, we adapted the C-score to our hourly presence-absence matrix and obtained comparable results to the GLM. For example, both the C-score and GLM showed that the seabass and porpoise have a significantly higher probability of co-occurrence during autumn and winter nights. This temporal aspect was crucial to make the discrepancy between co-occurrence – two species occupying the same space at the same time – and similarity in space occupancy – two species occupying the same space at any time. The GLM, from the perspective of the species with the lowest occurrence, effectively dealt with this resolution (thus answering the question formulated as: out of the total time a seabass was observed, how much time did it co-occur with a porpoise?).

The purpose of this study was to demonstrate the benefits of PAM and AT combined, whereby we opportunistically made use of already available datasets. Although a targeted ecological study on species co-occurrence patterns should have a study design with more relevant tagging locations (e.g., closer to the PAM and AT stations), this study provided insights on the co-occurrence of cod and seabass with harbour porpoise. The fish species were in the presence of porpoise at least one third (seabass) to nearly half (cod) of the time they were detected. The probabilities of co-occurrence of both cod and seabass with a harbour porpoise were found to be significantly higher at night, which was likely attributed to the patterns in occupancy. Seabass and cod were present rather continuously throughout the day, whereas porpoise was mainly present (or vocalizing) at night. Although this diel difference in co-occurrence was found for each season for seabass, there was a clear seasonal interaction in this diel pattern for cod.

The co-occurrence patterns would likely be attributed to dietary overlap as all species considered in this study were top predators whose diet included small pelagic fish such as mackerel, scads, anchovy and herring. Long-term echolocation diel patterns of porpoises are influenced by food availability and composition (Schaffeld et al. 2016) - they forage in deeper waters at night (Carlström 2005, Schaffeld et al. 2016), and during the colder seasons higher food consumption is necessary for the endothermic porpoises to be able to regulate their body temperature (Haelters et al. 2012, Kastelein et al. 2018, Rojano-Doñate et al. 2018). As opportunistic feeders, their distribution can greatly reflect the distribution of their prey (Link & Garrison 2002, Santos et al. 2004). Further research into the potential interaction between these species, which may exhibit seasonal avoidance or attraction towards each other, would benefit from investigating the relationship between co-occurrence and foraging behaviour from PAM data (Nuuttila et al. 2013, Todd et al. 2022) and vertical movement behaviour from AT data (Quayle et al. 2009, Reubens et al. 2014, Heerah et al. 2017).

Mooring scientific instruments together made for time and cost-efficient deployments and generated multiple datasets that were spatiotemporally synchronized. Aside from the C-POD and VR2AR acoustic receiver, moorings could be fitted with other scientific equipment such as the SoundTrap

hydrophone (Ocean Instruments NZ) and an acoustic Doppler current profiler (ADCP; Teledyne Marine) (Goossens et al. 2020). With the current development of large-scale networks of acoustic instruments (Mellinger et al. 2007, Risch et al. 2014, Abecasis et al. 2018, Reubens et al. 2019b), the combination of different acoustic technologies would further expand the data potential. The resulting long-term, high-resolution datasets could significantly contribute to other co-occurrence studies relying on sightings, strandings, catch and fishery observer data (Escalle et al. 2016, Pulver et al. 2016, Lamothe et al. 2019, Peltier et al. 2021), for which continuous sampling would not be possible. To better account for spatiotemporal autocorrelation and error, more complex statistical analyses could be applied, such as the Integrated Nested Laplace Approximation (INLA) for Bayesian inference (Martino & Riebler 2019) and models that consider imperfect detection and site characteristics (MacKenzie et al. 2004). This would contribute to identify multispecies hotspots, to understand species interactions, to inform on habitat function at a community level and to register distributional shifts due to global and ecosystem changes (Ward et al. 2015, Brownscombe et al. 2022).

AUTHOR CONTRIBUTIONS

AC analyzed the data and led the writing of the manuscript. JG conceived the study and contributed to the analysis and writing. ED, CM and JR elaborated and maintained the monitoring network and managed the data. ED and JR developed the deployment design. All authors critically revised the drafts and approved the final manuscript.

ETHICAL STATEMENTS

This research was carried out in line with official guidelines for animal welfare in Flanders, Belgium. Catching and tagging treatment of wild Atlantic cod and European seabass were performed under approved ethical certificate EC2017-080.

ACKNOWLEDGEMENTS

SUPPORTING INFORMATION S5
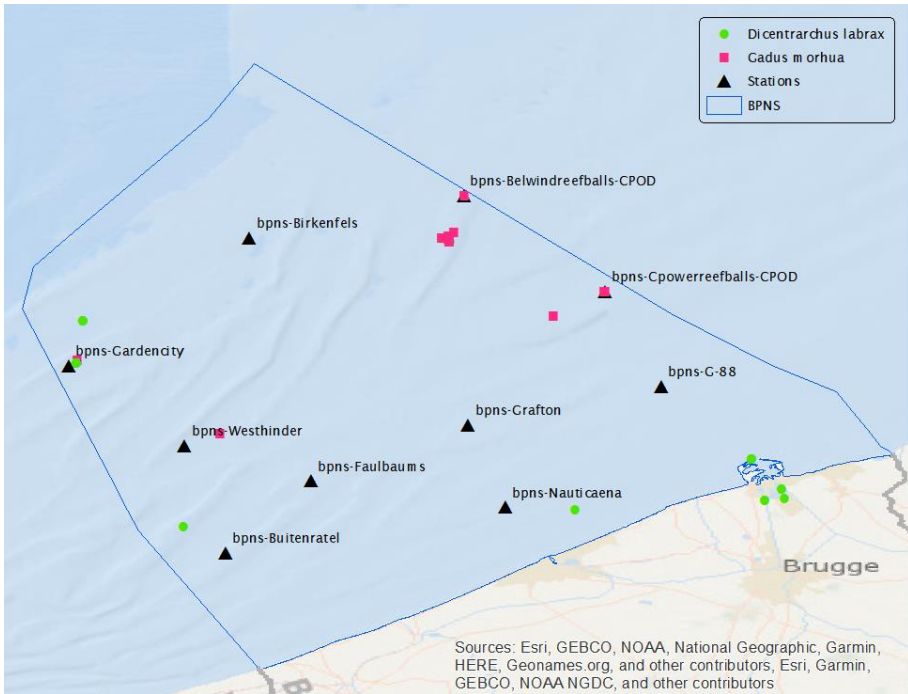
Figure S5.1. Map of release locations of tagged fish within BPAN.

Table S5.1. Reference to animal projects of each species from the European Tracking Network (ETN).

Species	Animal project dataset	References to animal projects
Alosa fallax	2015_fint: Twaite shad acoustic telemetry dataset in the Schelde-estuary and North Sea 2015	https://www.vliz.be/imis?module=dataset&dasid=5858
Anguilla anguilla	2015_PHD_VERHELST_EEL - Acoustic telemetry data for European eel (*Anguilla anguilla*) in the Scheldt estuary and southern North Sea (Belgium)	https://www.vliz.be/nl/imis?module=dataset&dasid=5850
	2019_Grotenete: Migration behavior of silver eels (*Anguilla anguilla*) in a system with a continuous transition from river, across estuary to the sea	https://www.vliz.be/nl/imis?module=dataset&dasid=6337
	BALANCE: Silver European Eel escapement success and migration patterns in River Ems	https://www.vliz.be/nl/imis?module=dataset&dasid=6634
	DAK: Decentralized Eel Management through Knowledge	https://www.vliz.be/nl/imis?module=dataset&dasid=6067
Chelon labrosus	SWIMWAY_2021: Wadden Tools – Swimway Wadden Sea	https://www.vliz.be/nl/imis?module=dataset&dasid=8030
Chelon ramada	SWIMWAY_2021: Wadden Tools – Swimway Wadden Sea	https://www.vliz.be/nl/imis?module=dataset&dasid=8030
Dicentrarchus labrax	Electronic tagging dataset of European seabass in the southern North Sea	https://www.vliz.be/nl/imis?module=dataset&dasid=6555
	SWIMWAY_2021: Wadden Tools – Swimway Wadden Sea	https://www.vliz.be/nl/imis?module=dataset&dasid=8030
Gadus morhua	2015_PHD_VERHELST_COD - Acoustic telemetry data for Atlantic cod (*Gadus morhua*) in the Scheldt estuary and southern North Sea (Belgium)	https://www.vliz.be/nl/imis?module=dataset&dasid=6581

	Rijke_Noordzee: Rijke_Noordzee	https://www.vliz.be/nl/imis?module=dataset&dasid=6534
	PCAD4CAD: Impact of airgun sound exposure on fish: integrating population-level modelling and collect	https://www.vliz.be/en/imis?module=project&proid=4861
fMustelus asterias	ADST Shark: ADST Shark	https://www.vliz.be/nl/imis?module=dataset&dasid=6557
Pleuronectes platessa	PhD_JolienBuyse: Using acoustic telemetry to study local and larger scale movements of plaice in relation to a Belgian offshore wind farm	https://www.vliz.be/nl/imis?module=dataset&dasid=6492
Raja clavata	SVNL-WS: Survival and distribution of 30 Vemco tagged, stocked juvenile thornback rays (*Raja clavata*), within the Westerschelde esutary and the Belgian part of the southern North Sea	https://www.vliz.be/nl/imis?module=dataset&dasid=5970

Table S5.2. Model selection for European seabass and porpoise co-occurrence. Final model in bold face.

Model	AIC	Remarks
cooc ~ dielf * seasonf + (1 | statf/seasonf)	3834.000	Chi-square test insignificance of dielf:seasonf [Pr(Chi) = 0.133]
cooc ~ dielf + seasonf + (1|statf/seasonf)	3833.600	Significant terms dielf [Pr(Chi) < 0. 000], seasonf [Pr(Chi) = 0.0166], but resulted to singular fit
cooc ~ dielf + seasonf + (1|statf)	3856.600	Significant terms dielf [Pr(Chi) < 0.000], seasonf [Pr(Chi) = 0.006].Variance of statf = 0.042. Since ICC (0.013) is close to zero, statf is an insignificant random effect.
cooc ~ dielf + seasonf	3872.500	Significant terms dielf [Pr(Chi) < 2.200e-16], seasonf [Pr(Chi) = 5.522e-10].

Table S5.3. Model selection for Atlantic cod and porpoise co-occurrence. Final model in bold face.

Model	AIC	Remarks
cooc ~ dielf * seasonf	4591.800	Chi-square test significance of dielf:seasonf [Pr(Chi) = 4.907e-08]

Table S5.4. Model selection for dolphins and porpoise co-occurrence. Final model in bold face.

Model	AIC	Remarks
cooc ~ dielf * seasonf + (1 | statf/seasonf)	--	Resulted to singular fit
cooc ~ dielf + seasonf + (1|statf/seasonf)	--	Resulted to singular fit
cooc ~ dielf + seasonf + (1|statf)	192.700	Chi-square test insignificance of seasonf [Pr(Chi) = 0.451] and dielf [Pr(Chi) = 0.052]
cooc ~ dielf*seasonf +seasonf+dielf	191.420	Chi-square test insignificance of dielf:seasonf [Pr(Chi) = 0.067]
cooc ~ seasonf+dielf	192.570	Chi-square test significance of seasonf [Pr(Chi) = 0.03568] and dielf[Pr(Chi) = 0.034]

II

EUROPEAN SEABASS MOVEMENTS
IN THE SOUTHERN NORTH SEA

CHAPTER 6

ELUCIDATING THE MIGRATIONS OF EUROPEAN SEABASS FROM THE SOUTHERN NORTH SEA, USING MARK-RECAPTURE DATA, ACOUSTIC TELEMETRY AND DATA STORAGE TAGS.

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ABSTRACT

Migration is a key ecological process that defines spatiotemporal dynamics and connectivity of populations. The movement ecology of European seabass, *Dicentrarchus labrax*, remains poorly understood, especially in the northern ranges of its distribution. The southern North Sea falls within the area of the "Northern stock" in the Celtic Seas and Greater North Sea ecoregions, which has not recovered from decades of unsustainable fishing pressure. To investigate migration patterns of seabass from the southern North Sea, we combined data from different projects, gathered using various tagging techniques: mark-recapture, acoustic telemetry and (acoustic) data storage tags. This resulted in 146 recaptures (out of 5598 externally marked seabass), 138 detected animals (out of 162 seabass fitted with a transmitter) and 76 archived depth and temperature series (out of 323 seabass with an archival tag) respectively. Tagged seabass were observed between 53.4°N in the Wadden Sea to 46.6°N in the Bay of Biscay. Using geolocation modelling, we distinguished different migration strategies, whereby individual fish migrated to the eastern English Channel, the Western English Channel, the Celtic Sea and the Bay of Biscay, or stayed in the North Sea. Although seabass are generally considered to migrate southwards during the colder months, a large

number of individuals (n = 62) was observed in the southern North Sea from December to February. However, no fish were detected in the Wadden Sea in these months, which was the most northern area in our study. A high number of seabass exhibited fidelity to the North Sea at least six months after tagging (90.5% of recaptures, 55.3 % for acoustic transmitters and for 44.7% of archival tags). Our results show that fine-scaled population structuring should be taken into account in fisheries assessment and that current seasonal fisheries closures are not aligned with the ecology of seabass in the North Sea.

INTRODUCTION

Migration is a crucial aspect of fish ecology and entails the directional movement of individuals and populations from one location or habitat to another (Secor 2015). Migration enables fish to undertake different life-history stages in distinct essential habitats, e.g. for feeding or spawning (Secor 2015, Dambrine et al. 2021). The spatiotemporal change in habitat use shapes population structuring, as it defines the connectivity between conspecifics. Individuals can exhibit fidelity to the locations where they feed or spawn. In the case of spawning sites, fish can return to their natal breeding area (natal homing) (Petitgas et al. 2013), or recurrently migrate to another breeding site, potentially through learned behaviour (Petitgas et al. 2006). A population can also display partial migration, whereby individuals exhibit different migratory life cycle patterns (Chapman et al. 2012, de Pontual et al. 2019).

The highly mobile European seabass, *Dicentrarchus labrax* L., is distributed across the Northeast Atlantic and the Mediterranean, which constitute separate genetic lineages (Souche et al. 2015). In the Northeast Atlantic, a seabass life cycle takes place in different habitats. After eggs are released in offshore spawning grounds, juveniles turn to shallow areas in coastal lagoons, estuaries and rivers that serve as nurseries. Adult seabass (at age 4-5 years and 32 – 36 cm length for males and 5 – 8 years and 40 – 45 cm for females) feed in these inshore areas, as well as around offshore sand banks and ship wrecks, in the period starting from March – June to September – November. As temperatures drop, seabass aggregate in deeper, offshore waters for spawning from December to June, with the exact timing depending on the location and latitude (Vázquez & Muñoz-Cueto 2014, López et al. 2015, Cambiè et al. 2016). The three main spawning areas are considered to be the

Bay of Biscay (Rochebonne Plateau), the western and eastern English Channel (Dambrine et al. 2021). In contrast to the low genetic differentiation within the Northeast Atlantic population, seabass movement patterns expose a complex population structure (Robinet et al. 2020). Individual seabass can reside in limited areas for long periods of time and some exhibit interannual fidelity to both spawning and feeding areas (Doyle et al. 2017, de Pontual et al. 2019, Stamp et al. 2021, Le Luherne et al. 2022).

An area with particularly limited knowledge on seabass movements and habitat use, is the North Sea. Seabass are known to occur in the coastal, estuarine and inshore areas along the Thames Estuary, Scheldt Estuary, Eastern Scheldt and Wadden Sea, which likely serve as nursery and feeding grounds (Pawson et al. 1987, Schnitzler et al. 2011, Cardoso et al. 2015, Tulp et al. 2016). Seabass marked near the Thames Estuary in summer were recaptured in the English Channel during spawning season (Pawson et al. 1987). Although seabass is generally considered to head southward for spawning, they may also spawn within the North Sea. In April and May 2011, stage 1 eggs (first 24 hours) were found in the North Sea along the English coast, the Dogger bank and the Voordelta (area stretching 3 to 15 km seaward along the Dutch coast from Walcheren to the Maasvlakte) (Tulp et al. 2016). Considering the temperature requirements for gonad development (minimum 9 °C for females), North Sea spawning is hypothesized to be possible during warmer years in the later months of the spawning season (April – May) (López et al. 2015, Beraud et al. 2018).

An essential tool to study (fish) movement ecology is tagging. The simplest and oldest tool consists of mark-recapture: a fish is captured and fitted with an external mark, after which a researcher depends on the recapture(s) of the animal to gain information on its movements. Fitting a fish with an electronic tag (internally or externally) vastly increases the information potential of an individual animal's movement. In acoustic telemetry, an animal-borne transmitter emits an acoustic signal that can be detected when the tagged animal is within the detection range of an acoustic receiver (Hussey et al. 2015). Detection data are accessed through the receiver and contain the timestamped information of the unique tag ID, potentially supplemented with a sensor measurement (Brownscombe et al. 2019). On the other hand, data

storage tags (DST) store sensor information (e.g. depth and temperature) in the tag memory, requiring the physical recovery of the tag to access the stored data (Metcalfe & Arnold 1997). The resulting data series provide high resolution, continuous information on the depth and temperature experienced by the tagged fish, and can be used for geolocation modelling to reconstruct trajectories at a lower resolution (as a result of model error) (Pedersen et al. 2008, Gatti et al. 2021). To benefit from the highly complementary information of acoustic telemetry and DST, the two technologies can be combined in one physical tag (Goossens et al. 2023) or by double-tagging (Liu et al. 2017). In this study, we combine mark-recapture, acoustic telemetry and DST data from seabass tagged in French, English, Dutch and Belgian waters to describe migration patterns of European seabass from the North Sea.

MATERIALS AND METHODS

Study area

The study area consisted of the southern North Sea (or Southern Bight; ICES division 4c) and its connected water bodies (Fig. 6.1). The complex hydrodynamics are influenced by strong tidal currents, saltwater inputs from the English Channel and freshwater inputs from rivers such as the Thames and Scheldt (Ivanov et al. 2020). The overall shallow area (maximum depth 91 m) is mainly characterized by sand banks, with seabed substrate being highly impacted by bottom trawling (Eigaard et al. 2017). Hard substrate habitats now mainly consist of man-made structures, such as ship wrecks and wind turbine foundations (Wright et al. 2020). The southern North Sea falls within the exclusive economic zones of the United Kingdom (UK), The Netherlands, Belgium and France and is heavy in anthropogenic impacts (e.g. climate change and overexploitation), whereby the North Sea fish community has undergone pronounced spatiotemporal changes in composition (Beukhof et al. 2019). Regarding fisheries management and assessment, seabass in the North Sea are classified into the Northern stock (central and southern North Sea, Irish Sea, English Channel, Bristol Cannel and Celtic Sea; ICES divisions 4b,c, 7a,d-h) (Fig. 6.1) (ICES 2020b). The other stocks in the Northeast Atlantic consist of North Spain and Portugal (southern Bay of Biscay and Atlantic Iberian waters; ICES divisions 8c,9b), the Bay of Biscay (northern and central

Bay of Biscay; 8ab) and West coast Scotland and Ireland (West of Scotland, West of Ireland and eastern part of southwest of Ireland; 6a,7b,j) (ICES 2012a).

Tagging

Tagging data originated from different projects over different time spans, using different methods of conventional and electronic tagging (Table 6.1, details on tag settings in Supporting information S6.1). Fish were caught from boats or from shore at different locations along the Belgian, British, Dutch and French coast in the southern North Sea (Fig. 6.1). Seabass were captured with hook and line, gillnets and fykes, and one seabass was caught with a longline. For angling, mostly artificial bait was used (plugs and shad lures), except for some offshore and estuarine locations where live bait was used (ragworms, lugworms and crabs. Between 2006 and 2021, 5598 seabass were fitted with Pederson discs (9.5 mm diameter; Floy Tag & Mfg. Inc., USA) along the Belgian coastline with the majority of captures coming from the Port of Zeebrugge. Electronic tags were surgically inserted in the abdominal cavity (Fig. 6.2). Data storage tags (DST) of the type Cefas G5 2Mb DST with a floatation collar (Cefas Technology Limited, UK) were used on 150 seabass caught off the French coast of Dunkirk in June 2014 and on 64 seabass caught in English waters along the coast of Suffolk in May 2015 and 2017. Acoustic tags of the types V9P, V13, V13AP and V16 (69 kHz, MAP114, protocol A69-9006; Innovasea Ltd., USA) were used on 22 seabass in Belgian waters between June 2018 and September 2020 and on 214 seabass in Dutch waters between May 2021 and September 2022. Acceleration sensor measurements of the V13AP transmitters were not used, as this information was outside of the scope of this study. Acoustic data storage tags (ADST; ADST-V9TP: 69 kHz, MAP114, protocol A69-9006; Innovasea Ltd., USA) were used on 109 bass in Belgian waters between 2018 and 2021. Seabass were tagged in coastal locations (less than 6 nautical miles from the shoreline) in Dutch, English, French and Belgian waters, as well as in offshore locations in Belgium (acoustic and ADST). Tagging was performed in accordance with the guidelines for animal experiments for the relevant national authorities under the ethical certificate and license numbers 01987.02 (France), EC2017-080 (Belgium), PPL 70/7734 (UK), AVD401002016613 and AVD40100202114609 (The Netherlands). Tagging procedures were explained in full detail in other publications that used these data sets (de Pontual et al. 2023, Goossens et al. 2023, Edwards et al. *in review*).
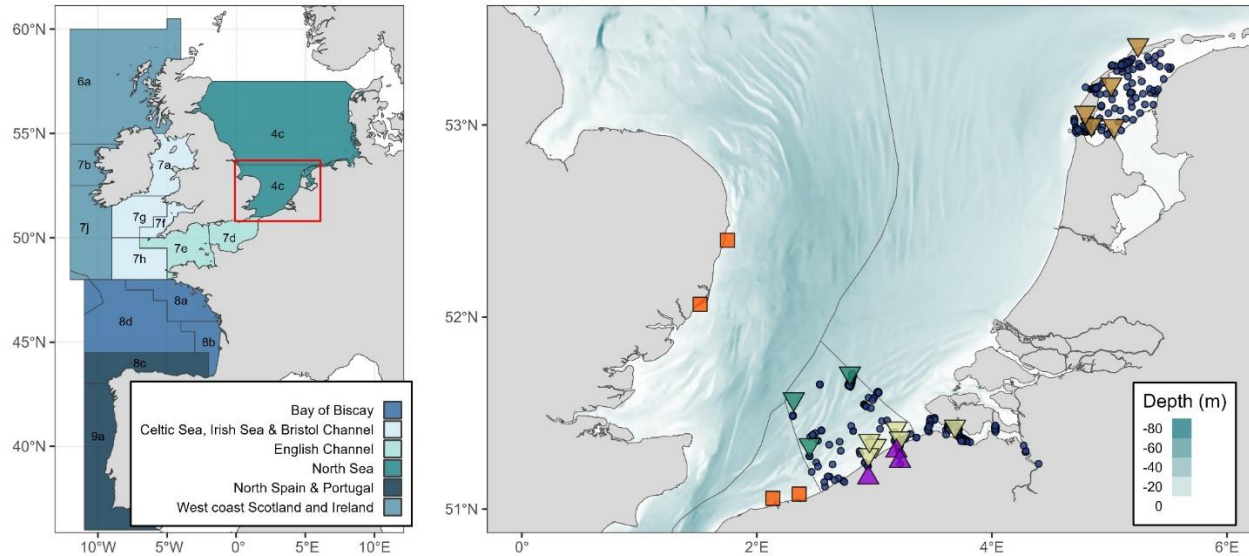
Figure 6.1. Left: Distribution of seabass population in Northeast Atlantic with current ICES stock division: the Northern Stock (central and southern North Sea + English Channel + Celtic Sea, Irish Sea and Bristol Channel: 4b,c, 7a,d-h), the stock of West coast Scotland and Ireland (West of Scotland, West of Ireland and eastern part of southwest of Ireland: 6a, 7b,j), the Bay of Biscay stock (northern and central Bay of Biscay: 8a,b. Note that 8d was also marked in blue, but is strictly seen not included in stock) and the stock of North Spain and Portugal (southern Bay of Biscay and Atlantic Iberian waters: 8c, 9a). Right: Map of tagging locations (purple: external tags; orange: DST; brown: acoustic, Wadden Sea; light yellow: ADST / acoustic, Belgian coast & Scheldt Estuary; dark green: ADST / acoustic, offshore) and acoustic receiver locations (blue dots) in the southern North Sea. Bathymetry data originate from the General Bathymetric Chart of the Oceans (GEBCO, 2014).

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Data collection differed between technologies. For the acoustic tags (including ADST), the tag ID and sensor information was transmitted (69 kHz, MAP114, protocol A69-9006) to acoustic receivers (VR2W, VR2AR and VR2Tx; Innovasea Ltd., USA) of permanent and temporary networks in the study area (Reubens et al. 2019b, Edwards et al. *in review*). From previous range testing in the Belgian part of the North Sea (BPNS), the median detection range distance (with 50% probability of observing the presence of a tagged seabass within a day's time) was estimated at 566 m (Goossens et al. 2022). Acoustic data and metadata was managed through the online database of the European Tracking Network (ETN; https://lifewatch.be/etn/), enabling direct access to detection data on other receiver arrays included in ETN. At the time of writing, detection data from fish tagged in the Wadden Sea were still being collected and were under limited disclosure. This dataset was therefore limited to a subset of the detections up to 30 April 2022 of 31 individuals which were detected by arrays outside of the Wadden Sea. For conventional tags, we relied on voluntary reporting by people encountering the marked fish (mainly fishers), who were asked to report the ID, date and location of recapture (and if possible: the length and weight of the recaptured seabass). To access archival sensor information, DST and ADST had to be recovered. To increase the recovery, floatable tags were used that could drift ashore if separated from the fish. For both conventional and archival tags, tag return was incentivized with rewards, ranging from 2 to 100 euro depending on the project and tag type. The tagging experiments of the different projects were publicised through various media, including posters, flyers, emails to fisheries and stakeholders, and articles in (mainly angler specific) websites and magazines.

Table 6.1. Number of seabass (N) and their length (median [range]), tagged with different tag types in different tagging areas.

Tag type	Tagging area	N	Length (cm)
Pederson discs	BE coast	5598	31.5 [9.0 – 81.0]
DST	FR Dunkirk	150	51.7 [43.2 – 69.1]
	UK Suffolk	64	58.5 [49.0 – 76.0]
Acoustic	Wadden Sea	31	51.6 [40.0-75.0]
Acoustic + ADST	PBARN coast	79	46.0 [34.0 – 74.0]
	PBARN offshore	52	47.0 [33.0 – 57.0]

Figure 6.2. Left: Pederson disc attached externally between dorsal and caudal fin. Right: Surgical insertion of an electronic tag (i.c. acoustic data storage tag) in the abdominal cavity.

Data processing

For the mark-recapture data, we calculated the distance between the release and recapture position, as well as the number of days between the two events. Some observations could not be used for these calculations, as they were communicated vaguely in terms of time (e.g. the month or year of recapture) and location (e.g. the EEZ). Telemetry data were analysed after a quality check. If an animal was detected only once on a receiver array, that detection was considered unreliable and hence removed. For long distance movements (more than 100 km distance between subsequent detections), we evaluated whether the movement was feasible (e.g. a single detection implying a movement of more than 100 km distance both back and forth within the same day was removed). A residence index (RI) was calculated to quantify daily presence in the North Sea and in the tagging area (Wadden Sea, coastal BPNS or offshore BPNS). If a seabass was detected at least once in a day, that day was considered as a detection positive day (DPD). RI was then calculated as the number of DPD out of the time at large, the period from the tagging event to the end of the battery lifetime or recapture of the fish. For some of the archival depth series, we could see that the depth sensor experienced drift, whereby depths strayed from a minimum of 0 m. To correct for depth drift, time series were processed by using a running minimum over a 7 day period.

For all tagging techniques, a fish was considered to exhibit fidelity to the North Sea if it was observed (through recapture, acoustic detection or trajectory reconstruction, see below) there at least 180 days (six months) after the

tagging event. For acoustic tags, we also calculated site fidelity to the area of tagging (Wadden Sea, coastal BPNS or offshore BPNS).

Geolocation

From archival data, trajectories were reconstructed with geolocation modelling using a hidden Markov model (HMM). As the model was fully described in previous publications (de Pontual et al. 2023, Goossens et al. 2023), we limited the explanation here to the alterations made. The choice of temperature reference field was based on the necessary spatial extent of the estimated trajectory. The 3D Dutch continental shelf model in flexible mesh (3D DCSM-FM) had a high spatial resolution (North Sea and coastal waters: 0.5' x 0.75', English Channel: 1' x 1.5'; latitude x longitude) (Zijl et al. 2021), but a limited spatial range (48.8°N-53.0°N, 3.2°W-5.0°E). The Atlantic Ocean Physics Reanalysis for the European North West Shelf (CMEMS-NWS Physics) model had a greater spatial range (which we limited to 44.0°N-56.0°N, 7.0°W-7.0°E), but a lower resolution (0.067° x 0.111°, latitude x longitude). 3D DCSM-FM temperature data were available for the years 2014-2016 and 2018-2020, whereas CMEMS-NWS Physics data were available for all years (since 1993) up to 30 June 2022 at the time of writing. If the spatiotemporal range of the trajectory allowed for it, we opted for the higher resolution model 3D DCSM-FM and otherwise we used CMEMS-NWS. The 3D DCSM-FM included bathymetry data, but we used the General Bathymetric Chart of the Oceans (GEBCO, 2014; resolution 0.5' x 0.5'). For the ADST resulting in both acoustic detections and archived sensor information, the detection likelihood was included (Goossens et al. 2023). Using the archival depth series, daily activity states were identified as low or high activity using a HMM (Heerah et al. 2017). The activity state identification was evaluated by visually checking in the archival depth series whether the low activity state did not include high activity vertical movements. If the states were considered reliable and if the model converged, the behavioural switch was included in the model (Pedersen et al. 2008, de Pontual et al. 2023).

We calculated trajectories as the most probable sequence of positions from the daily posterior probability distributions, using the Viterbi algorithm. Goossens et al. (2023) showed the estimation of seabass tracks performed with a median accuracy of 21.4 km (maximum 134.7 km) of daily position estimates.

As an additional validation, we calculated the distance between the daily position estimates of the Viterbi track with those of the maximum posterior mode and mean posterior tracks, as detailed by Woillez et al. (2016). A track was considered reliable if the median error was below 50 km and the maximum below 120 km (respectively the average errors for demersal and pelagic fish geolocation models (Gatti et al. 2021)). Tracks with median errors over 50 km or maximum error between 120 and 240 km were not visualized spatially, but they were included in temporal representation (see below).

Data visualisation

Data from all tagging techniques were visualized on a spatial and temporal dimension. To distinguish a relevant seasonal component, we explored data from all techniques in monthly time frames to determine which months were similar in space occupancy. Based on these explorations, we grouped observations into the seasonal component December – February, March – May, June – August and September – November. Recaptures with both date and location information were visualized as recaptures per season on a map. Acoustic detections of every tag ID were visualized over time in an abacus plot. Spatial visualizations of the acoustic telemetry data included a map with the locations of detections, as well as seasonal spatial network maps. For the latter, stations were grouped to calculate the number of detected animals and the counts of directed movements between different areas (Jacoby et al. 2012).

The daily position estimates derived from geolocation modelling of the archival data, were overlaid on ICES divisions to define whether a seabass was in the area of the North Sea (4b,c), the English Channel (7d,e), the Celtic Sea (7a,f,g,h) or the Bay of Biscay (8a,b,d). If the daily position estimate from the Viterbi track was located in another area than the estimate of the maximum posterior mode or the mean posterior track (see above), we considered the area of location of a seabass for that day as unknown. We visualized examples of archival depth and temperature series, as well as the depth and temperature experience (median, 50% and 95% confidence intervals) per area. An abacus plot visualised the daily area estimates over time for every tag ID. Daily position estimates of tracks (with median error was below 50 km and the maximum below 120 km, see above) were spatially visualised per season and per identified migration strategy.

Aside from the geolocation model, which was run in Python 2.7 (Van Rossum & Drake Jr 1995), all analyses and visualizations were performed in R software (R Core Team 2022).

RESULTS

Mark-recapture

Out of 5598 marked seabass, 146 were recaptured (2.6 %), whereby both date and location information was provided for 136 recaptures. The time period between capture and recapture (known for 137 seabass) ranged between one day and nearly four years (1,392 days) with a median of 285 days. Positions of recapture (n = 136, Fig. 6.3) showed 102 seabass (75.0 %) were caught within a range of 5 km of the release location. Another 22 seabass (16.2 %) were recaptured within 100 km distance within the BPNS, the Scheldt Estuary or Dunkirk. Twelve seabass (8.8 %) were observed to have roamed more than 100 km distance away within the southern North Sea, the English Channel and just south of the 48th parallel in the Bay of Biscay. Out of 84 seabass with at least 6 months at large, 76 were recaptured within the North Sea (90.5%).

Acoustic detections

Out of 162 tagged seabass, 137 were detected for a total of 864,730 detections on 246 receiver stations (Fig. 6.4). Two fish died shortly after tagging and one tag experienced a hardware issue preventing acoustic signal transmission. These tags were excluded from the analysis. Fidelity to the North Sea was observed for at least 85 animals (62.0% of detected seabass, 53.5 % of tagged seabass), whereby only three fish tagged in the Wadden Sea effectively returned to the same area (9.7 %) (Table 6.2). The highest residency was observed for fish tagged in Belgian coastal waters (median RI of 0.18 and 0.21 to the tagging area and North Sea, respectively). Lower values for RI were found for fish tagged offshore and in the Wadden Sea (median 0.01 to 0.04), but some fish were detected in the North Sea for approximately half of their time at large. Since large areas of the North Sea fell outside of the detection range of acoustic receiver stations, these values of RI should be regarded as underestimations. Fish tagged in the Wadden Sea were detected in offshore and coastal stations of the PBARN, but fish tagged in the BPNS or Scheldt Estuary were never detected in the Wadden Sea (Fig. 6.5). Fish tagged along

the Belgian coast were detected on offshore stations, but only two seabass tagged offshore were detected along the coast. Five individuals (n_{BE} = 3, n_{NL} = 2) were detected along the English coast in the English Channel between February and July, on a network that was active since 2021 (Fish Intel project). The pressure sensor measurements had a median of 7.8 m, with a maximum of 62.0 m registered in the English Channel. Temperature sensors registered a median of 15.2 °C, with the minimum and maximum values of 2.8°C and 28.4°C both registered in the secluded port area of Zeebrugge (discussed in more detail in Goossens et al. 2023).

The largest numbers of seabass were detected from June to August (n = 92) and from September to November (n = 117) (Fig. 6.6), which were also the months when the majority of seabass was tagged. Seabass were observed to move around between Dutch, Belgian and English receiver arrays mostly in the periods of March – May and September – November, with no large-scale movements registered within the periods of June – August and December - February. The lowest number of animals (n = 45) was detected from December to February, when most seabass was observed to have stayed at the port of Zeebrugge (n = 14), as well as around offshore wrecks and wind farms. From March to May, seabass (n = 80) were detected across the widest spatial range from the Wadden Sea to the western English Channel. The individuals detected in the western English Channel (n = 3) were never detected in the eastern English Channel, and vice versa (n = 2). Wadden Sea stations registered seabass throughout all seasons, except for December – February.
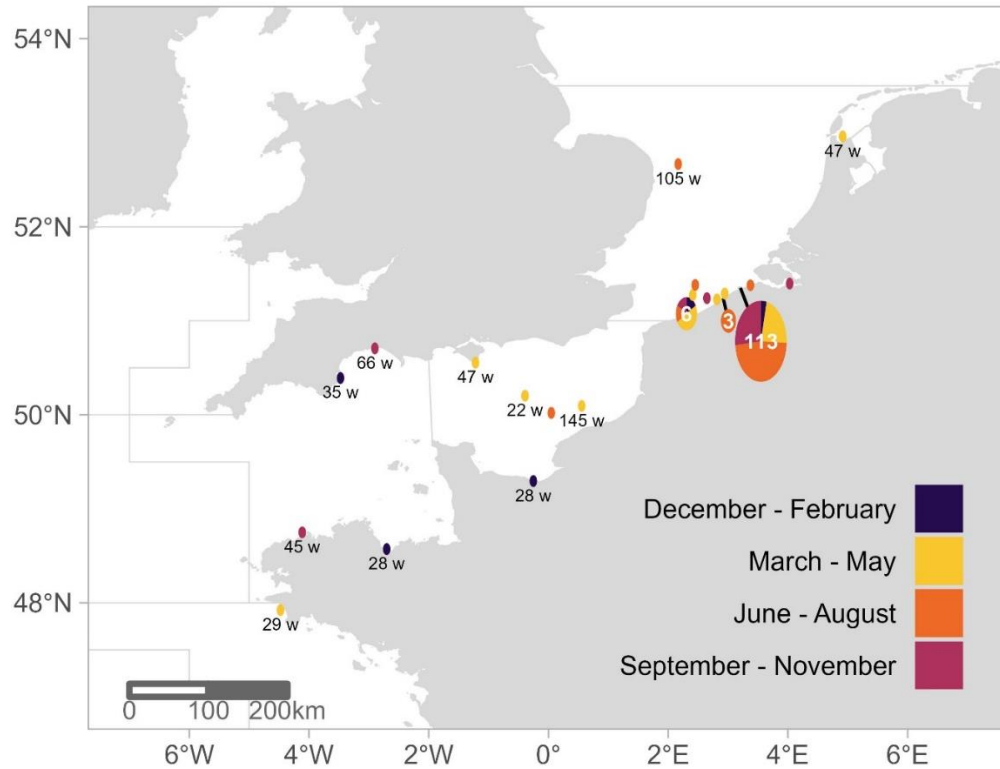
Figure 6.3. Recapture locations of marked seabass recaptures (n = 136), coloured by period of recapture. For long distance recaptures (for which the exact recapture date was available), the time at large was displayed in number of weeks (w).

Table 6.2. Acoustic telemetry results of site fidelity (seabass exhibiting fidelity out of the total number of detected animals), number of detection positive days (DPD, median [range]) and residency index (RI, median [range]) at receiver stations within the tagging area (TA) or the North Sea (NS).

TA	Fidelity -TA	Fidelity - NS	DPD - TA	DPD - NS	RI - TA	RI - NS
BE Coast	46/70 (65.7 %)	46/70 (65.7 %)	67 [1-366]	71 [1 – 366]	0.18 [0.00 – 0.92]	0.21 [0.00 – 0.92]
BE Offshore	20/36 (55.6 %)	21/36 (58.3 %)	21.5 [1 – 199]	24.5 [1 – 199]	0.05 [0.01 – 0.20]	0.05 [0.00 – 0.47]
Wadden	3/31 (9.7 %)	18/31 (58.1 %)	4 [1 – 109]	14 [1 – 111]	0.01 [0.00 – 0.32]	0.04 [0.00 – 0.33]
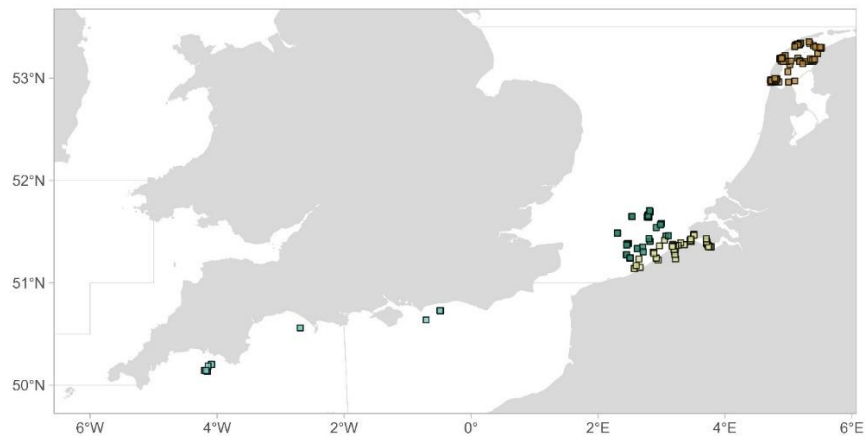
Figure 6.4. Locations of acoustic receivers with seabass detections, coloured by location (brown: Wadden Sea, light yellow: coastal PBARN, dark green: offshore PBARN, light blue: English Channel).

Figure 6.5. Abacus plot of acoustic data depicting a time line for individual tagged fish with the release (diamond) and detections (square) coloured by detection location (brown: Wadden Sea, yellow: coastal PBARN, green: offshore PBARN, light blue: English Channel). Fish were tagged from 2018 to 2022 and for each fish the detections were temporally aligned between tagging surveys using March 1 of the tagging year as a time reference.

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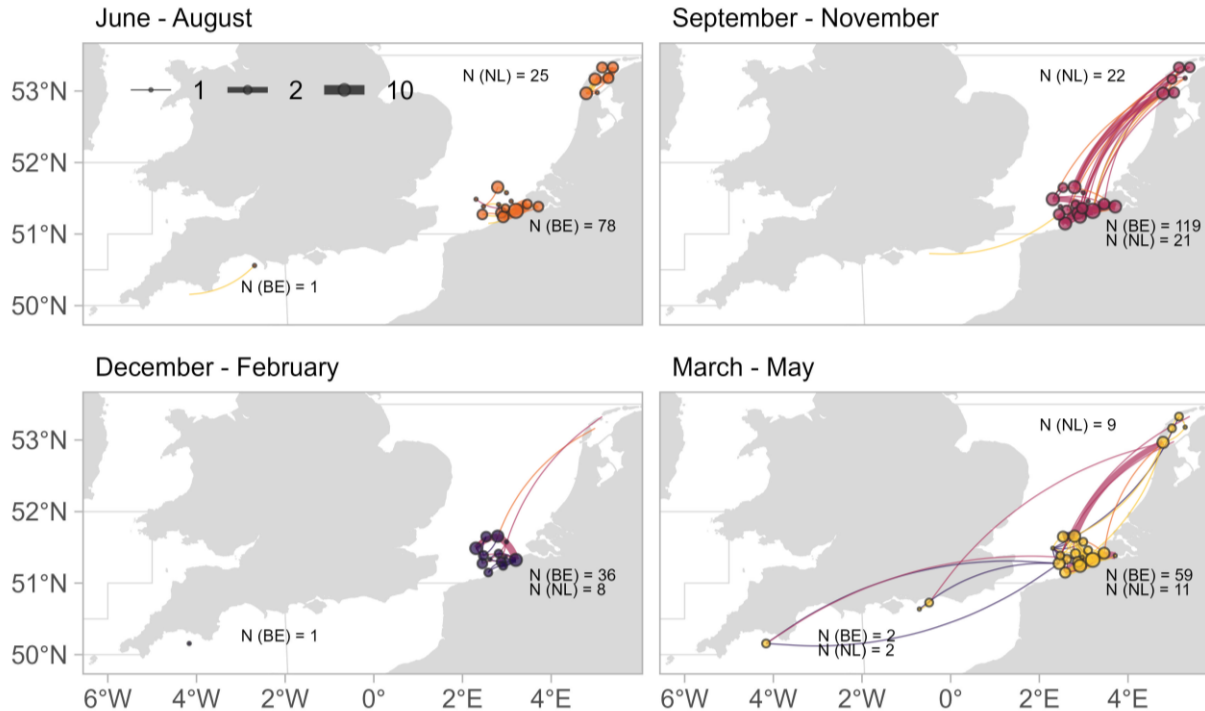
Figure 6.6. Spatial network maps for different periods: June – August (orange), September – November (pink), December – February (purple) and March – May (yellow). Nodes represent grouped receiver locations, are sized by the number of detected animals (n) and coloured by the period of detections. Edges represent frequencies of movement between receivers (right-hand curved from origin to destination receiver station) and are coloured by the period of detection at the origin station.

Archival data

The geolocation could be performed on 76 retrieved archival tags (n_{FR} = 48, n_{UK} = 18, n_{BE} = 10). Within the period that fish were evaluated to be alive, archived temperature measurements ranged between 4.3 and 32.3 °C, with a maximum depth of 173.5 m. The geolocation failed to converge for one tag and resulted in unreliable trajectories for six tags, producing 69 trajectories with a median of 330 days (range 33 – 734 days). The higher resolution 3D-DCSM reference field could be applied to 31 data series, with the remaining 38 requiring the larger spatiotemporal range of the CMEMS-NWS model. Behavioural switching could be applied to 17 tracks (24.6%). Eight out of ten recovered ADST rendered acoustic data, for which a detection likelihood was included. The warm temperature signal of power plant cooling waters was observed for 20 fish (28.6%), that spent a median 18 days in a warm water plume (range 4 – 235 days) (Fig. 6.7). Two fish experienced periods of high temperature variability in very shallow waters (Fig. 6.7), which we attributed to summer occupancy of inshore waters. Since the high variability of the temperature signal was not adequately represented in the temperature reference field, we only used the part of the data series before this behaviour for the geolocation. Out of the 69 estimated trajectories, 62 had sufficiently low error (distance between Viterbi track and mean or modal track: median 4.61 km, maximum 116.0 km) for spatial visualization (Fig. 6.8), but the remaining 7 were included in the temporal visualization (Fig. 6.10).

Seabass position estimates (n = 62) were located in the southern North Sea up to 52.9° N, the English Channel, the Celtic Sea and the Bay of Biscay up to 46.6° S (Fig. 6.8). From June to August (the period the majority of fish were tagged), seabass were mainly located in the North Sea and along the coast of the eastern English Channel. From September to November, seabass were widely distributed with high prevalence in the entire English Channel. From December to February, seabass were in the English Channel, as well as in the Celtic Sea and in offshore waters of the Bay of Biscay. Seabass also resided in the North Sea during winter in inshore waters in a port area and cooling waters, as well as deeper spots off the English coast of Norfolk and Suffolk (around 52.5°N, 2.0° E). From March to May, seabass were mainly in the western English Channel around the Cotentin peninsula and Channel Islands, as well as in the North Sea.

Depth and temperature experiences varied in time and space (Fig. 6.9). In all areas, seabass went to greatest depths during winter. In the North Sea, median temperatures were below 9°C from January to March. Temperature variance in the North Sea and English Channel was greater than in the Celtic Sea and the Bay of Biscay, but the greatest differences in temperature were found by seabass in cooling waters. Here, individual seabass would experience a median daily temperature change of 5.6°C (with a maximum of 16.5°C of temperature difference within one day), when entering/exiting the warm cooling waters.

From the 47 fish with data series of at least 6 months, 21 (44.7%) exhibited fidelity to the North Sea (Fig. 6.10). Remarkably, all of the fish tagged along the French coast of Dunkirk with longer data series left the North Sea (between August and December). Seabass tagged in the UK and Belgium either stayed in the North Sea or headed to the English Channel, with two fish going as far as the Celtic Sea. Migrations to the Bay of Biscay were limited to the seabass tagged in France (n = 8). Four different migration strategies or destinations were discerned for the seabass with data series over 90 days (n = 53) (Fig. 6.11): staying in the North Sea (n = 21), migration towards the eastern English Channel (n = 8), the western English Channel (n = 15) and towards the Celtic Sea and Bay of Biscay (n = 9). From the latter, four seabass returned to the North Sea, whereby the others went to the Bay of Biscay in winter, heading towards the southern coast of the English Channel in summer and five seabass returning to the Bay of Biscay in winter. The largest estimated travelled distance was over 3,000 km (Table 6.3).
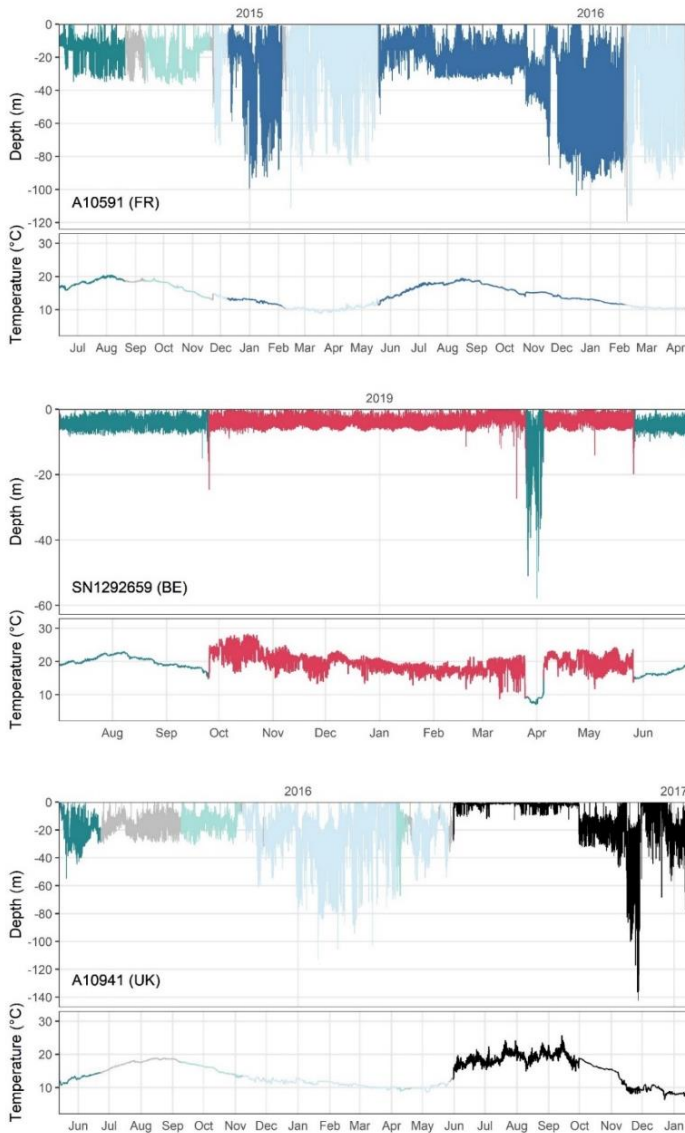
Figure 6.7. Exemplary time series of archived depth and temperature sensor measurements, coloured by the location of the daily position estimate (dark green: North Sea, light green: English Channel, light blue: Celtic Sea, dark blue: Bay of Biscay, red: cooling waters, grey: unsure, meaning daily position estimate of Viterbi track and mean or modal track were not in same area): an example of a seabass undertaking a migration (top), overwintering in cooling waters (middle) and showing shallow water occupancy with high temperature variability (bottom). For the latter, the black coloured data series were removed to estimate the trajectory.
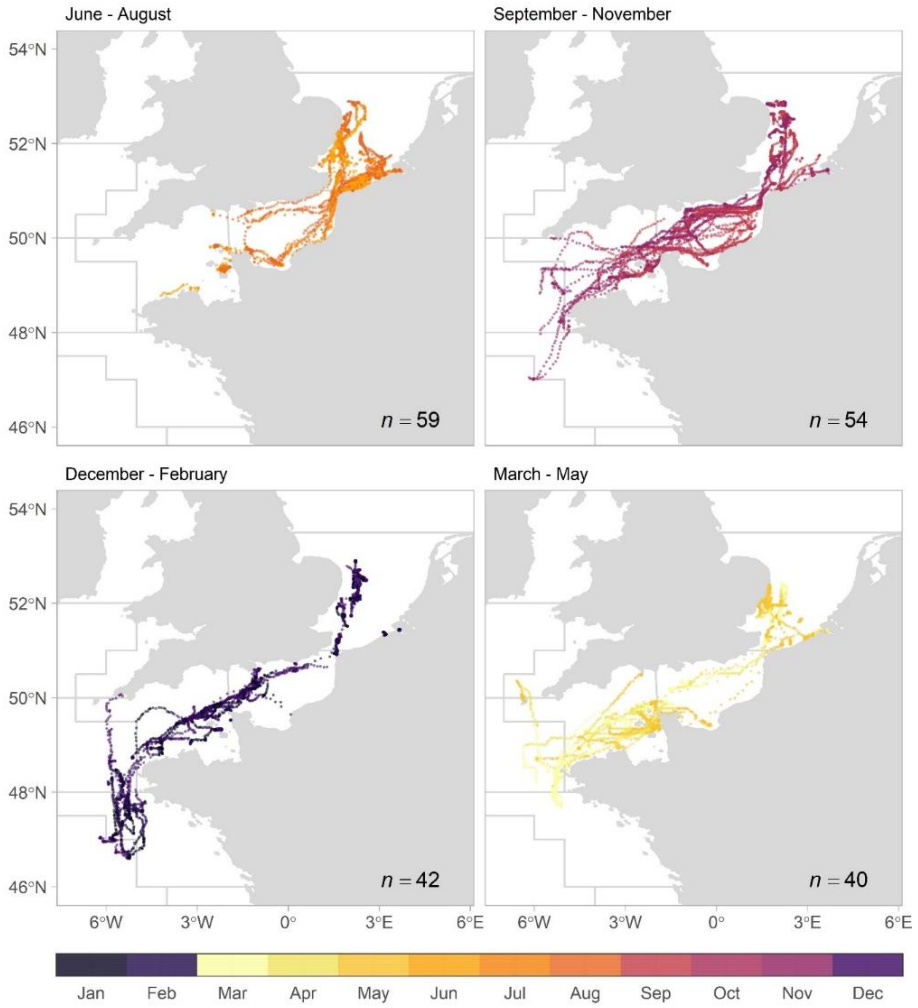
Figure 6.8. Daily position estimates of geolocated tracks of seabass (n = 62), coloured by month.
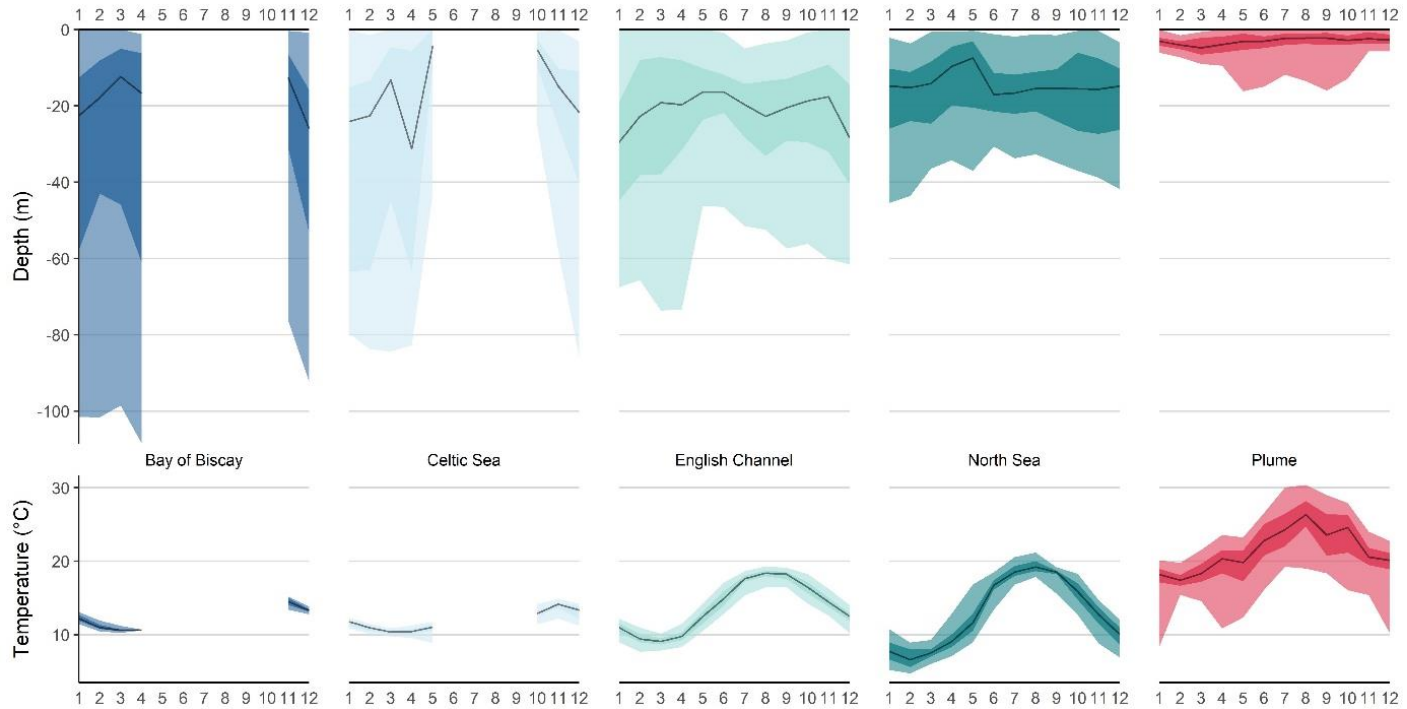
Figure 6.9. Plots of depth and temperature experience (black line: median; light and darker colouring: 95% and 50% confidence intervals, respectively) per month (x-axis), as experienced by seabass (n = 69) in different areas (dark green: North Sea, light green: English Channel, light blue: Celtic Sea, dark blue: Bay of Biscay, red: cooling waters).
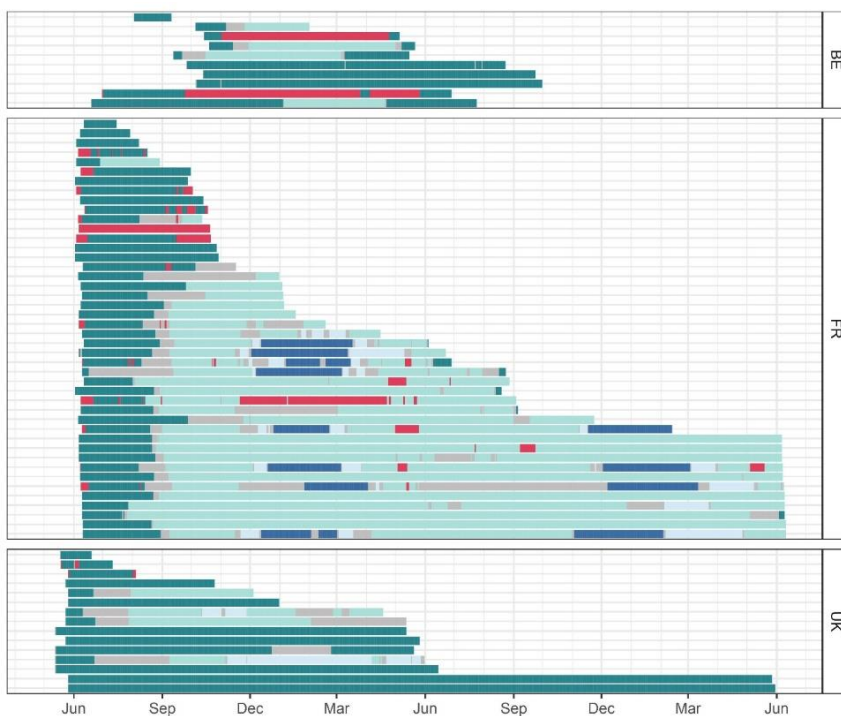
Figure 6.10. Abacus plot of archival data depicting a time line for the daily position estimates for individual tagged fish (n = 69), coloured by location (dark green: North Sea, light green: English Channel, light blue: Celtic Sea, dark blue: Bay of Biscay, red: cooling waters, grey: unsure, meaning daily position estimate of Viterbi track and mean or modal track were not in same area).

Table 6.3. Overview of the migration strategies with the number of seabass (n) and the individuals' distance travelled (km), estimated diffusion coefficient (D, km^2/day), experienced depth (m) and temperature (°C) displayed as median [range].

Strategy	n	Distance (km)	D (km^2/day)	Depth (m)	Temperature (°C)
North Sea	21	580 [208 – 1732]	5.5 [2.0 – 30.0]	6.9 [0 – 70.1]	15.0 [4.3 – 28.3]
English Channel E	8	840 [519 – 2663]	29.8 [16.1 – 90.0]	24.7 [0 – 90.5]	16.2 [6.9 – 20.8]
English Channel W	15	1582 [1024 – 2000]	30.0 [6.0 – 62.4]	19.8 [0 – 173.5]	14.5 [6.5 – 29.3]
Celtic Sea - Bay of Biscay	9	2496 [1648 – 3089]	61.2 [30.0 – 91.0]	17.3 [0 – 123.6]	14.1 [8.1 – 29.7]
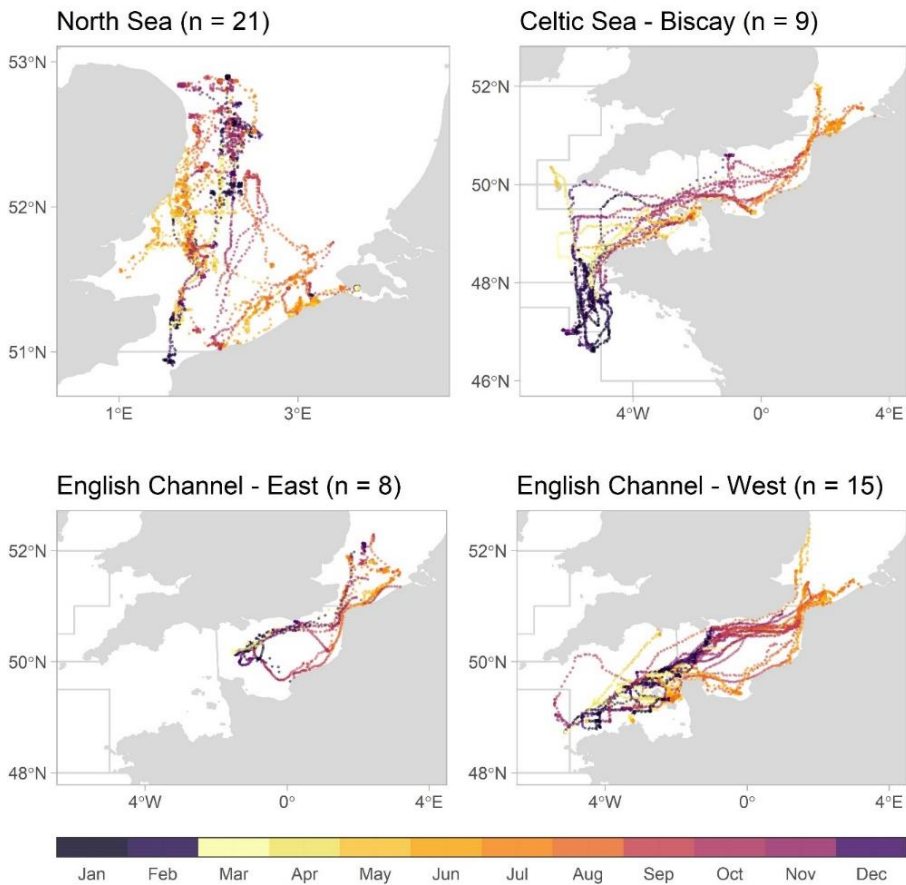
Figure 6.11. Maps of different migration strategies for seabass with data series over 90 days (n = 53), with daily position estimates coloured by month.

DISCUSSION

European seabass, tagged in the southern North Sea, were observed to inhabit an area from the southern North Sea to the northern Bay of Biscay (west of Brittany). In summer, seabass resided in the North Sea and along the coast of the English Channel. For the rest of the year, seabass were spread across the entire area, with high movement activity from September to November. Seabass from the Wadden Sea headed southwards to the Belgian EEZ and the English Channel, but the opposite movement was registered for only one individual (mark-recapture data). Several seabass from the tagging areas in Dunkirk and Belgian waters that headed northwards, went towards offshore

areas and coastal waters of Suffolk and Norfolk. Fidelity of seabass to the North Sea was seen for almost half of archival tags and more than half of acoustic tags.

Different geolocated trajectories of seabass, mainly of those staying in the North Sea throughout the year, were drawn to a deep location near the coast of Norfolk and Suffolk in the UK. Trajectories passed through this location throughout the year, with a seabass recapture (marked with a Pederson disc) in the summer of 2021 (Fig. 6.3). Since it's not known what a seabass spawning event looks like in terms of vertical movement behaviour (Heerah et al. 2017), tagging data alone wouldn't suffice to determine whether seabass spawn in the North Sea. Nonetheless, the observation of seabass eggs in the North Sea in 2011 (Tulp et al. 2016) proved it was possible. The temperature sensor measurements indicated North Sea spawning would have only been feasible from April onwards, since temperatures below 9°C would hamper female seabass gonad development (López et al. 2015). To better understand seabass behaviour in the North Sea, the location off the English coast of Norfolk and Suffolk (around 52.5°N, 2.0° E) would be a key position for an acoustic receiver array.

The individual dimension of seabass movements

Our results highlighted the importance of taking into account individual differences, as we observed different migration trajectories. The different strategies begged the question why a seabass would migrate over 3000 km when conspecifics travelled hundreds to thousands of kilometres less. Dambrine et al. (2021) showed that environmental covariates served as poor predictors for seabass spawning aggregations, indicating other mechanisms are at play, such as natal homing or learned behaviour. Natal homing would mean seabass return to the area where they hatched as an egg (Le Luherne et al. 2022), whereas they would follow other (older) adults if driven by learned behaviour (Petitgas et al. 2006). Migrations to the northern Bay of Biscay and the Celtic Sea (n = 11) were performed by seabass tagged in 2014 and 2015 (in French and UK waters), whereas fish tagged from 2016 onwards (n = 11) stayed in the North Sea or migrated to the English Channel. Potentially, seabass used to travel more southwards, but migrated less far in more recent years. Increased temperatures in the past decade may have made habitats

closer to home more suitable as spawning areas (Petitgas et al. 2013). Another explanation may be that the knowledge on southward migration routes was lost as a result of high fishing pressure that locally depleted seabass schools, including the older individuals who 'knew the way' (Petitgas et al. 2006, Doyle et al. 2017). If natal homing was at play, it could have been the case that recruitment to the North Sea from spawning aggregations in waters west of Brittany was poor in past years due to hydrodynamic conditions (Beraud et al. 2018), and that adult seabass in the North Sea in more recent years originated from spawning migration strategies closer to the North Sea.

Out of 36 bass tagged offshore (more than 6 nautical miles from the coast), we observed few of them along the coast. Three seabass were observed (two fish detected acoustically and one through its reconstructed trajectory) in coastal waters of the North Sea and another three were detected in coastal waters of the English Channel. Up until now, seabass tagging research always involved individuals captured in coastal locations (Doyle et al. 2017, O'Neill et al. 2018, Stamp et al. 2021, de Pontual et al. 2023). The generally assumed movement pattern of seabass - spawning in offshore locations during winter, but heading towards the coast in summer – may therefore have been biased by the logistical preference for coastal tagging locations. Ongoing tagging efforts in offshore locations (in the context of the Fish Intel project) will elucidate if seabass from offshore areas exhibit significant connectivity to the coast or if they undertake distinctly different movements than coastal seabass.

Complementary tagging techniques

The description of seabass migration patterns in this manuscript greatly benefited from applying different tagging techniques. The continuous data series from the DST allowed for the geolocation of entire trajectories, with the drawback that the modelled positions remained estimates rather than observations. Experts must therefore remain critical of the results of the geolocation model, which are useful, but cannot be considered as true paths. Acoustic data allowed to investigate fish movement in coastal areas where temperature reference fields might fail (e.g. the two fish with high temperature variability in inshore waters, Fig. 6.7). Acoustic data could validate trajectories of fish, either directly for which both data types were available (Goossens et al. 2023), or by corroborating the possibility of certain migration headings and

destinations. The latter was also true for conventional tags: Even though mark-recapture provides less data on a lower number of tagged fish (2.6% recaptures in this study and e.g. 4.5% reported by Pawson et al. (2007)), these data were highly valuable for ground-truthing model outcomes. Moreover, the mark-recapture project involved the collaboration of volunteer anglers who promoted the research in their networks, which we considered to have contributed to the notification of recaptures of both conventional and electronic tags.

Implications for fisheries management

The findings of this study are relevant for fisheries management and stock assessment. European seabass of the Northern stock experienced critical declines in the past fifteen years due to high fishing pressures and poor recruitment (ICES 2022b). The current stock delineation originated out of management practicalities, because of lacking biological information to substantiate stock structure (ICES 2012a).

Our data contested previous indications that the North Sea might consist of a separate unit (Pawson et al. 2007), although many seabass were seen to reside in the North Sea throughout the year. Eight seabass from the southern North Sea were shown to cross the boundaries of the Northern stock into the range of Bay of Biscay stock, although these migrations were not observed in recent years. The variation in individual migration strategies supported a high degree of fine-scaled population structuring, with previous research demonstrating the existence of separate entities (during the feeding season) distanced only few kilometres from each other (Goossens et al. *in review*). These migration strategies could be included in population dynamics and stock assessment models (Walker et al. 2020). Aside from optimizing existing models, this fine-scaled population structure should be accounted for when assessing the uncertainty of the relationship between fishing pressure F and stock biomass SSB (Alós et al. 2019). The effects of fisheries locally depleting groups of seabass and potentially erasing certain movement strategies on the stock unit or population as a whole remains poorly understood (Petitgas et al. 2006).

The individual variation in spatiotemporal habitat use should also be accounted for in fisheries management. Ever since 2016, EU fisheries measures include a seasonal closure for commercial seabass fishing in February and

March to protect spawning aggregations (EU 2016, 2023). Considering the different migration strategies, only a fragment of the population would be effectively protected during their spawning time by these measures. For seabass residing throughout the year in the North Sea, the seasonal closure would have to be in April and May. Moreover, the complexity in the structuring of the seabass population shows that these animals are not sufficiently understood to apply the principles of 'economic rationality' that seek to maximize yield (Ramesh & Namboothri 2018).

AUTHOR CONTRIBUTIONS

DATA AVAILABILITY STATEMENT

Data will be made available after publication through DOI.

ACKNOWLEDGEMENTS

SUPPORTING INFORMATION S6

Table S6.1 - Tag settings applied for external (Floy Tag & Mfg. Inc., USA), archival (CTL, UK), acoustic and acoustic data storage tag types (Innovasea Ltd., USA) for a number of tagged animals (N). Acoustic and archival tags transmitted and / or logged temperature (T), acceleration (A) and pressure (P) sensor measurements. The number of tags of each type was shown for ever. For estimated battery life, it should be noted that the ADST-V9TP was programmed to effectively stop transmitting after the set number of days, whereas the V13AP and V9P could continue transmitting as long as there was battery left. Signals were transmitted at predefined settings within a step of a fixed number of days at high (H) or low (L) transmitting power output between a minimum and maximum interval. Power output was 158 dB for V16, 152 dB for V13, 154 dB for V13AP, 151 dB for ADST-V9TP and 146 (L) or 151 (H) dB for V9P.

Tag type	Model	N	Country	Tagging period	Battery life (days)	Logging interval T–P(s)	Transmitting settings
External	Pederson disc	5598	BE	2006 – 2021	-	-	-
Archival	Cefas G5	150	FR	2014	730	90 - 90 (680 days); 180 - 180 (50 days)	-
	Cefas G5		UK	2014 – 2016	730	-	-
Acoustic	V13AP	11	BE	2018 - 2020	495	-	H 495 days (140 - 220 s)
		1	BE		198	-	H 30 days (30 - 60 s); H 168 days (140 - 220 s)
		5	NL	2021	278	-	H 278 days (50 – 100 s)
	V13	19	NL	2021	235	-	H 235 days (135 – 235 s)
	V16	8	NL	2021	1415	-	H 80 days (40 – 80 s)
	V9P	10	BE	2020	502	-	H 153 days (180 - 280 s); L 120 days (300 - 400 s); H 229 days (300 - 400 s)
Archival + Acoustic + External	ADST-V9TP Pederson disc	27	BE	2018 - 2019	354	180 - 90	H 90 days (240 - 360 s); H 150 days (120 - 240 s); H 104 days (240 - 360 s)
		40	BE	2018 - 2019	339	180 - 90	H 120 days (120 - 240 s); H 239 days (240 - 360 s)
		19	BE	2020 - 2021	400	180 - 90	H 120 days (180 - 200 s); H 280 days (300 - 400 s)
		23	BE	2020 - 2021	425	300 -90	H 70 days (180 - 280 s); H 355 days (300 - 400 s)

CHAPTER 7

USING ACOUSTIC TELEMETRY TO INVESTIGATE HABITAT USE OF EUROPEAN SEABASS IN THE SOUTHERN NORTH SEA

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ABSTRACT

The movement patterns of individual fish define population connectivity and population structuring. Knowledge on the movement behaviour of European seabass, *Dicentrarchus labrax*, is particularly scarce in the southern North Sea. We investigated seabass habitat use and connectivity in a study area comprising of the Belgian part of the North Sea (BPNS) and the Scheldt Estuary. From 2018 to 2021, 131 seabass were tagged with acoustic transmitters, that could be detected on a permanent receiver network in the study area, as well as on temporary arrays around artificial substrates. Seabass (n = 110) were detected across the entire study area up to the mesohaline estuarine zone. Individuals were mostly detected around their release location, with overall high site fidelity (n = 67, 63.2%) and with higher residency for seabass tagged along the coast (0.21) than in offshore areas (0.05). In terms of connectivity, three patterns were identified, whereby fish residing along the coast either stayed along the coast or headed offshore without ever being detected along the south-western coast. A third pattern was identified for seabass tagged at offshore locations, that mainly resided offshore and were never detected in the north-eastern coastal area. Seabass' highly localized behaviour, exhibited through high residency and individual variability in connectivity, demonstrated the complexity of population dynamics and the risk to local depletion.

INTRODUCTION

Movement is an essential aspect of ecology that enables organisms to make use of patchy and seasonally variable resources in different environments (Nathan et al. 2008, Lennox et al. 2019). Many marine fish migrate great distances between distinct habitats, e.g. for spawning or feeding (Secor 2015, Dambrine et al. 2021). Using these habitats differently, fish can display specific activity regimes (e.g. along circadian and tidal cycles) that vary among seasons, locations and individuals (Heerah et al. 2017, Spiegel et al. 2017). Individuals can be associated to specific locations to the extent that they exhibit long-term residency and interannual site fidelity to these areas (Kraft et al. 2023). Adding to the complexity, individual fish can vary in movement behaviour with some performing extensive seasonal migrations and others residing in an area throughout the year (de Pontual et al. 2019). Individual movement patterns are defining for the connectivity within species and thus characterize population structuring. As anthropogenic activities also operate at distinct spatiotemporal scales, information on movement ecology can inform conservation efforts.

In the Northeast Atlantic, the highly mobile European seabass (*Dicentrarchus labrax* L.) undertake seasonal migrations from summer feeding grounds along the coast and estuaries towards deeper offshore spawning grounds in colder months (Vázquez & Muñoz-Cueto 2014, López et al. 2015). Seabass occupy the pelagic and demersal parts of the water column and occur both solitary and in shoals (Anras et al. 1997, Quayle et al. 2009). Individuals can exhibit site fidelity to both feeding and spawning areas (Pawson et al. 2007, de Pontual et al. 2019, Stamp et al. 2021, Le Luherne et al. 2022). The localized behaviour of individuals implies a risk of local depletion of seabass targeted at specific locations by exhaustive fisheries activities (Pawson et al. 2008, Doyle et al. 2017).

The Northern stock (central and southern North Sea, Irish Sea, English Channel, Bristol Cannel and Celtic Sea; ICES divisions 4b,c, 7a,d-h) (ICES 2020b) and has not (yet) recovered from the declines in biomass due to high fishing pressure from the late 1990s to 2015 (ICES 2022b). Currently, seabass in this area is targeted by fisheries using lines and nets and is caught as bycatch by seines and bottom trawls. Next to commercial angling, seabass is a popular species

for recreational angling, which is estimated to account for nearly one fourth of fisheries biomass removals of the Northern stock (Radford et al. 2018, ICES 2022b). Since 2015, EU fisheries measures include a minimum landing size of 42 cm, commercial catch limitations, a recreational bag limit and a seasonal closure for commercial and recreational fishing (EU 2023). At the time of writing, the Northern stock seabass biomass is below the estimate for maximum sustainable yield (MSY $B_{trigger}$) (ICES 2022b).

Knowledge on seabass movement behaviour is particularly scarce in the southern North Sea. In our study area, the Belgian part of the North Sea (BPNS) and the Scheldt Estuary, information on seabass occurrence mainly derives from fisheries practices. Juvenile seabass occur in the upper reaches of the Scheldt Estuary (Brosens et al. 2015), with older individuals found in the lower part (Schnitzler et al. 2011, Tulp et al. 2016). Within Belgian waters, anglers target seabass from vessels, as well as from the beach (Verleye et al. 2022). Along the shore, high prevalence of (pre-)adult seabass has been described in port areas (Delbare 2012). Seabass is caught from the beach mostly during the summer months (Verleye et al. 2022), but offshore sand banks and artificial structures are considered seabass hotspots from April -May to September - November (Goossens, pers. comm.). Artificial substrates, such as offshore wrecks and wind farms, in the otherwise sandy surroundings of the southern North Sea, have been shown to attract different species (Reubens et al. 2013b, Wright et al. 2020), but a possible association of seabass to these structures remains undescribed.

Our research team was granted the opportunity to use a newly developed acoustic data storage tag (ADST), which promised to be a highly suitable technology to investigate seabass movement ecology in our study area at distinct spatial scales (Goossens et al. 2023). The archival depth and temperature series enabled the reconstruction of large-scale migrations (Woillez et al. 2016, Goossens et al. 2023), as described in detail in chapter 6. The tags also transmitted an acoustic signal that could be detected when a tagged fish was within the detection range of an acoustic receiver (Hussey et al. 2015). In this chapter, we used the acoustic telemetry feature to investigate European seabass movements in the BPNS and Scheldt Estuary. The objective of the study was to better understand patterns in presence, spatial connectivity

and habitat use, and thus to set a baseline of knowledge on seabass movement behaviour in this area of the southern North Sea.

MATERIAL & METHODS

Study area

The BPNS and Scheldt Estuary are part of the southern North Sea and are characterized by shallow (up to 40 m depth), subtidal sand banks with strong tidal currents (Ivanov et al. 2020). Hard substrate habitats consist mainly of artificial structures, like ship wrecks and wind turbines (Wright et al. 2020) The area is dense in anthropogenic activities, including fisheries, shipping, sand extraction and military exercises (Pecceu et al. 2016).

The study made use of permanent and temporary receiver arrays (Fig. 7.1). Acoustic receivers (VR2W, VR2AR and VR2Tx; Innovasea Ltd., USA) were installed as part of permanent networks with 107 unique receiver stations of the permanent Belgian acoustic receiver network (PBARN) (Reubens et al. 2019b) and the Belgian passive acoustic monitoring network (Chapter 5). In addition, temporary arrays were specifically purposed to investigate fish movements in the vicinity of artificial substrate, whereby receivers were installed on tripod moorings (Goossens et al. 2020). In this study, we specifically make use of arrays along the outer port walls of the Port of Zeebrugge, at an offshore radar tower, at the Garden City offshore wreck and in the southwestern area of the Belwind offshore wind farm. The active deployment period, as well as the number of receivers (1 – 28) of these temporary arrays varied over time (Fig. 7.5). More details on receiver deployment positions can be found in chapter 8 (Port of Zeebrugge), in Supporting Information S7.1 (Garden City wreck and radar tower), and in Buyse et al. (2023) and van der Knaap et al. (2021) (Belwind offshore wind farm).

Extensive range testing was carried out in the Belwind offshore wind farm, using the tripod frames. Telemetry analyses (see below) were performed using the resolution of single transmissions, hourly and daily time bins. These resolutions resulted in different detection ranges (transmitter-receiver distance with 50% detection probability of observing the presence of a tagged seabass under median environmental conditions within a set temporal

resolution): 402 m (single transmission), 502 m (hourly time bin) and 566 m (daily time bin) (Goossens et al. 2022).

Fish tagging

From 2018 to 2021, 131 seabass were tagged with transmitters of the type ADST-V9TP (109), V13AP (12) and V9P (10) (Table 7.1, Innovasea Ltd., USA). Commercial and recreational anglers captured the seabass using rod and line, except for one seabass caught with a longline (in the offshore wind farm). The majority of fish were caught using artificial bait (plastic lures and wobblers), except for some fish at the radar tower, offshore wind farm and estuary which were captured using live bait (ragworms, lugworms or crabs). Using a distance of 6 nautical miles as the delineation between coastal and offshore areas, 79 seabass (34.0 – 74.0 cm length) were tagged along the coast and 52 seabass (33.0 – 57.0 cm length) at offshore locations (Table 7.2). Transmitters were surgically inserted in the abdominal cavity. The tagging procedure is fully detailed in Goossens et al. (2023) and was approved under the ethical certificate EC2017-080. Detection data and metadata were managed through the online database of the European Tracking Network (ETN; https://lifewatch.be/etn/), enabling direct access to detection data on all receiver arrays.
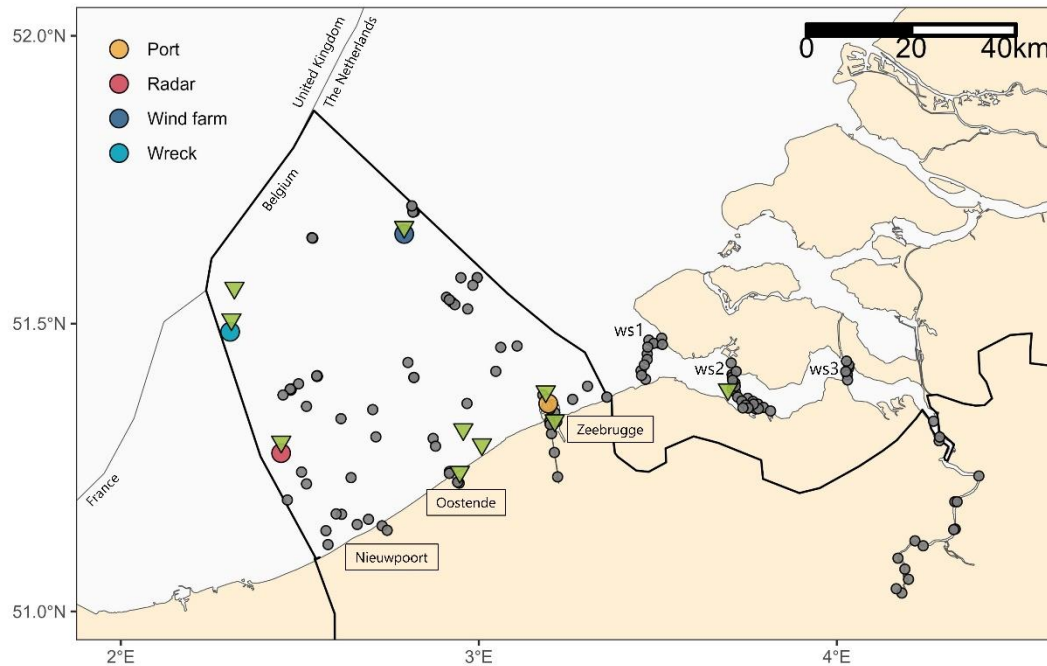
Figure 7.1. Map of the study area in the Belgian Part of the North Sea and the Scheldt Estuary with locations of fish release (green triangles) and acoustic receivers with active deployments during the study (grey circles). In the Scheldt Estuary, three bands of receivers stretch from shore to shore (ws1, ws2 and ws3). Temporary arrays were installed near artificial substrates at a port (dark yellow), an offshore radar tower (red), an offshore wreck (light blue) and an offshore wind farm (dark blue). Shape files originated from Marine Regions (https://www.marineregions.org/) and GRBgis (https://www.geopunt.be).

Table 7.1. Tag settings applied for different types of acoustic transmitters (Innovasea Ltd., USA) attached to a number of seabass (N). Sensor measurements of temperature (T), acceleration (A) and pressure (P) were transmitted at predefined settings within a step of a fixed number of days at high (H) or low (L) transmitting power output between a minimum and maximum interval. Power output was 154 dB for V13AP, 151 dB for ADST-V9TP and 146 (L) or 151 (H) dB for V9P. The ADST-V9TP were programmed to effectively stop transmitting after the set battery life, whereas the V13AP and V9P continued transmitting as long as there was battery left.

Transmitter type	N	Battery life (days)	Transmitter settings
V13AP	11	495	H 495 days (140 - 220 s)
	1	198	H 30 days (30 - 60 s); H 168 days (140 - 220 s)
V9P	10	502	H 153 days (180 - 280 s); L 120 days (300 - 400 s); H 229 days (300 - 400 s)
ADST-V9TP	27	354	H 90 days (240 - 360 s); H 150 days (120 - 240 s); H 104 days (240 - 360 s)
	40	339	H 120 days (120 - 240 s); H 239 days (240 - 360 s)
	19	400	H 120 days (180 - 200 s); H 280 days (300 - 400 s)
	23	425	H 70 days (180 - 280 s); H 355 days (300 - 400 s)

Table 7.2. Table of tagging metadata with number of seabass (N) tagged at different areas with length (cm), displayed as median [range], and the tagging period (months and years). Tagging areas were considered as coastal when they were within a distance of six nautical miles from shore.

Tagging area	N	Coastal / Offshore	Length (cm)	Tagging period
Zeebrugge port (outer)	41	Coastal	47.0 [38.0 – 74.0]	Jul – Oct (2018 – 2019)
Zeebrugge port (inner)	22	Coastal	46.5 [39.0 – 63.0]	Jun – Sep (2018 – 2020)
Scheldt Estuary	11	Coastal	40.0 [34.0 – 63.0]	Aug – Oct (2018 – 2019)
Oostende	5	Coastal	52.0 [37.0 – 57.0]	Jun – Aug (2018 – 2020)
Radar	14	Offshore	50.5 [42.0 – 57.0]	Sep (2021)
Wreck	30	Offshore	46.0 [42.0 – 57.0]	Oct – Dec (2019 – 2021)
Wind farm	8	Offshore	44.0 [33.0 – 53.0]	Jun – Oct (2018 – 2020)

Detection data metrics and visualization

For this chapter, only detections within the BPNS and Scheldt Estuary were included. A residence index (RI) was calculated to evaluate presence in the study area. A day was considered to be a detection positive day (DPD) if a seabass was detected at least once during that day. A residence index (RI) was calculated as the number of DPD out of the time at large, starting from the release date until the end of the battery lifetime or recapture of the fish. A fish was considered to exhibit site fidelity if it was detected in the study area at least 180 days (six months, a period long enough to have performed a spawning migration) after the release date. Acoustic detections of every tag ID were visualized over time in an abacus plot. Connectivity in the area was investigated by visualizing spatial networks, whereby grouped receiver stations represented the nodes and the counts of directed movements in between these locations were the edges (Jacoby et al. 2012). For this network representation, receivers were grouped by vicinity (with receiver stations within a group at a maximum distance of 3.6 km), except for the inner harbour of Zeebrugge and receiver bands ws1 and ws2 (Fig. 7.1), which were grouped as such (whereby receivers were at a maximum distance of 10.7 km). After exploration of these spatial networks of individual seabass, we visually identified different movement patterns. To visualize a seasonal component, we split the year into June – August, September – November, December – February and March – May (Chapter 6).

Habitat use at artificial substrates

The detection information at the receiver arrays near artificial substrates (port, radar, wreck and wind farm) was used to explore depth occupancy and to model seasonal presence. For this, we limited the data set to individuals that were detected at least 10 days at the temporary arrays around the artificial substrates. Depth occupancy at each array was visualised with a boxplot depicting depth measurements during day and night, which were categorized using the times of sunrise and sunset extracted with the R package *suncalc*.

We used a generalized linear mixed-effects modelling framework (GLMM) (Zuur et al. 2009) to model seasonal patterns in presence. A separate model was constructed for each array, whereby each model dataset was limited to the period of active battery life times of both receivers and transmitters, that

were detected at least 10 days in the array. We opted for these separate models because comparing presence between differently set up arrays (where a fish's absence in one array might imply its presence in another) and comparing depth use at different bathymetries wouldn't make sense. For the dependent variable, an individual seabass was categorized as present (1) or absent (0) for each calendar day. Presence was then modelled in a GLMM, following a Bernoulli distribution with fish ID as a random factor to take individual variability into account. The fixed variable month was included as the cyclical functions of its sine and cosine components to account for seasonality, following a similar approach as Dudgeon et al. (2013). Model selection was performed by stepwise backward selection by applying an analysis of variance (ANOVA) test to the full model and a model excluding one of the terms (single-term deletion). The model with a significantly lower Akaike Information Criterion (AIC) value was selected. The analyses were performed using the R package *lme4* (Bates et al. 2015).

In supporting information S7.2, we documented an onset for a more in-depth analysis of diel and tidal variation in depth occupancy and activity, but this analysis would need to be improved and elaborated with more tagging data (data were still collected at the time of writing).

RESULTS

Detection data metrics and visualization

In total, 795,662 detections of 110 seabass (out of 131 tagged) were registered by 154 stations. Two fish died shortly after tagging and one tag experienced a hardware issue preventing acoustic signal transmission. These fish were excluded from the analysis (leaving a total of 110 fish). Seabass were detected across the entire range of the BPNS (Fig. 7.2). In the Scheldt Estuary, seabass were only detected up until the second receiver band between Borssele and Terneuzen (ws2, Fig. 7.1). Individual seabass showed high variation in detection patterns, with RI varying between 0.00 and 0.92 and median RI of 0.21 and 0.05 for individuals tagged in coastal and offshore areas, respectively.

Looking at individual detections over time (Fig. 7.3), we saw that seabass were mainly detected in the area where they were released. Seabass tagged along the coast were mostly detected between April and October. Seabass tagged

offshore were more commonly detected until January (n = 11). Only a few seabass (n = 3) tagged offshore were detected at coastal stations and none were detected in Zeebrugge or the Scheldt Estuary. Out of all tagged individuals, only five were detected in the offshore area in February and March, namely at the radar tower (n = 1, 2 DPD), offshore wind farm (n = 1, 2 DPD) and at the wrecks Garden City (n = 1, 2 DPD) and Birkenfels (n = 3, each 1 DPD). Some seabass stayed during winter in the inner port of Zeebrugge, which is discussed in detail in chapter 8. For the calculation of site fidelity, we excluded animals that were recaptured within 180 days after release, as well as the animals that died (n=2) or whose tag experienced the above-mentioned hardware issue (n=1). Site fidelity to the study area was thus seen for 46 out of 70 (65.7%) seabass tagged along the coast, and for 21 out of 36 (58.3%) seabass tagged offshore.
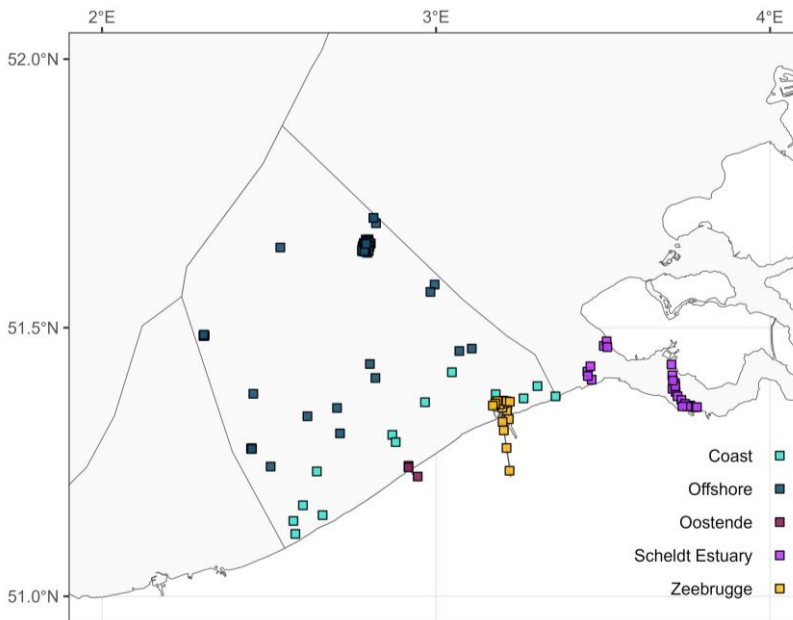
Figure 7.2. Locations of acoustic receivers with seabass detections, coloured by area (coastal, less than 6 nautical miles from shore: turquoise; offshore, more than 6 nautical miles from shore: dark blue; port of Oostende: burgundy; port of Zeebrugge: yellow; Scheldt Estuary: purple).
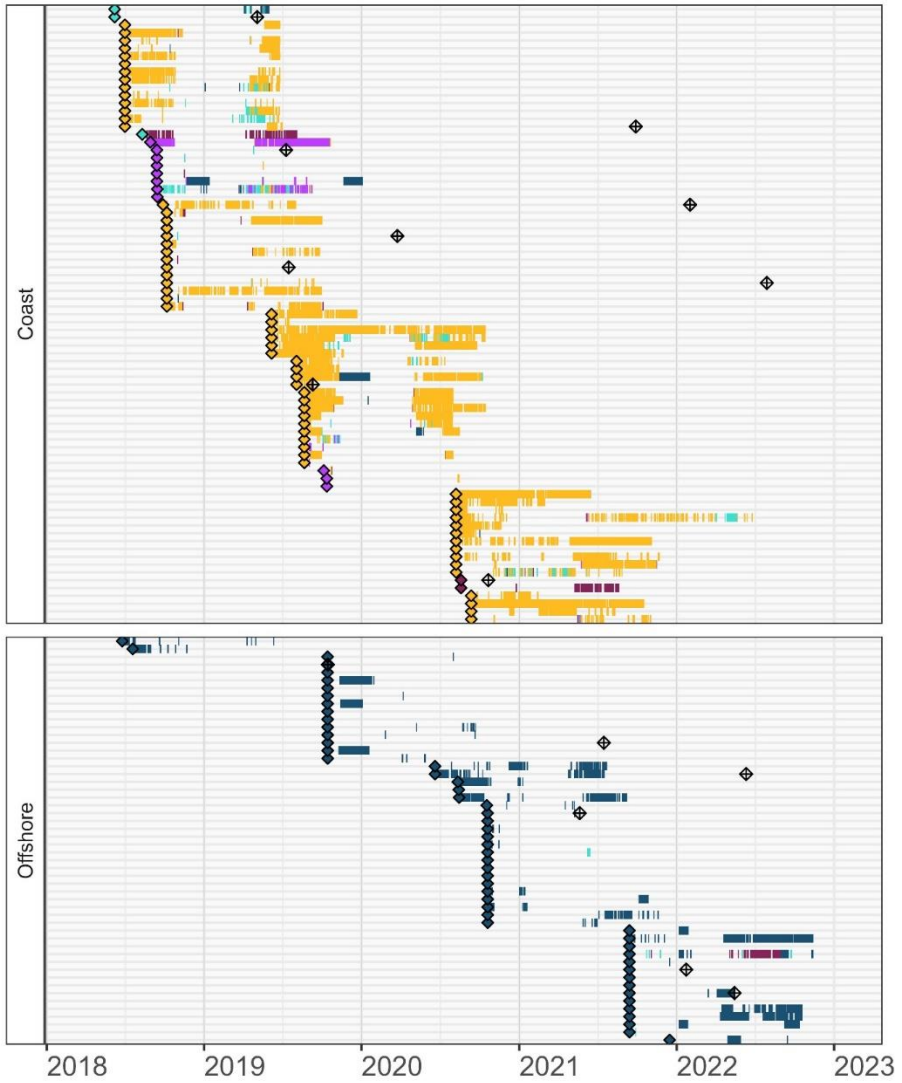
Figure 7.3. Abacus plot of acoustic data for seabass tagged along the coast (top) and in offshore areas (bottom), depicting a time line for individual tagged fish with the release (diamond), tag recovery (crossed diamond) and detections (square) coloured by location of detection (coastal, less than 6 nautical miles from shore: turquoise; offshore, more than 6 nautical miles from shore: dark blue; port of Oostende: burgundy; port of Zeebrugge: yellow; Scheldt Estuary: purple).
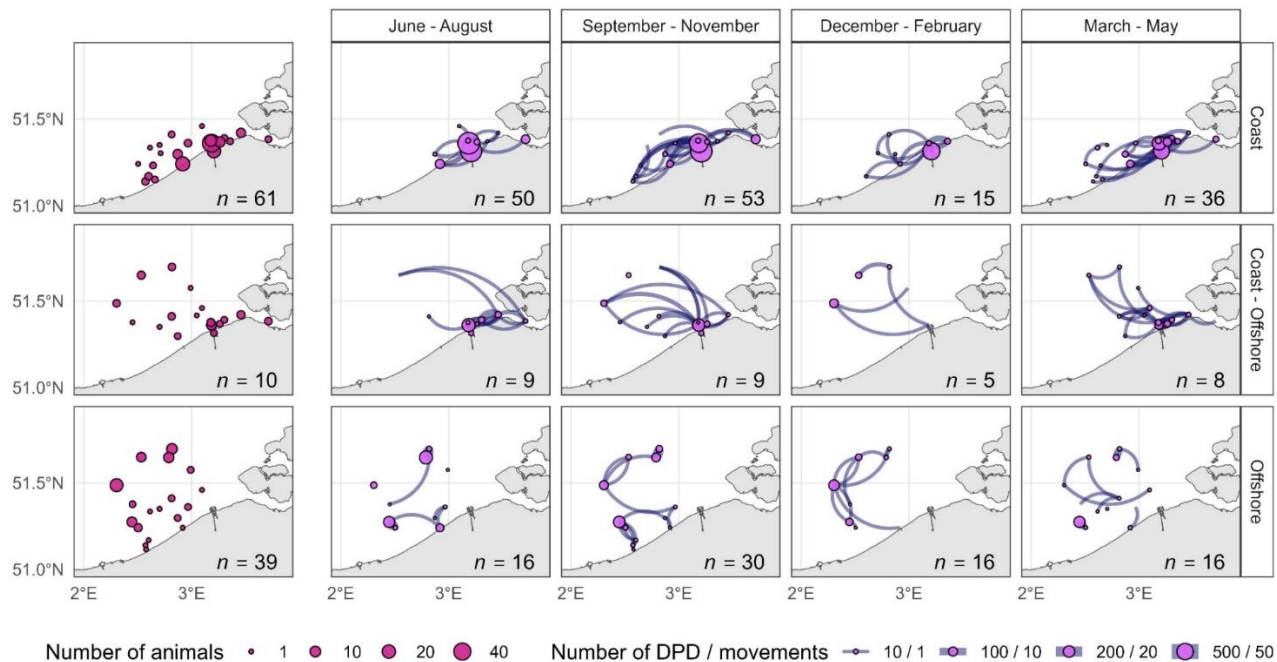
Figure 7.4. Space use of individuals classified into different strategies: coastal (top, n = 61), coastal with link to offshore areas (middle, n = 10) and offshore (bottom, n = 39) with the number of animals detected at grouped receiver stations (left, pink). The right plots show spatial network maps for different periods with nodes sized by the number of detection positive days (DPD, fuchsia) and edges sized by frequencies of movement between grouped receiver stations (right-hand curved from origin to destination). For each graph, the number of detected animals (*n*) is marked in the bottom right corner.

After visual exploration of individual spatial networks, we identified three spatial network patterns (Fig. 7.4): seabass that were tagged along the coast and were only detected in stations near the coast (strategy 'coast', n = 61), seabass that were tagged along the coast and showed connectivity to offshore stations (strategy 'coast – offshore', n = 10), and seabass that were tagged offshore and showed limited connectivity to the coast (strategy 'offshore', n = 39). For the strategy 'coast', the area of Zeebrugge seemed in strong connection with Oostende and the Scheldt Estuary. Seabass from the coast moved south-westwards along the coast mainly between September and November, returning the same way between March and May. Four seabass displayed a particular movement pattern when returning to Zeebrugge between April and June: the seabass first moved more northwards to the Scheldt Estuary (even after having been detected at Zeebrugge) to then return to Zeebrugge where they exhibited residency during the summer months. For the 'coast – offshore' strategy, the connectivity between Zeebrugge and Scheldt Estuary was also observed, but these seabass were never detected in Oostende or any other station along the south-western shore. These seabass went more offshore after spending summer along the coast; five individuals were detected at offshore stations during the winter. From March to May, eight (out of ten individuals) returned to the coast. Seabass tagged offshore (strategy 'offshore') were rarely detected in coastal areas with only three individuals detected in south-western coastal stations. None of the 'offshore' seabass were ever detected in Zeebrugge or the Scheldt Estuary.

Habitat use at artificial substrates

When investigating the detection data at the artificial substrates, it was important to take into account that the number of receivers at different locations varied over time (Fig. 7.5). The number of detected seabass varied between the different arrays (n_{port} = 28, n_{radar} = 8, n_{wreck} = 8, n_{wind} = 6) (Fig. 7.6). Seabass were mainly detected at depths corresponding to the depth of the seabed (where the receivers were installed) at the port, radar tower and wreck site (Fig. 7.7). Depth occupancy (median [Q1, Q3] in m) at these sites were 3.79 [2.43, 5.42] at the port, 7.52 [6.62, 9.03] at the radar tower and 27.1 [25.5 – 28.6]. In the offshore wind farm, seabass occupied a larger (interquartile) range of depths, and was mostly detected at greater depth during the day (22.4 [19.7,

26.2]) than at night (15.8 [12.0, 21.2]). This overall diel difference in depth use was observed for four of six seabass detected at the offshore wind farm.

For each array, the full presence model was chosen with fixed variable month (defined as the sine and cosine components) and the random factor ID (Table 7.3). Seasonal patterns in presence showed highest probability of presence π during the warmer months at the port and wind farm, with near zero (median) probability of presence from December to April (Fig. 7.7, Table 7.4). The wreck site showed the inverse pattern with highest π in November – January. The model for the radar tower, rendered non-zero probabilities throughout the year (except for December, for which we did not have data yet). However, we did not register seabass presence here in February, and only one seabass (2 DPD) was detected in March. This indicated the patterns in presence at the radar tower may not be entirely fit to investigate with a cyclical seasonal component.
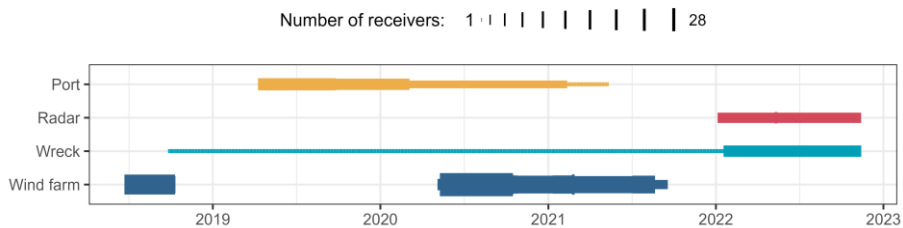
Figure 7.5. Time line of the number of available receivers for the acoustic receiver arrays at a port (yellow), an offshore radar tower (red), an offshore wreck (light blue) and an offshore wind farm (dark blue).
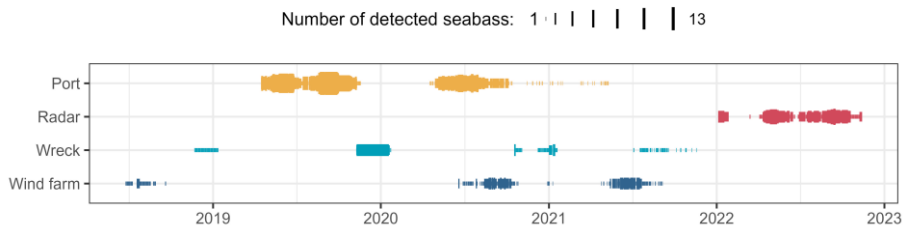
Figure 7.6. Time line of the number of individual seabass detected at the acoustic receiver arrays at a port (yellow), an offshore radar tower (red), an offshore wreck (light blue) and an offshore wind farm (dark blue).

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Table 7.3. Overview of model selection for generalized linear mixed models of presence (following a Bernoulli distribution) at the acoustic receiver arrays at the port, offshore radar tower, offshore wreck and offshore wind farm. For each area, the full model M1 was compared to models with single-term deletions (M2 and M3) using the Akaike Information Criterion (AIC) and p-value of the ANOVA (with p < 0.001 indicated as *). The AIC of the selected models were indicated in bold.

| | AIC | | | |
Model	Port	Radar	Wreck	Wind farm
M1: $\pi \sim$ Month + (1|ID)	**5019.8**	**2009.0**	**1796.3**	**1422.6**
M2: $\pi \sim$ Month	6047.1*	2504.6*	1946.3*	1469.7*
M3: $\pi \sim$ (1|ID)	6720.5*	2239.4*	2313.7*	1862.6*
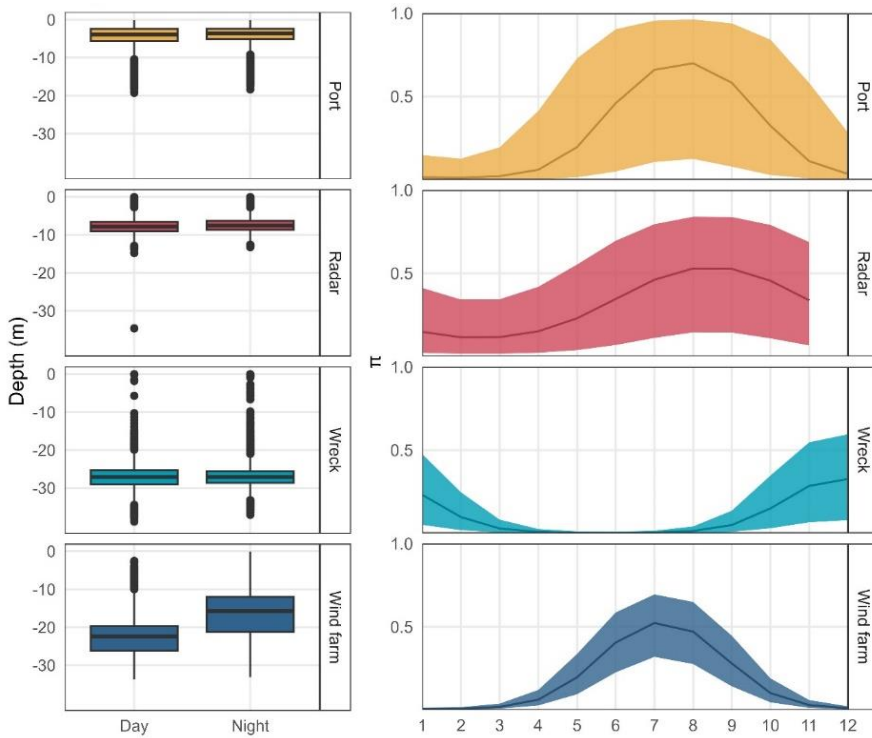
Figure 7.7. Left: Boxplot of transmitted depth (m) measurements, as detected during day and night at the acoustic receiver arrays at a port (yellow, n = 28), an offshore radar tower (red, n = 8), an offshore wreck (light blue, n = 8) and an offshore wind farm (dark blue, n = 6). Right: Output of predicted probability of presence π (median and range).

Table 7.4. Summary of generalized linear mixed models of presence (following a Bernouilli distribution) for each area with fixed effect estimates and standard error (SE), as well as the standard deviations (SD) of the random effect ID. Significant effects had p-values of <0.001 (*) and <0.05 (^).

	Port	Radar	Wreck	Wind farm
N	28	8	8	6
Fixed effect (SE)				
Intercept	-1.76 (0.26)*	-1.19 (0.47)^	-3.32 (0.35)*	-2.51 (0.27)*
Sine(2π/12 x month)	-2.08 (0.07) *	-1.14 (0.08)*	-0.28 (0.10)^	-1.50 (0.13)*
Cosine(2π/12 x month)	-1.58 (0.07) *	-0.33 (0.09)*	2.52 (0.16)*	-2.06 (0.15)*
Random effect SD				
Fish ID	1.32	1.30	0.93	0.56

DISCUSSION

Presence in Belgian waters & Scheldt Estuary

Seabass were detected in marine waters across the entire study area. Several seabass exhibited seasonal residency and site fidelity to the BPNS. Highest residency was observed along the coast in the period from April-May to October-November, indicating the coastal zone would serve as a feeding area. As expected, the majority left the coastal area during the colder months. In the offshore area of the BPNS (where receiver coverage was less dense and more fragmented than along the coast), seabass detections were more scarce. Seabass were observed in the offshore area throughout the year, with albeit very few detections in February and March, which corresponds to the timing of seabass aggregations in spawning grounds to the south-west of the study area, e.g. the English channel (López et al. 2015, Dambrine et al. 2021).

Seabass were detected in the Scheldt Estuary, but only in the marine waters. Recreational anglers did mention catches further upstream in the more brackish waters of the Scheldt (from ws3 onwards, Fig. 7.1), but we did not capture nor detect any seabass in this area. Although seabass as a species would tolerate a wide range of salinity (especially in the younger life-history stages), coping with variation in salinity may involve a high energetic cost (Vázquez & Muñoz-Cueto 2014).

Seasonal patterns in presence differed at the different artificial substrate sites. Higher presence was observed from May to October at all sites, except for the

offshore wreck where higher seabass presence was detected from November to January. Considering this timing and its offshore location, the wreck might serve as a pre-spawning stop before heading towards spawning grounds (Vázquez & Muñoz-Cueto 2014). Seabass seemed to occupy a deeper part of the water column during the day than at night in the offshore wind farm, but no circadian pattern was seen in the other sites. Using archival depth series, seabass has been observed to seasonally switch in diel patterns in depth occupancy and activity rhythm (Quayle et al. 2009, Heerah et al. 2017). Our telemetry results might therefore add a spatial component to this seasonal pattern, whereby seabass would alter vertical movement behaviour according to their location, for example in relation to available prey or a different function they use the habitat for. Considering only six seabass were detected at the offshore wind farms, this might also reflect individual variation in movement behaviour.

The importance of offshore artificial structures for European seabass is further investigated by ongoing tagging research in the context of the Fish Intel project. Additional acoustic and archival data can substantiate how more individuals use these habitats, which would enable to improve models of presence and activity (Supporting information S7.2) and could be complemented with other analysis techniques, such as spectral analysis for temporal patterns (Reubens et al. 2014) and 3D positioning for fine-scale spatial patterns (Baktoft et al. 2019).

Connectivity

We found that the connectivity in the area differed between individuals, whereby we identified three patterns. These different strategies demonstrate fine-scaled population structuring. As the geolocation modelling in chapter 6 showed that some seabass headed south towards the English Channel and some stayed in the North Sea, the different movement patterns within the BPNS could imply that these seabass headed for different destinations. For example, seabass residing in and around Zeebrugge in summer were observed to 1) stay in the port during winter, 2) head offshore, or 3) move south-westwards along the coast. A similar pattern of breeding partial migration (Shaw & Levin 2011) was described for seabass off the coast of the Iroise Sea, where residents and migrants separated to breed (de Pontual et al. 2019).

Looking into these individual patterns of connectivity, we found that four seabass made a stopover near the Scheldt Estuary (ws1) before returning to their summer residency area (Zeebrugge). Seemingly anecdotic, it was remarkable that these individuals first headed northwards (whereby one was even detected in Zeebrugge on its way north) to only then return to the area they had spent the previous summer and would spend the next. The observation could have been related to roaming behaviour before heading to the area of residency, or potentially even to a flawed orientation (e.g. due to habitat alteration due to the many anthropogenic activities). Another explanation consisted of individuals partaking in different spawning events at different locations throughout the year. Physiologically, seabass are able to spawn multiple times within a year (1 to 5 times for females, 1 to 8 times for males, as observed in aquaculture research) (Superio et al. 2021), and stage 1 seabass eggs had been observed in this area in April – May 2011 (van Damme et al. 2011, Tulp et al. 2016). A targeted spawning or egg survey could elucidate whether seabass spawn in the Voordelta (area west of the Dutch coast from Walcheren to the Maasvlakte).

Management implications

The importance of artificial substrates for European seabass was already fairly clear at the beginning of this study. For catching the fish, we relied on anglers and their knowledge of seabass hotspots in the BPNS, which were almost always related to artificial structures. Moreover, the importance of these habitats had been demonstrated for other fish species (Reubens et al. 2013b, Wright et al. 2020). These structures would therefore make good candidates for the spatial protection of the North Sea fish community, which represented one of the historically most heavily fished systems in the world (Beukhof et al. 2019). For the areas in our study, no recreational nor commercial fishing was allowed in the wind farm and port, due to safety regulations. Fishing was allowed at the offshore wreck and the radar tower, which were both considered hotspots to target shoals of seabass. Even if we lacked information at the time of writing to make strong statements about habitat use at the offshore artificial substrates, enough information is at hand to understand that spatial fisheries closures would likely benefit seabass recovery.

The biomass of the Northern seabass stock has not yet recovered to a level that can be ascertained as sustainable (ICES 2022a). Seabass' highly localized behaviour, exhibited through high residency and individual variability in connectivity, demonstrated the complexity of population dynamics and the risk to local depletion (Doyle et al. 2017). In light of the precautionary approach (Proelss & Houghton 2012), constituting the guiding principle of EU fisheries and environmental policy, conservation action can and should be taken to protect local seabass.

AUTHOR CONTRIBUTIONS

JG wrote the manuscript and analysed the data. JG, JR and PV tagged the fish, maintained the receiver network and managed the data. All authors contributed to the design of the study and critically revised the manuscript.

ACKNOWLEDGEMENTS

SUPPORTING INFORMATION S7.1 – ARTIFICAL SUBSTRATE RECEIVER ARRAYS
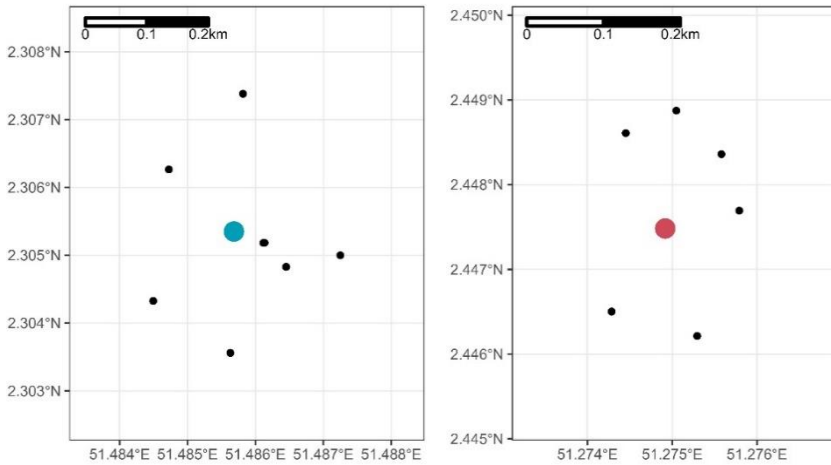
Figure S7.1.1 – Positions of acoustic receivers in the arrays at the Garden City wreck (left) and at the radar tower (right). The number of deployed receivers varied over time (Fig. 7.5).

SUPPORTING INFORMATION S7.2 – HABITAT USE ARTIFICAL SUBSTRATE

In this supporting document, we detail the onset of an in-depth analysis of habitat use at the four receiver arrays at different artificial substrates (port, radar, wreck and wind farm). Tagging efforts were ongoing on the time of writing, which will provide additional detection data as input for the models in the analyses below. We also provide some considerations and potential adaptations for future elaboration of the models.

Methods

We investigated the habitat use of individuals that were detected at least 10 days at the temporary arrays around the artificial substrates. We used a generalized linear mixed-effects modelling framework (GLMM) (Zuur et al. 2009) similarly to Dudgeon et al. (2013), to analyse patterns in presence, depth use and activity in the arrays. Activity was enumerated as hourly mean vertical distance (in m) between detections, whereby an hour had to contain at least 3 transmitted pressure sensor measurements to be included in the analysis. For the fixed factor diel phase, the time of day was categorized as day and night, using the times of sunrise and sunset extracted with the R package *suncalc*. Tidal data were extracted from 'Meetnet Vlaamse Banken' at the Westhinder measuring station (51°23'18" N, 2°26'16" E). This lead to the categorization of the tidal data into low, rising, high and falling tide, whereby the stages high and low included the peak tide plus one hour before and after.

Because of the inherently different nature of the dependent variables presence (binary), depth use and activity (continuous), models were set up differently. For the dependent variable 'presence', an individual seabass was categorized as present (1) or absent (0) per level of diel and tidal phase for each calendar day, rendering maximum eight records per day. Presence was then modelled in a GLMM, following a Bernoulli distribution, with the fixed factors month, diel phase and tidal phase and with fish ID as a random factor to take individual variability into account. The dataset for each array was limited to the period of active battery life times of both tags and receivers. The fixed variable month was included as the cyclical functions of its sine and cosine components to account for seasonality (Dudgeon et al. 2013). Depth use was evaluated in a GLMM following a Gamma distribution with a log link function, using the fixed

factor Diel phase with the random effects of fish ID and month. Tidal phase was not included, because of its direct relation to depth. Using a GLMM with a Gamma distribution with a log link function, activity was modelled against the fixed factors area (port, radar, wreck and wind farm), tidal phase and diel phase, and the random effects fish ID nested within area, as well as month. Since activity was calculated per hour, each hour was assigned the diel and tidal phase that took up most of the time within that hour (i.e. 30 minutes or more).

For the presence and depth use models, separate GLMMs were set up for each receiver array (port, radar, wreck and wind farm). We opted for these separate models because comparing presence between differently set up arrays (where a fish's absence in one array might imply its presence in another) and comparing depth use at different bathymetries would not make sense. Activity on the other hand, could be compared between areas while accounting for differences between individuals by nesting the random effect ID within area. In the presence model, month was included as a fixed factor since presence and absence could be determined for every date within the temporal range of the model. However, the datasets for the depth and activity models were limited to the instances with transmitted depth measurements. Month was therefore included as a random effect in the depth use and activity GLMMs.

Model selection was performed by stepwise backward selection by applying an analysis of variance (ANOVA) test to the full model and a model excluding one of the terms (single-term deletion). The model with a significantly lower Akaike Information Criterion (AIC) value was selected. We applied the Tukey's honestly significant difference (HSD) test to the chosen model as a post-hoc test. Analyses were performed using the R packages *lme4* (Bates et al. 2015) and *afex* (Singmann et al. 2022).

Results

Different binomial regression models were selected for the different arrays, with the full model (including fixed factors month, diel and tidal phase) selected for the port and wind farm (Table S7.1). Diel phase was removed for the wreck and tidal phase was removed for radar. Seasonal patterns in presence showed highest probability of presence π during the warmer months at the port and wind farm, with (near) zero probability of presence from

December to April (Fig. S7.1, Table S7.2). At the radar tower, we registered seabass presence throughout the year (except for December, for which we did not have data yet), with highest π from July to October. The wreck site showed the inverse pattern with highest π in November – January. Diel differences were found in the areas radar (higher π at night), port and wind farm (lower π at night), but the effect was small. Higher π was predicted during falling tide, compared to rising and high tide for all areas, but the effect sizes were small.

For the GLMMs on depth use, the full model was selected for all areas (Table S7.3). Seabass were detected at significantly shallower depth at night in all areas (Table S7.4, Fig. S7.2), but the effect estimate was extremely small for the port, radar and wreck site, resulting in predicted diel difference of 0.5 m or less. At the offshore wind farm, seabass was predicted to be 5.1 m deeper during the day than during the night (with low variance between individual fish: SD 0.02 for the random effect fish ID). For the activity GLMM, the full model was retained (Table S7.5). Highest activity was found at the Garden City wreck with lowest activity registered at the radar tower and offshore wind farm (Table S7.6, Fig. S7.3). Activity was found to be significantly higher at night and at falling tide in comparison with high and low tide, although effect sizes were very small.

Improvements to be made

The major difficulty with these models was that statistically significant differences were found, even when those diel and tidal differences in some cases were too slight to be considered of practical (in this case: ecological) relevance. Including detection data of more fish (in light of the ongoing tagging efforts) might therefore render clarity on the existence of these differences. We included tidal phase following a similar approach of Dudgeon et al. (2013), but tidal phase could be accounted for differently in the model, either by applying a different time window or using another variable, such as current velocity. Moreover, diel and tidal factors might be more appropriately accounted for with spectral analysis (Reubens et al. 2014).

Table S7.1. Overview of model selection for generalized linear mixed models of presence (following a Bernoulli distribution) at the acoustic receiver arrays at the port, offshore radar tower, offshore wreck and offshore wind farm. For each area, the full model M1 was compared to models with single-term deletions (M2, M3 and M4) using the Akaike Information Criterion (AIC) and p-value of the ANOVA (with p < 0.001 indicated as *). The AIC of the selected models were indicated in bold.

Model	AIC Port	Radar	Wreck	Wind farm
M1: π ~ Month + Diel phase + Tidal phase + (1|ID)	**25569.5**	15296.4	8442.3	**8002.8**
M2: π ~ Month + Tidal phase + (1|ID)	25580.1*	15319.2*	**8440.3**	8088.0*
M3: π ~ Month + Diel phase + (1|ID)	27125.4*	**15295.8**	8461.6*	8017.6*
M4: π ~ Diel phase + Tidal phase + (1|ID)	30227.8*	16718.1*	12232.9*	9802.0*

Table S7.2. Summary of generalized linear mixed models of presence (following a Bernouilli distribution) for each area with fixed effect estimates and standard error (SE), as well as the standard deviations (SD) of the random effect ID. Significant effects had p-values of <0.001 (*).

	Port	Radar	Wreck	Wind farm
N	28	8	8	6
Fixed effect Estimate (SE)				
Intercept	-2.95 (0.23)*	-1.51 (0.4)*	-5.26 (0.42)*	-3.14 (0.31)*
Diel phase: night	-0.11 (0.03)*	0.2 (0.04)*	-	-0.53 (0.06)*
Sine(2π/12 x Month)	-1.77 (0.03) *	-1.03 (0.03)*	-0.22 (0.05)*	-1.77 (0.07)*
Cosine(2π/12 xMonth)	-1.14 (0.03) *	-0.16 (0.03)*	4.12 (0.12)*	-1.82 (0.07)*
Tidal phase: rising	0.02 (0.04)		0.06 (0.08)	0.05 (0.08)
Tidal phase: high	-1.51 (0.06) *	-	0.01 (0.09)	-0.18 (0.08)^
Tidal phase: falling	0.48 (0.04) *	-	0.33 (0.08)*	0.18 (0.08)^
Random effect SD				
Fish ID	1.21	1.14	1.15	0.73

Table S7.3. Overview of model selection for generalized linear mixed models of depth use (following a Gamma distribution with log link) at the acoustic receiver arrays at the port, offshore radar tower, offshore wreck and offshore wind farm. For each area, the full model M1 was compared to models with single term deletions (M2, M3 and M4) using the Akaike Information Criterion (AIC) and p-value of the ANOVA (with p < 0.001 indicated as *). The AIC of the selected models were indicated in bold.

	AIC			
Model	Port	Radar	Wreck	Wind farm
M1: Depth ~ Diel phase + (1|ID) + (1|Month)	**144131.0**	**835580.3**	**195700.0**	**425401.2**
M2: Depth ~ Diel phase + (1|ID)	145077.5*	845105.1*	195997.3*	427024.3*
M3: Depth ~ (1|ID) + (1|Month)	144141.0*	836857.0*	195926.9*	438702.6*
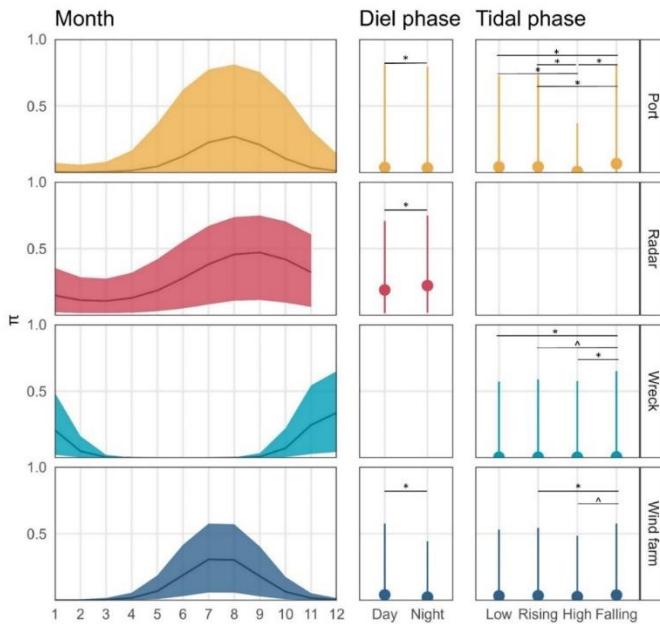
Figure S7.1. – Output of predicted probability of presence π (median and range) at the acoustic receiver arrays at a port (yellow), an offshore radar tower (red), an offshore wreck (light blue) and an offshore wind farm (dark blue). Significant effects had p-values of <0.001 (*) and <0.05 (^).

Table S7.4. Summary of generalized linear mixed models of depth use (following a Gamma distribution with log link) for each area with fixed effect estimates and standard error (SE), as well as the standard deviations (SD) of the random effect ID. Significant effects had p-values of <0.001 (*).

	Port	Radar	Wreck	Wind farm
N	28	8	8	6
Fixed effect (SE)				
Intercept	1.49 (0.08)*	1.82 (0.23)*	3.23 (0.02)*	3.16 (0.07)*
Diel phase: night	-0.02 (0.01)*	-0.04 (0.001)*	-0.02 (0.001)*	-0.25 (0.002)*
Random effect SD				
Fish ID	0.17	0.01	0.01	0.02
Month	0.09	0.14	0.01	0.04
Residual	0.53	0.22	0.09	0.21

Table S7.5. Overview of model selection for generalized linear mixed models of activity (following a Gamma distribution with log link). The full model M1 was compared to models with single term deletions (M2, M3, M4 and M5) using the Akaike Information Criterion (AIC) and p-value of the ANOVA (with p < 0.001 indicated as *). The AIC of the selected model was indicated in bold.

Model	AIC
M1: Depth ~ Area + Diel phase + Tidal phase + (1|Area:ID) + (1|Month)	**3359**
M2: Depth ~ Area + Diel phase + (1|Area:ID) + (1|Month)	3371*
M3: Depth ~ Area + Tidal phase + (1|Area:ID) + (1|Month)	3379*
M4: Depth ~ Diel phase + Tidal phase + (1|Area:ID) + (1|Month)	3388*
M5: Depth ~ Area + Diel phase + Tidal phase + (1|Area:ID)	3526*
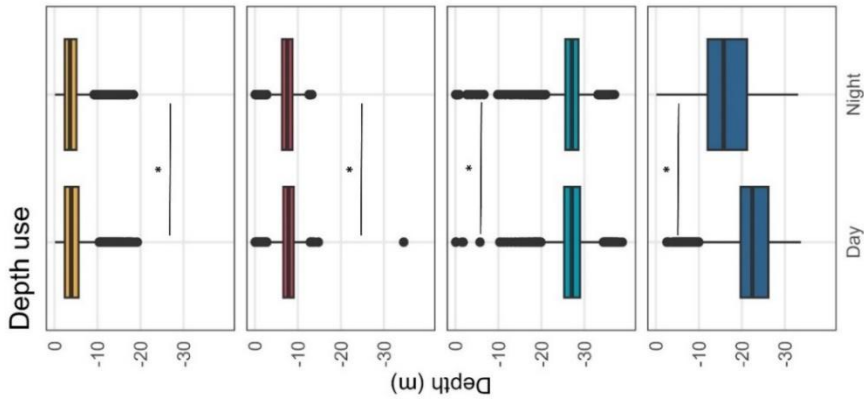
Figure S7.2. Boxplot of depth (m) measurements, as detected in the different receiver arrays during day and night. Significant effects of the GLMMs were indicated by the *p*-values of <0.001 (*).

Table S7.6. Summary of generalized linear mixed model of activity (following a Gamma distribution with log link) with fixed effect estimates and standard error (SE), as well as the standard deviations (SD) of the random effects fish ID nested in Area (Area : Fish ID) and month. Significant effects had *p*-values of <0.001 (*) and <0.05 (^).

Fixed effect Estimate (SE)	
Intercept	-1.01 (0.21)*
Area: wreck	1.48 (0.27)*
Area: radar	-0.19 (0.26)
Area: port	0.70 (0.22)^
Diel phase: night	0.06 (0.01)*
Tidal phase: rising	0.05 (0.02)^
Tidal phase: high	0.01 (0.02)
Tidal phase: falling	0.07 (0.02)*
Random effect SD	
Area : Fish ID	0.35
Month	0.11
Residual	0.71
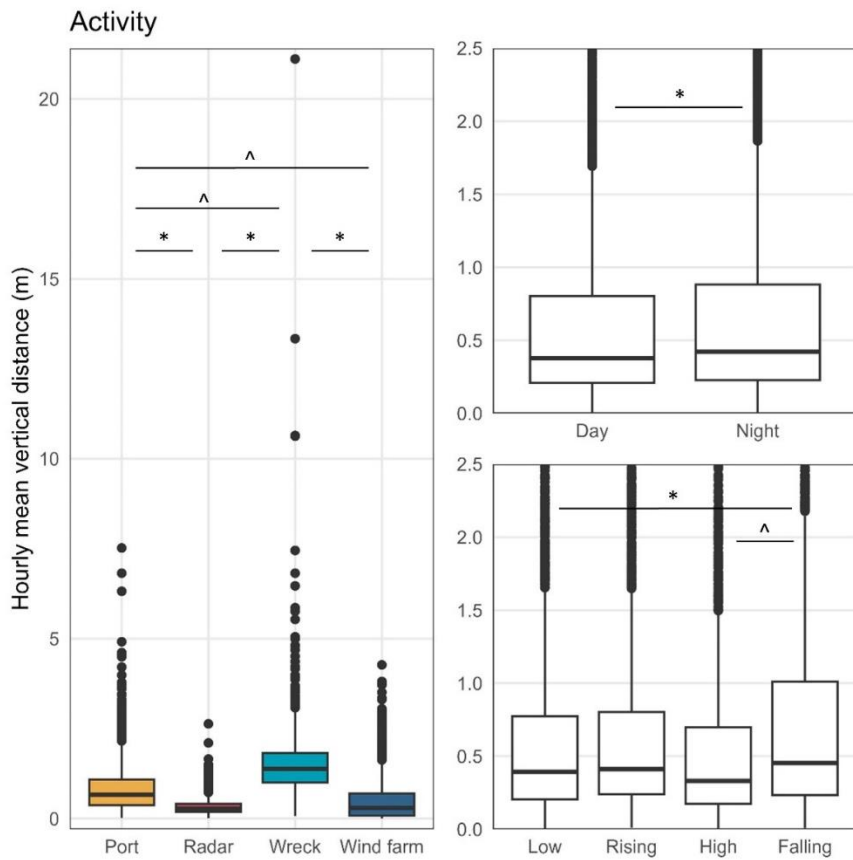
Figure S7.3. Boxplot of hourly mean vertical distance, as detected in the different receiver arrays during day and night and the tidal phases low, rising, high and falling. Significant effects of the GLMM was indicated by the p-values of <0.001 (*) and <0.05 (^).

CHAPTER 8

NOT ALL ARE EQUAL BEFORE THE LAW: FISHERIES MEASURES PROTECT EUROPEAN SEABASS GROUPS WITH DISTINCT HABITAT USE DIFFERENTLY

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ABSTRACT

We investigated the movements of European seabass, *Dicentrarchus labrax*, to understand habitat use and connectivity to evaluate how individual seabass are protected by the spatiotemporal fisheries restrictions in place. We tagged seabass with acoustic transmitters in a study area in the Port of Zeebrugge (Belgium) in the southern North Sea. The 370,200 detections of 57 seabass in the study area revealed high residency in the period from late March - May to September - November, as well as high site fidelity (70.7 %). Whereas the large majority of seabass left the area in winter, thirteen seabass stayed in the harbour experiencing temperatures as low as 2.8 °C. Two groups of seabass were identified having different core movement areas in the inner and outer harbours, although movement between the two areas was possible. The

distinct differences in habitat use between these groups resulted in a significantly different level of exposure to fisheries under the same policy framework. By quantifying a fish' protection based on the spatiotemporal fisheries management in place, our study underlines the importance of taking into account movement behaviour when evaluating conservation measures.

INTRODUCTION

The vulnerability of a fish to being captured by a certain fishery is at the intersection of the spatiotemporal dynamics of both the fish and fisheries (Abesamis et al. 2014). The failure to recognize these spatiotemporal dynamics, and their scale, can lead to flawed fisheries management (Kerr et al. 2017, Cadrin 2020). An example is the case of the European seabass, *Dicentrarchus labrax*. After more than a decade of excessive exploitation (ICES 2022b), the European Parliament and Commission committed in 2015 to the preservation of seabass (EU 2015e). Fisheries measures include catch restrictions, gear limitations and a spatial and seasonal closure for commercial fisheries, as well as a bag limit and a catch-and-release season for recreational fisheries (EU 2022a, b). Underlining the limited understanding of both seabass fisheries and ecology (Steadman et al. 2014), the countless alterations of seabass fisheries measures, often amended within the year, illustrate the ad-hoc, changeful nature of the management.

For assessment purposes, ICES divides seabass in the Northeast Atlantic in four stocks: southern Bay of Biscay and Atlantic Iberian waters (ICES divisions 8c,9b), northern and central Bay of Biscay (8ab), West of Scotland, West of Ireland and eastern part of southwest of Ireland (6a,7b,j), and the "Northern stock" which includes the central and southern North Sea, Irish Sea, English Channel, Bristol Cannel and Celtic Sea (4b,c, 7a,d-h) (ICES 2020b). Our study area is located in the North Sea, where seabass fisheries are managed under the EU multiannual plan (MAP) for Western Waters since 2019 (EU 2019b). The yearly ICES advice for the Northern stock provides the estimates of fishing mortality (F) based on this MAP (ICES 2022b). F is estimated to have been below the reference point for maximum sustainable yield (MSY) from 2016 onwards, since the emergency measures have been in place. At the time of writing, the biomass has not fully recovered (ICES 2022b). Understanding the

effect of the fisheries measures on the protection of seabass could aid the conservation management.

European seabass is a highly mobile fish. The species tolerates a wide range of temperatures (2-32°C) and salinities (0-40 ppt) and predates on various prey species of crustaceans, polychaetes, bivalves, gastropods, cephalopods and fish (Vázquez & Muñoz-Cueto 2014, López et al. 2015). These fast-moving predators generally feed along the coast, in estuaries and lagoons, but head to offshore deeper and warmer waters for winter spawning (López et al. 2015). Despite low genetic differentiation across the Northeast Atlantic population (Souche et al. 2015, Robinet et al. 2020), individual movement patterns illustrate a complex population structure. Mark-recapture (Pawson et al. 2007) and electronic tagging studies (Doyle et al. 2017, O'Neill et al. 2018, de Pontual et al. 2019, Stamp et al. 2021, de Pontual et al. 2023) have revealed interannual site fidelity to both feeding and spawning areas. Individual seabass exhibited long-term residency, staying in limited areas for long periods of time. The behaviours of long-term residency and interannual fidelity put seabass at risk of local depletion (Doyle et al. 2017), a mechanism that can contribute to the slow recovery of fish populations (Petitgas et al. 2006).

Seabass movement ecology has only been limitedly studied in the North Sea (Quayle et al. 2009, de Pontual et al. 2023). Our study area, the port of Zeebrugge (Belgium), is considered a hotspot for recreational angling due to its high seabass abundance (Deputter pers. comm.). In marine waters, seabass fisheries measures are legislated in a yearly Council Regulation (EU 2022a). The national (i.c. the Department of Environment of the Flemish government) jurisdiction stipulates seabass fisheries measures for inland waters (Flemish Government 2017). Additionally, the port authorities regulate the access to the port of Zeebrugge by means of maritime security measures. Depending on their space use over time, seabass will therefore be differently exposed to fisheries regulated on different policy levels. This semi-confined study area is therefore a clear example of the interplay of spatiotemporal dynamics of both the fish and fisheries. In this study we investigated local seabass movements to 1) thoroughly understand habitat use and connectivity in the port area, and to 2) evaluate the prevailing spatiotemporal fisheries restrictions by quantifying how seabass are protected by these measures.

MATERIAL & METHODS

Study site

Seabass were tracked in the Port of Zeebrugge (Belgium, Fig. 8.1), which consists of an outer, marine harbour and an inner harbour which are connected through two shipping lock complexes. The main shipping lock, Vandamme, operates multiple times a day for regular and large ship traffic, whereas the smaller lock, Visart, is rarely operational. The outer harbour shores consist of sandy beaches, straight quay walls and large, concrete stones, that surround the two seaside port walls on either side. The shipping canal Boudewijn connects the port with the city of Bruges. The canal water is not used to discharge excess of freshwater, but seawater is regularly fed into the Boudewijn canal via an opening on the west side of the Vandamme shipping lock to maintain a specific water level. Both the inner harbour and the canal are lined with straight quay walls, as well as sandy beaches and oyster reefs.

Seabass fishing in the study area is regulated under different spatiotemporal fisheries measures on different policy levels (full overview of legislation in Supporting information S8.3). Maritime security measures spatially limited fishing in the port to specific zones because of safety regulations (blue lines in Fig. 8.1). An additional spatial closure consisted of the zone 200 m inland of the Vandamme shipping lock where seabass fishing was specifically prohibited to halt seabass poaching that was prevalent in this area (Flemish Government 2017). Temporal closures covered January to June in riverine waters and February – March (2018-2019) or February (2020 -2022) in marine waters. Recreational angling inside the port was considered to mainly take place during day (Goossens pers. comm.).

Fish tagging and acoustic monitoring array

During the summers of 2018 to 2020, 63 European seabass were caught in the inner (22) and outer (41) harbour (Fig. 8.1) with rod and line by recreational anglers using plastic lures and wobblers. Fish were tagged with transmitters of the type ADST-V9TP (45), V13AP (9) and V9P (9) (Innovasea Ltd., USA; details in Supporting information S8.1). Through a small surgery at the ventral side of the fish, the transmitters were placed in the abdominal cavity, as approved

under the ethical certificate EC2017-080 (for more details about the tagging procedure, we refer to (Goossens et al. 2023).
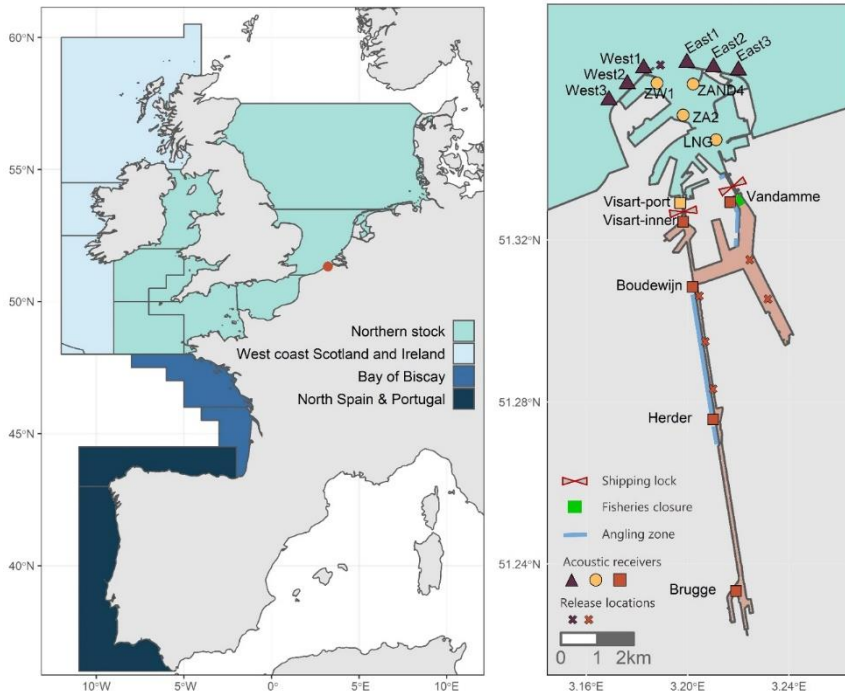
Figure 8.1. Left: Map of seabass ICES stock division in the Northeast Atlantic with the location of the study area (orange dot). Right: Map of the study area in the port of Zeebrugge with two shipping locks, Vandamme and Visart. Angling is only allowed in specific zones (light blue), as imposed by the port authorities, and one location is specifically closed for seabass fishing (green), as legislated by the Flemish government. Locations of fish release (cross) and of receivers, deployed on tripod frames (triangle), navigation buoys (circle) and harbour infrastructure (square), were coloured by harbour zone (port walls: purple; outer harbour: yellow; inner harbour: orange). Shape files originated from ICES (https://gis.ices.dk), Marine Regions (https://www.marineregions.org/) and GRBgis (https://www.geopunt.be).

Table 8.1. Overview of deployment period and attachment type for each acoustic receiver station (tripod mooring, navigation buoy or harbour infrastructure).

Harbour zone	Station name	Receiver attachment	Start date	End date
Port walls	West1	Tripod mooring	11/4/2019	10/2/2021
	West2	Tripod mooring	11/4/2019	3/3/2020
	West3	Tripod mooring	11/4/2019	3/3/2020
	East1	Tripod mooring	11/4/2019	12/5/2021
	East2	Tripod mooring	11/4/2019	3/3/2020
	East3	Tripod mooring	11/4/2019	3/3/2020
Outer harbour	ZOKN	Navigation buoy	27/6/2018	19/3/2019
	ZW1	Navigation buoy	19/3/2019	11/8/2022
	ZAND4	Navigation buoy	27/6/2018	11/8/2022
	LNG	Navigation buoy	25/11/2020	11/8/2022
	ZA2	Navigation buoy	25/11/2020	13/4/2022
	Visart-port	Harbour infra.	25/11/2020	13/4/2022
Inner harbour	Visart-inner	Harbour infra.	11/1/2021	8/11/2022
	Boudewijn	Harbour infra.	12/6/2018	8/11/2022
	Vandamme	Harbour infra.	12/6/2018	8/11/2022
	Herder	Harbour infra.	11/1/2021	8/11/2022
	Brugge	Harbour infra.	25/11/2020	8/11/2022

Acoustic receivers (VR2W, VR2AR and VR2Tx; Innovasea Ltd., USA) were placed strategically to study fish movements along the port walls, the outer and inner harbour, and the Boudewijn Canal (Fig. 8.1). Due to practical and budgetary reasons, the receiver array changed considerably in lay-out between the earliest deployment in June 2018 and last recovery in November 2022 (Table 8.1). Receivers were attached to existing harbour infrastructure and navigation buoys with steel cable, metal chain and stone (Reubens et al. 2019b), as well as tripod moorings deployed on the seabed (Goossens et al. 2020). Previous range testing in the Belgian part of the North Sea (BPNS) resulted in estimated detection ranges (defined here as the transmitter-receiver distance with 50% detection probability of observing a tagged animal's presence under median environmental conditions) of 502 m (hourly time bin) and 566 m (daily time bin) for observing European seabass (Goossens et al. 2022). The hard surfaces

of the harbour infrastructure (e.g. concrete walls) might have caused acoustic signal reflection (Vergeynst et al. 2020b). Data and metadata were managed using the online database of the European Tracking Network (ETN; https://lifewatch.be/etn), enabling us to directly access transmitter detections on other arrays, such as the permanent Belgian acoustic receiver network (PBARN) (Reubens et al. 2019b).

Data analysis

All analyses were performed in R software (R Core Team 2022), using the packages lme4 (Bates et al. 2015) and afex (Singmann et al. 2022). R scripts are made available on the GitHub repository https://github.com/JolienGoossens/SeabassTelPort.

Data processing

For each seabass, the time at large (TAL) was defined as the period from the tagging event to the last detection or recapture of the fish. Detection data were organized in hourly and daily time bins throughout the TAL. If a fish was detected at least once in an hour or day, we considered that time bin as detection positive hour (DPH) or detection positive day (DPD). DPD were categorized as day or night using the R package suncalc for extracting the times of sunrise and sunset (Thieurmel & Elmarhraoui 2022). For the time steps when an animal wasn't detected, information on its probable whereabouts could be deducted from its previous and/or next location of detection, building on the concept of epistemic uncertainty (Bruneel et al. 2020). Seabass had to pass through one of the shipping locks (detection stations Vandamme, Visart and Visart-inner) to leave the inner harbour. Therefore, we considered a seabass to likely be present in the inner harbour if the previous and following detection were located in the inner harbour. If the last detection of a transmitter was registered in the inner harbour, the fish was considered to likely have been in the inner harbour for the remaining TAL. In all other cases, the seabass was considered to likely be in the outer harbour or at open sea. These likely locations (LL) were used for visualization and in the fisheries vulnerability model (see below). An overview of analysis metrics and methods and their spatiotemporal resolutions is provided in table 8.2.

Table 8.2. Overview of analysis metrics and methods, listing the applied temporal resolution (hour or day) and range (month or time at large, TAL) and spatial resolution (receivers station, harbour zone, entire study area or likely location, LL).

Metric / Method	Time scale		Space scale	Purpose / Definition
	Resolution	Range	Resolution	
Site fidelity	-	TAL	Zone	Percentage of detected animals that
		TAL	Study area	returned or stayed in the area six months after tagging
Residence index (RI)	Hour	Month	Zone	Percentage of time an animal spent at a
	Day	Month	Zone	receiver out of its time at large
	Day	TAL	Station	Input of the correspondence analysis (CA)
Correspondence Analysis (CA, calculated with RI)	Day	TAL	Station	Multivariate analysis (station & fish ID) to visualize association of fish with stations
Empirical derived Markov Chain (EDMC)	Hour	TAL	Station	Calculate transition probability of one station to another
Eigenvector centrality (EVC)	Hour	TAL	Station	Quantify the use of a receiver station
GLMM Spatial closure	Hour	TAL	Station	Model to compare presence and activity at Vandamme
GLMM Fisheries protection	Hour	Month	Study area + LL	Model protection from fisheries measures for individual seabass

Habitat use and network analysis

First, we investigated spatiotemporal patterns in seabass' use of the study area. A seabass was considered to exhibit site fidelity if it was detected in the study area at least six months after the tagging event. Site fidelity thus reflected if a fish returned to or stayed in the study area for the subsequent feeding period. The residence index (RI) was used to evaluate what percentage of time an individual fish spent at a particular location. For visual comparison of RI between harbour zones, daily and hourly RI per month were calculated as the number of DPD and DPH out of the total number of days or hours within that month (within the TAL, e.g. if a fish was tagged within that month, only the time bins after the tagging event were considered). Daily RI was also calculated per receiver station as the detected daily time bins out of the tagged fish' TAL to be used in the correspondence analysis (CA).

We used network analysis to discern spatial patterns in seabass' use of the study area. CA was applied to infer grouping of stations and animals, based on the amount of time individual seabass spent at each station. Given a contingency table of daily RI for every animal ID at every receiver station, Chi-square distances quantified the similarity of how individual seabass frequented different stations. As a multivariate statistical method, CA enabled to visualize multidimensional complex data in fewer dimensions, where the distances between data points reflect the similarity between them (van Dam et al. 2021). The interconnectedness between the different stations in the harbours was investigated using Empirical derived Markov Chain (EDMC) analysis (Stehfest et al. 2015), following the approach of (Garcia et al. 2015). We calculated transition probabilities from one station to the other, as well as eigenvector centrality (EVC) which quantified the use (the centrality) of that station in relation to the use of the stations it is connected to. In contrast to (Garcia et al. 2015), we didn't regard a lack of detection as a true absence, as we considered the scarcity of our receiver array would wrongly inform the Markov process on absence. CA was performed with the R package FactoMiner (Lê et al. 2008) and EMDC was applied with the code of (Stehfest et al. 2015). For the visual exploration of the spatial network, the counts of directed movements between receiver stations were plotted on a map of the study site (Jacoby et al. 2012).

Spatial closure

Seabass fishing was prohibited around Vandamme station (see above). As recreational seabass angling in the port was assumed to mainly take place during daylight hours (Goossens pers. comm.), we compared circadian patterns in presence and activity within the protected area (station Vandamme) and outside of it. Presence was modelled as the number of DPH in a generalized linear mixed model (GLMM) with a Poisson distribution. A GLMM following a Gamma distribution with a log link function was used for activity, enumerated as hourly mean vertical distance (in m) between detections for tags with a pressure sensor and as the hourly mean acceleration (3D, in m/s^2) for accelerometer tags. For the dependent variables, the selected distributions were evaluated and validated by visual exploration of the raw data and Pearson residuals. Explanatory variables were day/night, station and their interaction, with fish ID as a random effect. Model selection was performed with single-term deletion using Chi-square tests and the Akaike Information Criterion (AIC) (Zuur et al. 2009).

Fisheries vulnerability

From a fish' perspective, how much time would a fish spend in an area where and at a time when no fishing was allowed? A seabass was considered to be protected from fishing (both commercial and recreational) if the legislation prohibited fishing at that location and time (full overview of legislation in Supporting information S8.3 and chapter 9) under different management scenarios (Table 8.3). We assigned a seabass to be 'exposed' (0) or 'protected' (1) per hourly time bin, using DPH as well as likely locations. For the assumed locations, seabass was considered to be subject to riverine management (national, i.c. Flemish, jurisdiction) in the inner harbour zone and to the yearly fisheries measures (Council Regulations) outside of the inner harbour zone. For every seabass, we calculated the number of 'protected' hours out of the total hours in a month. The probability of protection π was predicted with a GLMM with a binomial distribution. Explanatory variables were tagging location (outer or inner harbour, fixed) and the random effects of month and fish ID nested in tagging location. Model validation was performed through visual inspection of residuals and through Chi-square tests comparing the full model with single term deletions. Using the model, we investigated how this

predicted protection π varied under different hypothetical management scenarios (Table 8.3).

RESULTS

Habitat use

Out of the 63 tagged seabass, 57 were observed in the port counting a total of 370,200 detections (Fig. 8.2). Seabass were detected at all stations in the study area, except for Visart-port. An additional 26,785 detections were registered on marine stations of the PBARN, including detections of two fish that weren't detected in the port array (making a total of 59 detected seabass). One seabass was caught after 38 days off the coast of Dunkerque (France), 50 km southwest of the tagging location, and was not included in the calculation of site fidelity. Site fidelity to the study area was seen for 41 out of 58 detected seabass with a TAL exceeding 6 months (70.7%,Table 8.4). High daily RI (median 0.19, range 0.00 – 0.92) showed high seabass presence, with lower hourly RI (median 0.04, range 0.00 - 0.52) indicating they would not spend the entire day around the receiver stations.

The majority of seabass were detected in the study area until September – November (n = 48, 77.4%) and a lot returned the next year from late March to May after seemingly leaving the area (n = 31, 50.0%) (Fig. 8.2). Remarkably, thirteen seabass (39.0 – 57.0 cm total length at release) were detected in the harbour in winter (January – March): twelve in the inner harbour and one at the outer port and along the port walls. During winter the transmitted sensor measurements showed a minimum water temperature of 2.8°C in the port (median 6.9°C in winter). The differential temporal use of harbour zones was also reflected in the monthly variability of RI (Fig. 8.3). While mean daily RI per month in the inner port was 0.07 to 0.18 throughout the year, seabass were largely absent from the port walls and outer port from December to March. Out of five transmitters with TAL of nearly 2 years, three revealed interannual variability in habitat use. One fish stayed in the port during winter 2021, but left in 2022. Another seabass was tagged in summer 2020, left the port late autumn and didn't return until the summer of 2022.

Table 8.3. Management scenarios used to predict the probability of protection of individual seabass. An individual seabass was considered 'protected' (1) in an hourly time bin if it met the condition of the mentioned likely location (LL) or a detection positive hour (DPH) at a specific station. If it didn't meet any of the conditions, the individual was considered as 'exposed' (0) for that hour bin. The measures taken into account for the different scenarios are marked with X. For names of detection stations, see table 8.1 and figure 8.1).

Scenario	Spatial closure Maritime access	Spatial closure Vandamme	Temporal closure EU	Temporal closure riverine	No fishing at night
Condition for protection	DPH any station excl. Boudewijn, Herder, Vandamme	DPH Vandamme	LL marine waters (during closed period)	DPH or LL inner harbour (during closed period)	DPH or LL inner harbour at night
Maritime access measures	X				
Current regulation	X	X	X	X	
Current regulation without seasonal closure EU	X	X		X	
Current regulation without seasonal closure riverine	X	X	X		
Current regulation without spatial closure Vandamme	X		X	X	
Current regulation without spatial closure Vandamme, without fishing at night	X		X	X	X
Current regulation without fishing at night	X	X	X	X	X
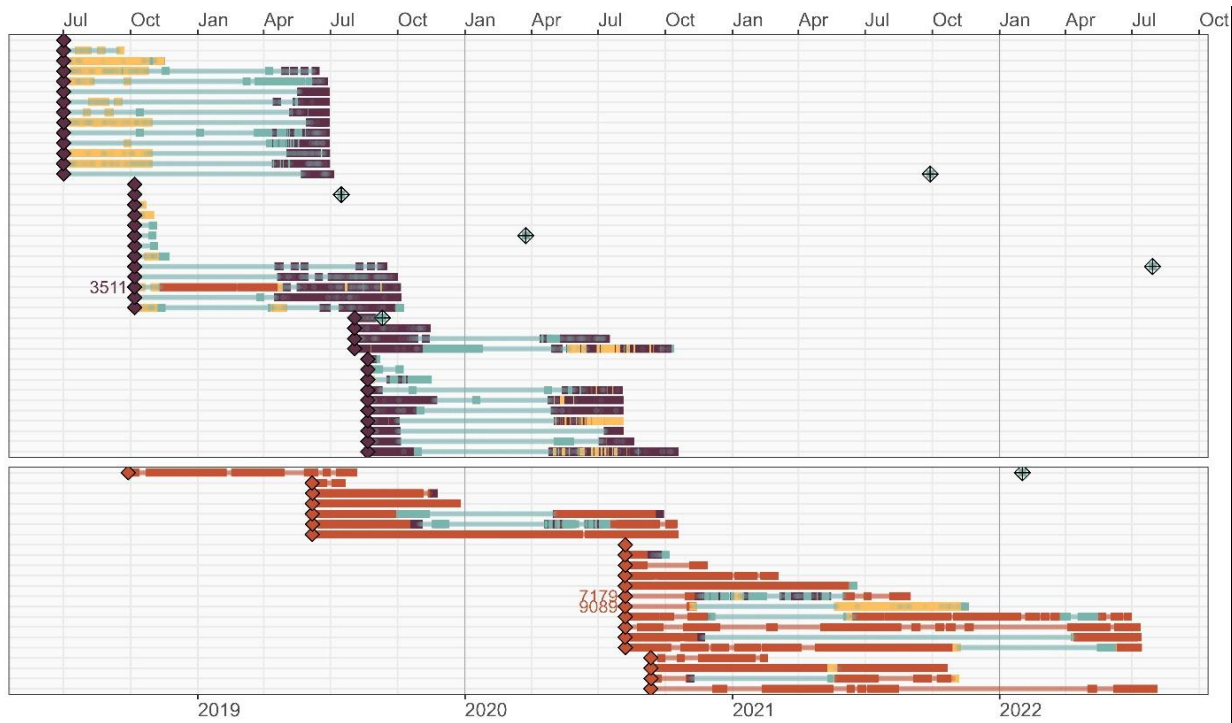
Figure 8.2. Abacus plot depicting a time line (x-axis) for individual fish (y-axis) tagged along the port walls (top) and inner harbour (bottom) with detections (bold) and likely locations (translucent), as well as the events of release (diamond) and tag recovery (crossed diamond) and coloured by location zones (port walls: purple; outer harbour: yellow; inner harbour: orange; marine waters: light blue). The ID numbers of three seabass (3511, 7179 and 9089) were highlighted: these individuals were found to deviate in habitat use patterns through the correspondence analysis (Fig. 8.4).

Table 8.4. Results of site fidelity (seabass exhibiting site fidelity out of the total number of detected animals with a time at large longer than six months) to the entire study area and to the tagging zone (inner or outer harbour) and daily and hourly residence index (RI, median [range]).

Tagging location	Length (cm)	Site fidelity		Daily RI	Hourly RI
		Study area	Tagging zone		
Inner harbour	46.5 [39.0-63.0]	16/21 (76.2%)	15/21 (71.4%)	0.29 [0.03-0.92]	0.12 [0.01-0.52]
Outer harbour	47.0 [38.0-74.0]	25/37 (67.6%)	25/37 (67.6%)	0.16 [0.00-0.56]	0.02 [0.00-0.20]
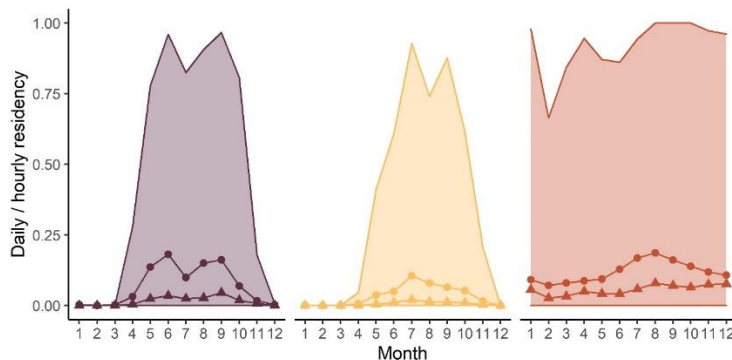
Figure 8.3. Mean daily (circle) and hourly (triangle) value for residence index(RI), calculated for each month as the percentage of time an individual fish spent in the different harbour zones (port walls: purple; outer harbour: yellow; inner harbour: orange), with the 95% quantile of daily RI (shaded area).

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Network analysis

The CA revealed a clear grouping of fish' habitat use, based on tagging location (Fig. 8.4). The first two dimensions of the CA accounted for 27.71% and 24.42% of the total variation. Fish tagged in a specific zone would mainly be associated to the stations in that zone and have a similar RI at stations as the ones tagged in the same zone. Three exceptions were noted (these ID numbers were also stated in Fig. 8.2). Tagged along the port walls, ID 3511 didn't undertake a winter migration, but instead spent the winter in the inner port. ID 7179 performed the opposite movement, using stations along the port walls and in the outer port, performing a habitat use dissimilar to the majority tagged in the inner port. The seabass with ID 9089 was the only individual observed to frequent stations LNG and ZA2. However, these stations were not deployed throughout the entire study period.

The highest values for EVC (Fig. 8.5) were found for the stations West1 (0.23), Vandamme (0.28) and Boudewijn (0.30), indicating these stations were highly frequented and served as transition points. Station Vandamme was the key transition location between inner and outer port. At least 13 fish travelled through the shipping lock, making 16 movements from inner to outer port and 10 from outer to inner port. One fish was not detected at Vandamme during this travel, which was likely due to a missed detection rather than another route. The transition probability matrix showed that movements were strongest within harbour zones. Station West1 (located near the fish capture site) served as the main transit point between the port walls and the outer port. Transition probabilities were generally highest for the same station, indicating high residency. This was less true for the port walls, where there were a lot of transits between the stations, likely due (in part) to the closer proximity between the stations here. In the inner port, the stations Herder and Visart-inner were strongly connected to Boudewijn.
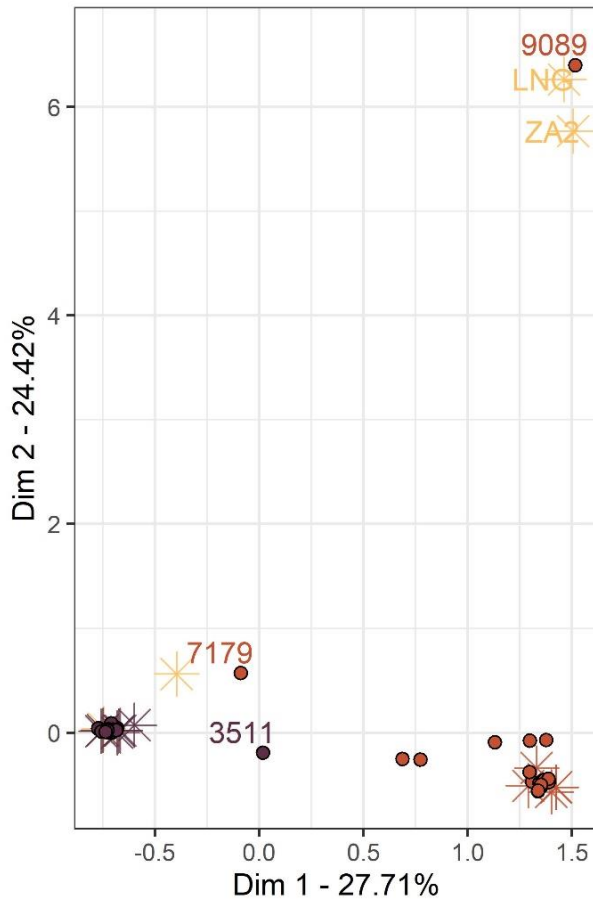
Figure 8.4. Chi-square distances along two dimensions between individual fish (circles) and receiver stations (stars), as calculated by correspondence analysis on daily residence indices. Colours reflect the harbour zones of the receiver position or animal release location (port walls: purple; outer harbour: yellow; inner harbour: orange).
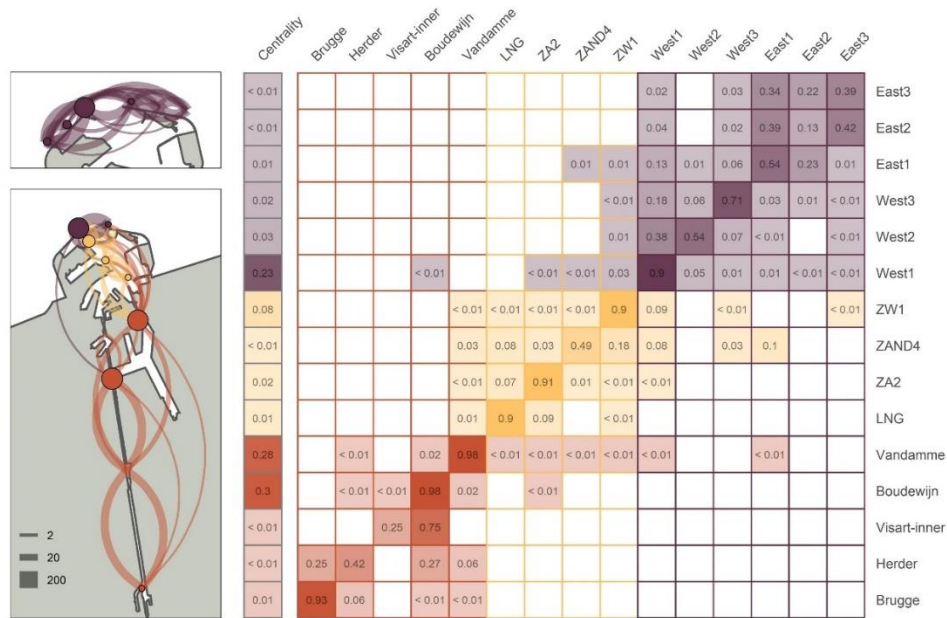
Figure 8.5. Spatial network maps of the port wall zone in detail (top left) and the entire harbour (bottom left) with nodes representing receiver location, sized by eigenvector centrality (right), and edges representing frequencies of movement between receivers (right-hand curved from origin to destination receiver station, coloured by zone of origin receiver). The transition probability matrix (D) with cells coloured by origin station (y-axis) and grid lines coloured by destination station (x-axis). Colours correspond to location zones (port walls: purple; outer harbour: yellow; inner harbour: orange).

Spatial closure

In total, 21 tagged seabass were detected at Vandamme station (9,832 DPH), where fishing was prohibited. Since Boudewijn station was the only station with comparable detection numbers (n = 18, 11,665 DPH), we limited the comparison in circadian habitat use to these two stations (Fig. 8.5), considering only the fish that were detected at both stations. Model output and validation of the GLMMs were detailed in Supporting information S8.2. The GLMM of presence resulted in a significant interaction between the factors station and day/night, indicating seabass spent more hours at Vandamme during the day and at Boudewijn during the night. In terms of both vertical distance travelled and acceleration, seabass were significantly more active during the day and at Vandamme with no significant interaction effect (Table 8.5).

Table 8.5. Output of (generalized) linear mixed models of presence and activity, listing the distribution and number of fish (N) used for the model, as well as the fixed effect estimates and standard error (SE) and the standard deviation (SD) of random effects. Significant effects had p-values of <0.001 (*) and <0.05 (^).

Model	Presence	Activity	Activity
Response variable	Number of DPH	Hourly mean vertical distance (m)	Hourly mean acceleration (3D, m/s^2)
Distribution	Poisson	Gamma	Gamma
N	18	18	6
Fixed effect (SE)			
Intercept	5.64 (0.27)*	0.07 (0.07)	0.06 (0.11)
Night	0.35 (0.01)*	-0.36 (0.06)*	-0.28 (0.05)*
Vandamme	0.31 (0.01)*	0.67 (0.07)*	0.13 (0.05)^
Night:Vandamme	-0.10 (0.02)*	-	-
Random effect SD			
Fish ID	1.16	0.13	0.13
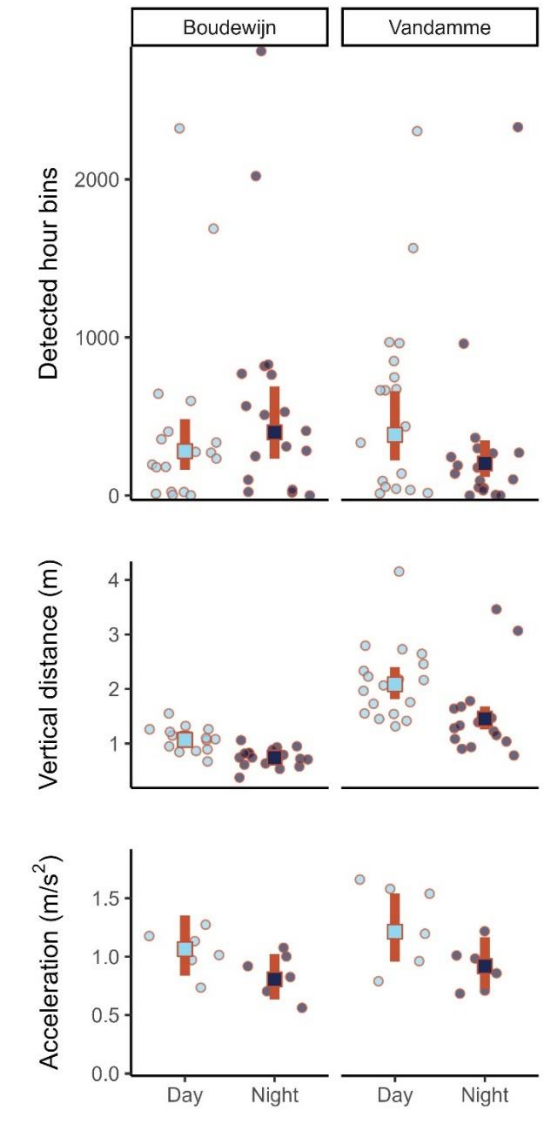
Figure 8.6. Diel differences in presence and activity at receiver stations Boudewijn and Vandamme, as evaluated with generalized linear mixed models (GLMM). Plots display observed values (circles) and GLMM fitted value and 95% confidence interval (squares and lines) for detected hourly time bins per fish (top, n = 18), hourly mean vertical distance (m) travelled between detections (middle, n = 18) and hourly mean acceleration (m/s^2) (bottom, n = 6) during day (light blue) and night (dark blue). GLMMs showed significant differences (p<0.05) between day and night and between stations for all metrics, and a significant interaction effect for the presence model (Table 8.5).

Table 8.6. Summary of generalized linear mixed model output for the different scenarios with fixed effect estimates and standard error (SE), as well as the standard deviations (SD) of the random effects ID and month. Median [range] values of the predicted probability of protection π were shown for individual seabass tagged in the outer (π_{outer}) and inner (π_{inner}) harbour. Significant effects had p-values of <0.001 (*) and <0.05 (^).

Scenario	π_{outer}	π_{inner}	**Fixed** (SE)	**ID** SD	**Month** SD
Maritime security measures	0.02 [0.00-0.21]	0.00 [0.00-0.05]	-4.35 (0.60)*	2.05	2.84
Current regulation	0.17 [0.04-0.34]	0.35 [0.03-0.70]	1.86 (0.31)*	1.13	4.19
Current regulation without seasonal closure EU	0.02 [0.00-0.34]	0.33 [0.03-0.70]	2.89 (0.43)*	1.60	1.46
Current regulation without seasonal closure rivers	0.16 [0.00-0.29]	0.10 [0.00-0.46]	-0.67 (0.44)	1.63	1.74
Current regulation without spatial closure Vandamme	0.17 [0.00-0.34]	0.24 [0.00-0.55]	1.11 (0.37)^	1.36	4.87
Current regulation without spatial closure Vandamme, without fishing at night	0.18 [0.00-0.43]	0.53 [0.25-0.81]	2.90 (0.30)*	1.13	3.71
Current regulation without fishing at night	0.18 [0.00-0.43]	0.63 [0.25-0.83]	3.13 (0.31)*	1.16	3.70

Fisheries vulnerability

When linking spatiotemporal patterns of seabass' habitat use to the protection in space and time, full models were the most appropriate for all scenarios, except for the scenario excluding the riverine seasonal closure (details on model validation in Supporting information S8.3). Under the prevailing measures in place during the study (Fig. 8.6), the protection probability of the fish tagged in the outer harbour (median π_{outer} 0.17, 95% CI 0.04-0.34) was predicted to be significantly lower than those of the inner harbour group (median π_{inner} 0.35, 95% CI 0.03-0.70). The high inter-individual variability in protection of the inner harbour group, particularly from January to June (excluding February), was attributed to the differences in habitat use of fish staying in the inner harbour and those who left during the winter.

Comparing the different scenarios showed that seabass fisheries measures increased π markedly in comparison with the scenario considering only the maritime security measures (Table 8.6). Seasonal closures increased π for both groups, but the EU seasonal closure of marine seabass fisheries mostly impacted seabass tagged at the port walls (median estimate π_{inner} increase of 0.15), while the riverine fisheries measures increased π_{inner} by 0.25. The closure of the small area around the shipping lock Vandamme hardly impacted π_{outer} but caused a reduction of π_{inner} by 0.11. When we regarded fishing in the inner harbour during the night as non-existent, the median predicted π_{inner} was as high as 0.63.
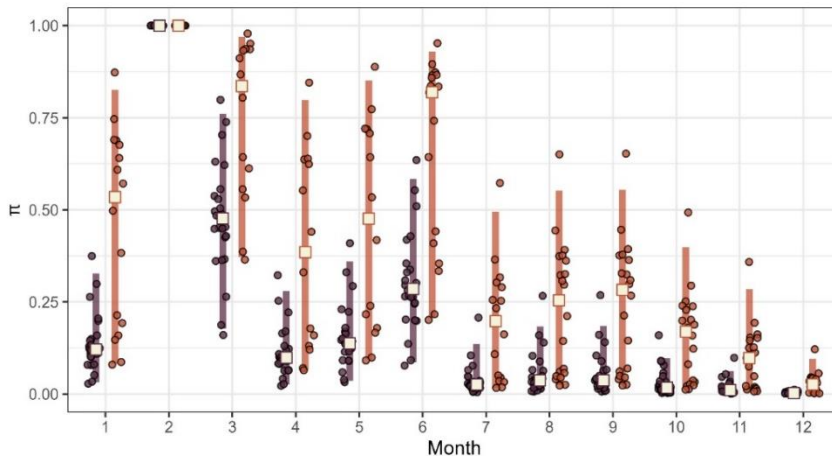
Figure 8.7. Predicted probability of protection π for individual fish (square: median; lines: 95% prediction intervals; circles: predictions for individuals)tagged in the outer (π_{outer} purple) and inner harbour (π_{inner} orange), under the regulations in place during the study (scenario current regulation).

DISCUSSION

Habitat use in the study area

Our results show that seabass exhibited residency and site fidelity to such an extent that we considered two different groups in the relatively small study area of the port of Zeebrugge. Largely sticking to their turf, these two seabass groups used the space in the study area differently. Seabass tagged in the inner or outer harbour were mainly detected at stations in these respective zones. Both groups generally exhibited high summer residency until October-November, which resumed from April-June onwards. The inner harbour seabass that left the port area during winter, spent limited time in the outer port when transiting seawards. Corroborating previous findings of high summer residency and site fidelity to small inshore areas (Doyle et al. 2017, Stamp et al. 2021), our results of two groups or population subunits at merely 3 to 15 km apart implied a complex population structure

The majority of seabass were not detected in the port during winter, when they were presumably undertaking migrations. However, at least thirteen seabass were in the study area in winter, enduring temperatures considered

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too low for gonad maturation (minimum 9 °C for females, (López et al. 2015). Potentially, some seabass don't migrate every year and skip spawning (Le Luherne et al. 2022), as illustrated by two of the seabass with tag battery times exceeding one year. Another possibility could be that some seabass never perform spawning migrations. Twelve of the overwintering bass stayed in the inner harbour, where it was possible that these seabass were not able to pass through the shipping lock. However, at least thirteen tagged bass moved from inner to outer harbour and vice versa in a seemingly targeted way.

The area specifically closed for seabass fishing at Vandamme station proved to be highly frequented by the seabass tagged in the inner harbour. The Vandamme shipping lock was the transition point between the inner and outer parts of the harbour. As seabass also frequented the Vandamme station without passing through the lock, it was impossible to conclude from our data to what extent the shipping lock could have obstructed fish movement. Local anglers stated that seabass would predate on prey fish that were gushed when the sluice opened (Deputter pers. comm.), which our findings seemed to corroborate. The diel patterns in presence and activity showed seabass were present at Vandamme mostly during the day, exhibiting high activity. At night seabass were less active and showed higher presence at station Boudewijn, a key point of passage in the inner harbour. These findings add a horizontal dimension to previously described diel vertical movement pattern (Quayle et al. 2009, Heerah et al. 2017, de Pontual et al. 2019). Interestingly, fishing was allowed at Boudewijn, but angling would mainly take place during the day. Thus, during the day seabass were mainly at Vandamme, where seabass fishing was prohibited, and headed to Boudewijn at night, when fishing was assumed to be rare. Seabass' spatiotemporal movement patterns therefore increased the protection that the spatial closure provided.

Quantifying fisheries exposure

By modelling the fisheries protection an individual seabass would benefit from, considering its habitat use, we found that seabass from the inner harbour group had a higher probability of being protected from capture. For both inner and outer harbour groups, the current seabass fisheries regulation framework increased the predicted protection substantially compared to the maritime access regulations. As expected from the diel habitat use patterns,

the spatial closure at Vandamme especially contributed to seabass protection when inner harbour fishing at night was considered to be non-existent. In the model, seasonal closures were found to have a high impact on the predicted protection. Based on the spatiotemporal patterns in fish movement and fisheries closures, protection of seabass varied throughout the year, but was consistently higher for the inner harbour group. Although aquatic tagging data has been used in numerous ways to contribute to conservation policy (Brooks et al. 2018, Hays et al. 2019, Lowerre-Barbieri et al. 2019b, Brownscombe et al. 2022), we believe we are the first to quantify a fish' protection based on the spatiotemporal fisheries management in place. The approach demonstrated a direct application of how detailed knowledge on habitat use can inform and improve fisheries management for a better conservation policy of species and habitats.

In our approach, linking habitat use to management measures, some concerns should be taken into account when interpreting the results. First of all, we used fisheries legislation, but didn't quantify fishing pressure as data on the relevant spatiotemporal scale were non-existent. Qualitative knowledge on fisheries practices could be incorporated (Marshall et al. 2023) in a similar way as the assumption that seabass angling at night in the inner harbour was rare. In light of ecosystem-based management, fish movement could also be linked to natural predation or anthropogenic stressors, such as the thermal stress and oxygen limitation in the inner harbour during heat waves or the ongoing expansion of port infrastructure. Moreover, a high probability of protection at a certain point in time would be meaningless if the exposure to fisheries was extremely high at another point in time (e.g. when leaving a protected area, a fish has to transit a passage that is blocked with nets). Quintessential to movement ecology research, spatiotemporal scale and resolution should be carefully considered. We used hourly time bins, whereby one detection could suffice to classify a fish as protected within an hour, although seabass could have roamed outside of a protected zone within 60 minutes (Pita & Freire 2011). For hourly time steps without detections, we inferred a fish' likely location which unequivocally came with error (Bruneel et al. 2020). Moreover, the likely locations presented great unevenness in spatial scale, when comparing the confinement of the inner harbour with the vastness of the potential marine range of seabass.

Our approach illustrates that different population subunits can be differentially affected or protected by the same policy framework. Quantifying the level of protection a management measure provides for an individual fish reveals the fisheries policy consequences of the common behaviour of residency and site fidelity. The behaviours of residency and site fidelity illustrate that habitat selection is highly driven by conservatism, rather than by a continuous search for the optimal habitat (Petitgas et al. 2006). As telemetry scientists call to design studies specifically to assess habitat suitability (Rudolfsen et al. 2021, Brownscombe et al. 2022), we must be wary of ignoring (learned) individual behaviour. According to the 'Entrainment hypothesis' (Petitgas et al. 2006), fish generally stick to the places and migration routes they know. Conservatism of (successful) life-cycle patterns can then be dependent on old adults transferring this knowledge and behaviour to younger individuals. Local depletion, i.e. the loss of population subunits, potentially entails the loss of learned life cycle patterns, hampering the resilience and recovery of populations that experienced overfishing (Petitgas et al. 2006, Steadman et al. 2014, Doyle et al. 2017). Behavioural conservatism of seabass and the consequential population structuring (Doyle et al. 2017, O'Neill et al. 2018, de Pontual et al. 2019, Le Luherne et al. 2022, de Pontual et al. 2023) can thus aid to clarify why the Northern seabass stock biomass has not recovered and has repeatedly been overestimated (ICES 2022c). As the value of including behavioural ecology in fisheries assessment and management is increasingly highlighted (Walker et al. 2020, Malone & Polivka 2022), our results highlight the importance of considering conservatism and entrainment in fisheries assessment and management.

By setting out from individual fish vulnerability rather than from a fisheries need, this study compels to recognize the complexity of ecological reality. When investigating fish as a commodity by default, this economic viewpoint may bias biologists and fisheries managers to ignore the complex reality of fish' learning behaviours, personalities and variability in movement ecology (Bolnick et al. 2011, Knott et al. 2021, Vigliano Relva & Jung 2021). Moreover, the plea for straightforward, simplified advice to environmental managers (Kraak et al. 2010) is in stark contrast to the distrust when sharing detailed information with stakeholders, who would very much know how to apply this knowledge (Glenn et al. 2012, Crossin et al. 2017). Rather than averaging out

the individual variability in habitat use, ecological research and environmental policy should take into account the plurality of behaviours (Spiegel et al. 2017). Although the range of biological complexities and scientific uncertainties may seem overwhelming to include in policy, they directly relate to the precautionary approach, the supposed guiding principle of environmental and fisheries management (United Nations 1995, EU 2013). For species exhibiting the abovementioned conservatism, frequented habitats and locations will likely be important to a population subunit. Rather than validating the importance of specific habitats in separate case studies, we could assume that these fish are resident to these areas, until proven otherwise. This reversed 'burden of proof' would specifically counter the risk of local depletion, which can be of utmost urgency in light of habitat loss (Stamp et al. 2022) and cumulative impacts of anthropogenic stressors (Hodgson & Halpern 2019). A true application of the precautionary approach would thus depart from the vulnerability of a fish based on its behaviour to then set out what type and extent of fisheries would be sustainable.

AUTHOR CONTRIBUTIONS

JG led the analysis and writing. GDP, JR, TM, ET, PV and JG designed the study. GDP, JR, PV and JG carried out the field work. DV, ET and JG investigated policy measures. All authors read and reviewed the drafts and approved the final manuscript.

DATA AVAILABILITY

Data are available in the DOI repository. All scripts are available on the GitHub repository https://github.com/JolienGoossens/SeabassTelPort.

ACKNOWLEDGEMENTS

SUPPORTING INFORMATION S8.1 - TAG SETTINGS

Table S8.1.1. Tag settings applied for different tag types (Innovasea Ltd., USA): V13AP (50 mm length, 13 mm diameter, 10.4 g weight in water), V9P (31 mm length, 9 mm diameter, 4.9 g weight in water) and ADST-V9TP (65 mm length, 13 mm diameter, 8.5 g weight in air). Tags transmitted temperature (T), acceleration (A) and/or pressure (P) sensor measurements. The number of tags of each type was shown for every year of deployment. For estimated battery life, it should be noted that the ADST-V9TP was programmed to effectively stop transmitting after the set number of days, whereas the V13AP and V9P could continue transmitting as long as there was battery left. Signals were transmitted at predefined settings within a step of a fixed number of days at high (H) or low (L) transmitting power output between a minimum and maximum interval. Power output was 154 dB for V13AP, 151 dB for ADST-V9TP and 146 (L) or 151 (H) dB for V9P.

Transmitter type	# tags	Estimated battery life (days)	Step 1	Step 2	Step 3
V13AP	1 (2019)	196	H 30 days (30 – 60 s)	H 168 days (140 – 220 s)	
	8 (2019: 7; 2020: 1)	490	H 495 days (140 – 220 s)		
V9P	9 (2020)	502	H 153 days (180 – 280 s)	L 120 days (300 – 400 s)	H 229 days (300 – 400 s)
ADST-V9TP	10 (2019)	339	H 90 days (240 – 360 s)	H 150 days (120 – 240 s)	H 104 days (240 – 360 s)
	30 (2018: 28; 2019: 2)	354	H 120 days (120 – 240 s)	H 239 days (240 – 360 s)	
	5 (2020)	400	H 120 days (180 – 200 s)	H 280 days (300 – 400 s)	

SUPPORTING INFORMATION S8.2 – DIEL PATTERNS VANDAMME

Model selection details and the visualization of Pearson residuals for the selected models (Fig. S8.2.1) for the comparison of the habitat use between the stations Vandamme and Boudewijn was provided below.

Presence

The day/night pattern in detected hour bins (per animal) of the stations Vandamme and Boudewijn was analysed with a generalized linear mixed model (GLMM) following a Poisson distribution (Table S8.2.1). Explanatory variables were day/night (fdn), station (fstation) and their interaction, in addition to the random effect fish ID (fid). The full model (M1) was evaluated with Chi-square tests against models excluding one of the terms in the formula (M2 and M3). The full model (M1) was selected as the final model.

M1: y ~ fdn * fstation + (1| fid)
M2: y ~ fdn * fstation
M3: y ~ fdn + fstation + (1| fid)

Table S8.2.1. Overview of model selection with Akaike Information Criterion (AIC) and the p-value of the Chi-square test comparing a model with single term deletion (M2 and M3) to the full model (M1).

Model	AIC	p
M1	23,778	NA
M2	43,858	<0.001
M3	25,849	<0.001

Activity: vertical distance

The day/night pattern in hourly mean vertical distance (m) travelled (per animal) at the stations Vandamme and Boudewijn was analysed with a GLMM following a Gamma distribution with a log link function (Table S8.2.2). Explanatory variables were day/night (fdn), station (fstation) and their interaction, in addition to the random effect fish ID (fid). The full model (M1) was evaluated with Chi-square tests against a models excluding the interaction. Model M2, excluding the interaction, was selected as the final model.

M1: $y \sim$ fdn * fstation + (1| fid)
M2: $y \sim$ fdn + fstation + (1| fid)

Table S8.2.2. Overview of model selection with Akaike Information Criterion (AIC) and the p-value of the Chi-square test a model with single term deletion (M2) to the full model (M1).

Model	AIC	p-value
M1	62.3	NA
M2	60.3	0.95

Activity: acceleration

The day/night pattern in hourly mean acceleration (m/s^2) (per animal) at the stations Vandamme and Boudewijn was analysed with a GLMM following a Gamma distribution with a log link function (Table S8.2.3). Explanatory variables were day/night (fdn), station (fstation) and their interaction, in addition to the random effect fish ID (fid). The full model (M1) was evaluated with Chi-square tests against a models excluding the interaction. Model M2, excluding the interaction, was selected as the final model.

M1: $y \sim$ fdn * fstation + (1| fid)
M2: $y \sim$ fdn + fstation + (1| fid)

Table S8.2.3. Overview of model selection with Akaike Information Criterion (AIC) and the p-value of the Chi-square test a model with single term deletion (M2) to the full model (M1).

Model	AIC	p-value
M1	-10.7	NA
M2	-11.1	0.22

SUPPORTING INFORMATION S8.3 – PROTECTION MANAGEMENT

Fisheries policy in the study area

In the study area of the port of Zeebrugge and surrounding waters, different fisheries measures were in place that restricted seabass fishing in space and time (Table S8.3.1). EU seasonal closures of fishing on the Northern seabass stock applied to commercial fisheries in February and March, while the period restricting recreational fisheries to catch-and-release for recreational fisheries varied throughout the years (EU 2018b, c, 2019a, 2020, 2021a, b, 2022a). Under the jurisdiction of the Flemish Department of Environment, seabass fisheries in inshore waters (only recreational allowed) were restricted to catch and release from January to June (Flemish Government 2017). On the same policy level, seabass fishing was prohibited throughout the year at the Vandamme shipping lock (Flemish Government 2017). Finally, some port areas were prohibited for fishing because of safety aspects, under the jurisdiction of the Zeebrugge Port authority and Maritime Access of the Flemish Department of Mobility and Public works (see Fig. 8.1 in main text).

Model selection and output

For every scenario, the protection probability was modelled with a logistic GLMM with explanatory variables tagging location (fgroup) and the random effects month (fmonth) and fish ID (fid), nested in tagging location. The full model (M1) was evaluated with Chi-square tests against models excluding one of the terms in the formula (M2, M3 and M4). The formulas of these models are:

M1: π ~ fgroup + (1|fgroup / fid) + (1|fmonth)
M2: π ~ fgroup + (1|fmonth)
M3: π ~ fgroup + (1|fgroup / fid)
M4: π ~ (1|fgroup / fid) + (1|fmonth)

Based on the single-term deletions, the full model (M1) was retained for every scenario (Table S8.3.2). The predicted probabilities of protection π were visualized in the figure below.

Table S8.3.1. Overview of fisheries measures in place at the time of the study, with the relevant policy level, the period the policy is in place and the area to which it applies, as well as the acoustic receiver stations or likely locations (LL) in that area. Measures marked with * specifically apply to seabass fishing.

Policy level	Measure	Period	Area	Receiver stations
EU	Seasonal closure commercial fisheries*	February – March	Northern stock	LL: Sea
EU	Catch & release recreational fisheries*	Jan – Sep 2018 Jan – Mar 2019 Nov 2019 – Feb 2020 Dec 2020 – Feb 2021 Dec 2021 – Feb 2022	Northern stock	LL: Sea
Department of Environment (Flemish government)	Catch & release recreational fisheries*	January – June	Rivers	LL: inner harbour
Department of Environment (Flemish government)	Spatial closure*	Always	Vandamme (inner port side of shipping lock)	Vandamme
Port authority	Fishing not allowed in specific zones	Always	Port	ZAND4, ZW1, ZOKN, LNG, ZA2,Visart-port Visart-inner
Maritime access	Fishing not allowed in specific zones	Always	Port walls	West1, West2, West3, East1, East2, East3

Table S8.3.2. Overview of model selection for each scenario with Akaike Information Criterion (AIC) and the p-value of the Chi-square test comparing the model (M2, M3, M4) to the full model (M1).

Scenario	Model	AIC	p
Maritime security measures	M1	12414.1	NA
	M2	28724.1	<0.001
	M3	26467.6	<0.001
	M4	12451.2	<0.001
Current regulation	M1	126575.1	NA
	M2	169595.2	<0.001
	M3	311637.1	<0.001
	M4	126601.8	<0.001
Current regulation without seasonal closure EU	M1	100518.0	NA
	M2	163798.0	<0.001
	M3	160461.2	<0.001
	M4	100549.1	<0.001
Current regulation without seasonal closure rivers	M1	84479.9	NA
	M2	118787.6	<0.001
	M3	197579.2	<0.001
	M4	84480.1	0.13
Current regulation without spatial closure sluice	M1	126954.8	NA
	M2	171540.0	<0.001
	M3	343403.4	<0.001
	M4	126961.2	0.004
Current regulation without spatial closure sluice, without fishing at night	M1	116850.7	NA
	M2	164940.8	<0.001
	M3	239879.0	<0.001
	M4	116903.7	<0.001
Current regulation, without fishing at night	M1	118864.6	NA
	M2	169164.7	<0.001
	M3	237313.1	<0.001
	M4	118920.9	<0.001

Maritime security measures
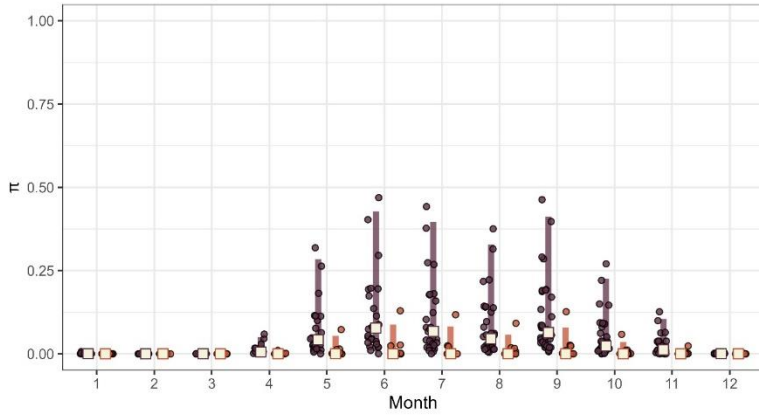
Current regulation
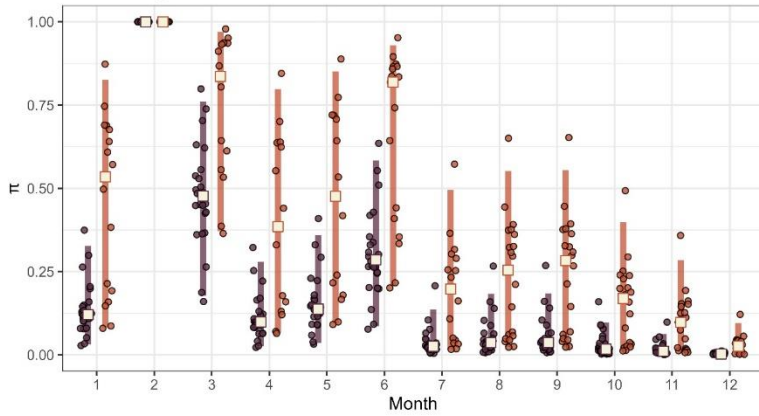
Current regulation without seasonal closure EU
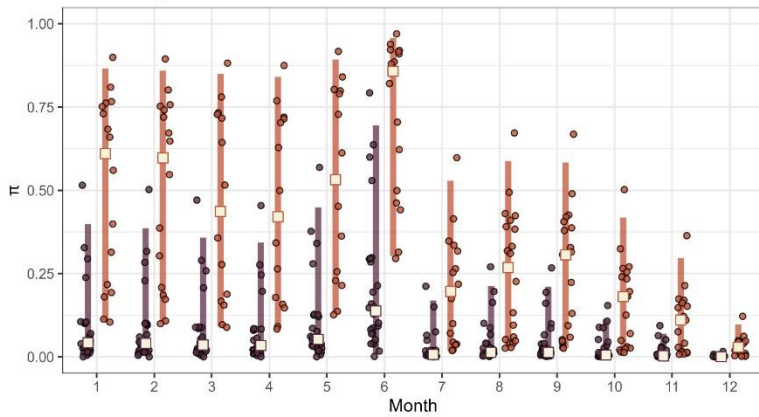
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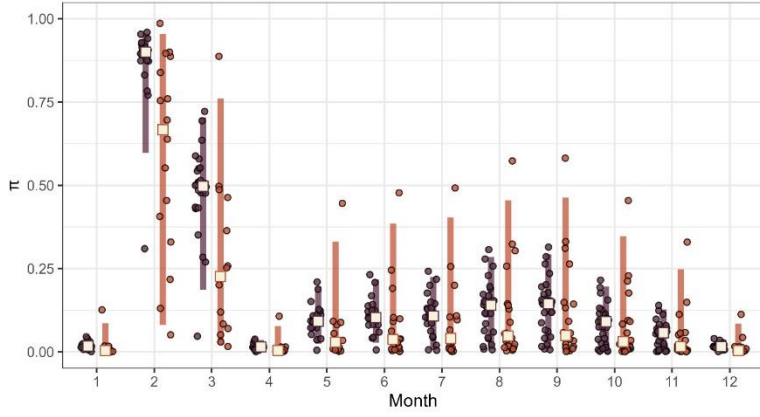
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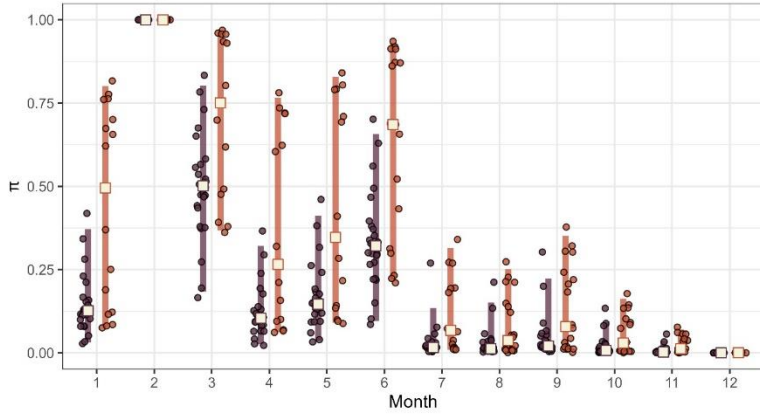
Current regulation, without fishing at night
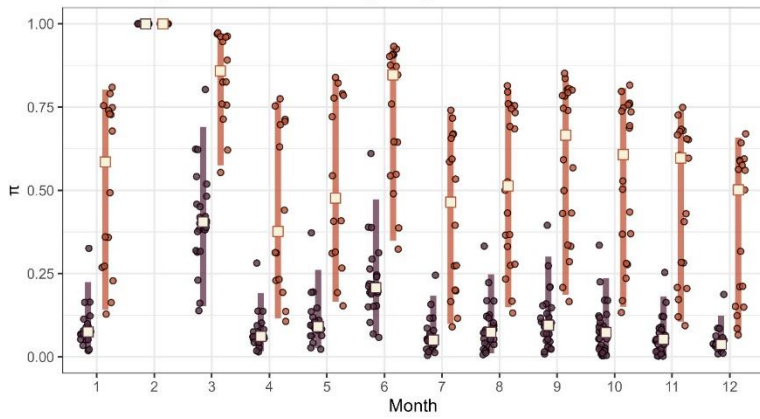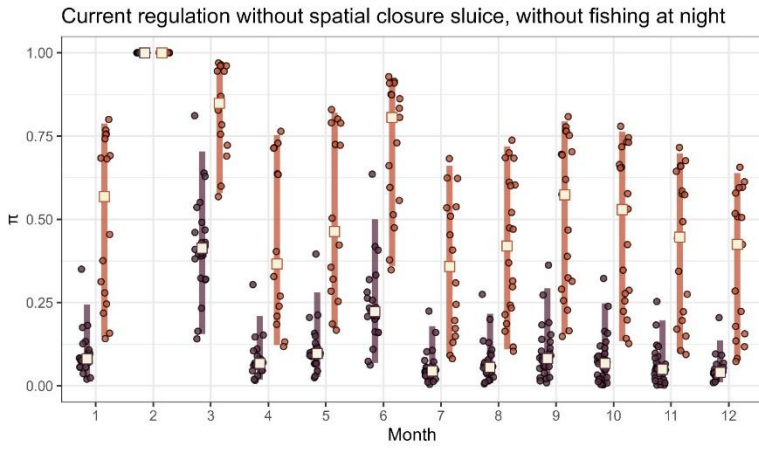
Figure S8.3.1 – Predicted probability of protection π for individual fish (square: median; lines: 95% prediction intervals; circles: predictions for individuals) tagged in the outer (π_{outer} purple) and inner harbour (π_{inner} orange), under the hypothesized regulations of the different scenarios.

III

FISHERIES POLICY

CHAPTER 9

LESSONS (STILL NOT) LEARNED FROM A DECADE OF EUROPEAN SEABASS FISHERIES POLICY

AUTHORS Jolien Goossens, Damian Villagra, Pieterjan Verhelst, Els Torreele, Jan Reubens

ABSTRACT

The Northeast Atlantic population of European seabass, *Dicentrarchus labrax* L., faced critical declines in biomass over the past two decades as a result of high fishing pressures. At the time of writing, the spawning stock biomass estimates of Northeast Atlantic stocks were below or just at the limit of maximum sustainable yield (MSY), or could not be estimated because of data limitation. From 2015 onwards, the EU took emergency measures and included seabass fisheries in multi-annual management plans. The multitude of legal documents, often adapted within a year's time, made it difficult to keep oversight of policy evolution, even within a decade of time. We provided an overview of seabass fisheries management measures since 2015, which we contextualized in the EU policy framework. In addition, we discussed the specific case of Belgium, where commercial seabass angling was at an administrative impasse due to indirect effects of a national fisheries policy system designed to accommodate demersal mixed fisheries. We highlighted three issues in (seabass) fisheries policy, common to both the European and Belgian national policy: 1) cases of decision-making procedures that lack transparency and the genuine participation of environmental organisations, 2) the failure to apply the precautionary principle, and 3) the lack of a social contract for the right to fish in the current profit maximisation framework. We plea that seabass angling could represent an exemplary small-scale fishery

with low environmental impact and high socio-economic gains, but a drastic cultural change towards marine stewardship would be required.

INTRODUCTION

European seabass, *Dicentrarchus labrax* L., are fast-moving predators that are known to tolerate a wide temperature range and predate on various prey species (Vázquez & Muñoz-Cueto 2014). The geographic range of European seabass spans from the Mediterranean Sea and Atlantic waters of Morocco and Canary Islands to the coasts of Scotland and Scandinavia in the North Sea (López et al. 2015). With rising temperatures, the suitable habitat for seabass has been expanding northwards and higher recruitment and juvenile survival rates have been noted in the northern range (Hind 2006, Colman et al. 2008). Here, we will focus on seabass in the Northeast Atlantic, which constitutes a separate lineage from Mediterranean populations, as drawn from genetic studies (Souche et al. 2015, Robinet et al. 2020). Seabass' high market value and iconic status make the species highly targeted by both commercial and recreational fisheries (Williams et al. 2018). Seabass has been caught in different marine regions, as both target and bycatch species mainly with rod and line, pelagic and bottom trawlers, nets and seines (ICES 2020b). Seabass fisheries in Northwest Europe rapidly expanded in the 1970s and 1980s, likely due to the high prices offered for seabass (Pawson 2008). Offshore fisheries (mainly mid-water pair trawlers) targeted (pre-)spawning aggregations during the colder months of November to April, while seabass in their feeding areas were caught with nets and lines from the shoreline and on boats (Pawson et al. 2007).

From the 1990s onwards, seabass fisheries measures were introduced on national levels. In the UK, there was concern for economic losses due to growth-overfishing, the harvesting of fish before they reach the size that would theoretically optimize the yield per recruit (Pawson et al. 1987, Colman et al. 2008). To protect juveniles in estuaries and cooling water outlets, 34 bass nursery areas were closed for seabass fishing (Ministry of Agriculture Fisheries and Food & Welsh Office Agriculture Department 1990). In France and the UK landings of the offshore seabass trawling fisheries were limited to 2 and later 5 tonnes per week to contain market forces (Colman et al. 2008). As the first country to prioritize recreational fishing over the commercial sector, Ireland

banned commercial fishing of wild seabass in 1990. Measures for recreational fisheries included a ban on seabass fishing using nets from boats, a bag limit (a maximum number of fish to be kept per day per person) of two seabass, along with a closed season for seabass angling from May to June (Minister for the Marine 1990, Colman et al. 2008, STECF 2014). On a European level, the minimum conservation reference size (MCRS) was put at 36 cm in 1998 (Table 9.1), despite the recommended 45 cm (Pawson et al. 1987).

In the 2010s the alarm was raised on the poor state of European seabass in the Atlantic, when both seabass biology and fisheries were considered to be poorly understood (Steadman et al. 2014). After years of excessive fishing, seabass was exploited to exhaustion (ICES 2022b, c). In its first assessment of the data-limited seabass population in the Northeast Atlantic in 2012, the International Council for the Exploration of the Sea (ICES) advised a maximum removal of 6000 tonnes, roughly a 25% reduction of the estimated commercial landings (ICES 2012b). In 2012, ICES experts delineated four seabass stocks in the Northeast Atlantic (Fig 9.1): North Spain and Portugal (southern Bay of Biscay and Atlantic Iberian waters; ICES divisions 8c,9b), Biscay (Northern and central Bay of Biscay; 8ab), West coast Scotland and Ireland (West of Scotland, West of Ireland and eastern part of southwest of Ireland; 6a,7b,j) and the Northern stock (central and southern North Sea, Irish Sea, English Channel, Bristol Cannel and Celtic Sea; 4b,c, 7a,d-h). This stock delineation was based on pragmatic considerations, since convincing biological evidence for the stock identity was lacking (ICES 2012a). Two of the stocks are considered data-limited, namely the stocks of North Spain and Portugal, and West coast Scotland and Ireland (ICES 2020a, 2021). Since 2013, ICES assessed the Bay of Biscay and the Northern stocks (Fig. 9.2), with Stock synthesis (Methot & Wetzel 2013), using fisheries-dependent and survey data on age and length, as well as biological information on growth rate and maturity (ICES 2018, 2020b). These model outputs were then applied to the framework of maximum sustainable yield (MSY), the highest yield without causing the stock to collapse in the long term (Walker et al. 2020). For the Bay of Biscay stock, fishing pressure (F) exceeded F_{MSY} (0.14) on and off for several years since the 1980s and spawning stock biomass (SSB) was estimated below MSY $B_{trigger}$ (16,688 tonnes) between 2016 and 2019 (ICES 2022c). Fisheries on the Northern stock exerted pressures higher than F_{MSY} (0.17) between 1996 and 2016, with F

estimates reaching up to 0.31, thus exceeding the limit (F_{lim} = 0.25) and precautionary (F_{pa} = 0.20) reference points. The Northern stock biomass fell below MSY $B_{trigger}$ (14,439 tonnes) ever since 2014 and was estimated below B_{lim} (10,313 tonnes) from 2016 to 2019 (ICES 2022b). The behaviours of residency and forming spawning aggregations added to the vulnerability of seabass to (local) depletion (Pawson et al. 2007, Doyle et al. 2017).

Emergency measures were taken on a European level from 2015 onwards. Despite the taken measures and the proclaimed commitment to the conservation of European seabass on European (EU 2015e) and national levels (De Snijder et al. 2014, Ares & Sutherland 2016), recovery of seabass in the Atlantic has been precariously slow (ICES 2022b, c). In this paper, we contextualize seabass fisheries policy frameworks over the past decade in the European Union and the specific case of Belgium. Belgium constitutes an interesting case study, because policy measures for commercial seabass fisheries are currently at an awkward standstill because of administrative reasons. It is important to state that the reality of how fisheries are managed results from the intertwined effects of different fisheries management measures (quota allocation systems, licensing of vessels, spatiotemporal restrictions etc.), as well as socioeconomic, political and cultural contexts (e.g. national labour laws, market regulation, colonial and patriarchal power structures), and of course biological aspects, such as biomass and population dynamics (Bavington et al. 2004, Pauly 2018, Said et al. 2020, Reid et al. 2021). Likewise, compliance to fisheries policy will be an interaction of different factors (Grilli et al. 2019, Oyanedel et al. 2020). Here, we provide an overview of seabass policy, fully realizing that we don't cover all aspects of an ongoing history. Our goals are 1) to describe the European framework of seabass fisheries policy, providing an overview of the legislation, 2) to frame the management of seabass fisheries in Belgium and 3) to highlight key issues in the policy framework. By analysing and discussing the policy context of the past decade, we hope to contribute to seabass conservation policy in the future.
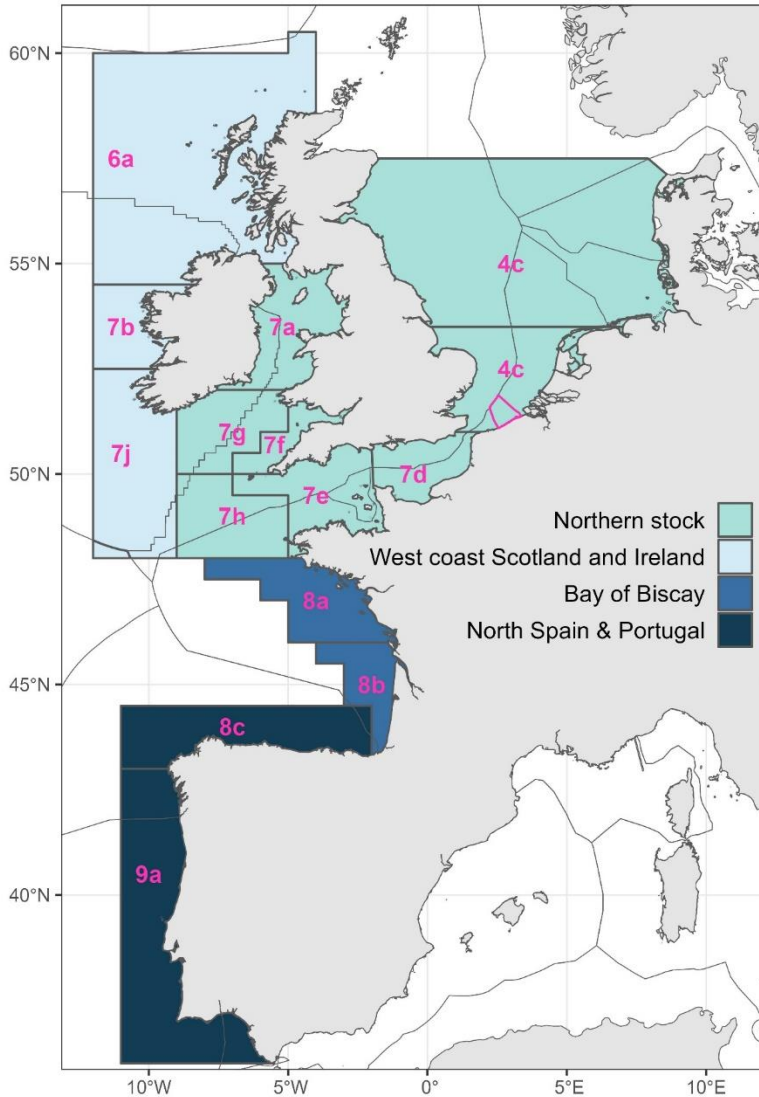
Figure 9.1. ICES stock divisions for European seabass in the Northeast Atlantic: southern Bay of Biscay and Atlantic Iberian waters (North Spain and Portugal; ICES divisions 8c,9b), northern and central Bay of Biscay (Biscay; 8ab), West of Scotland, West of Ireland and eastern part of southwest of Ireland (West coast Scotland and Ireland; 6a,7b,j) and the central and southern North Sea, Irish Sea, English Channel, Bristol Cannel and Celtic Sea (Northern stock; 4b,c, 7a,d-h). The map shows the exclusive economic zones (EEZ), with the Belgian EEZ highlighted in pink. Shape files originated from ICES (https://gis.ices.dk) and Marine Regions (https://www.marineregions.org).

Table 9.1. Chronological overview of EU level legislative documents defining the minimum conservation reference size (MCRS, cm) for European seabass.

Year	Document	Area	MCRS (cm)
1989	4056/89	Regions[1] 2 – 3	32
1990	4056/89	Regions[1] 2 – 3	36
1998	850/98	Regions[1] 1 – 5	36
2015	2015/1316	Region[1] 2	42
2019	2019/1241	North Sea + North Western Waters	42
		South Western Waters	36
		Mediterranean Sea	25
2020	2020/123	Recreational fisheries in	42
2021	2021/92	4b,c, 6a, 7a-k + 8a,b	
2022	2022/109		

Regions as defined in EEC 3094/86. In the terminology of the defined ICES stocks in the Northeast Atlantic, the West coast Scotland and Ireland stock is within Region 1, the Northern stock in Region 2 and the stocks of North Spain and Portugal and Bay of Biscay in Region 3.
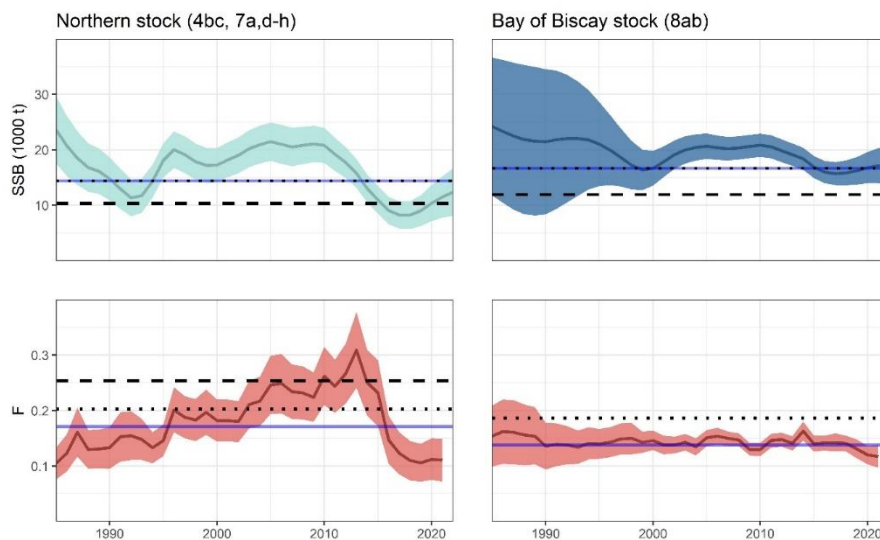
Figure 9.2. Time series (1985 – 2022) of spawning stock biomass (SSB, top) and fishing mortality (F, bottom) as assessed by ICES for the Northern (left) and Bay of Biscay stock (right). Horizontal lines indicate thresholds for the limit reference point (dashed), precautionary reference point (dotted) and maximum sustainable yield (blue). Data were accessed through the R package *icesSAG* (Millar et al. 2022).

EUROPEAN SEABASS FISHERIES MANAGEMENT

European fisheries policy framework

The legislative framework of European Union fisheries for the following decade is set out in the common fisheries policy (CFP), ever since 1983. The CFP constitutes a Council Regulation, meaning that member states have to implement the regulation literally and directly, as opposed to e.g. a framework directive, that delineates goals to be achieved and needs to be transposed into national law. After decades (and centuries) of excessive extraction of marine wildlife, the 2013 CFP envisioned a far-reaching reform of European fisheries with the long-term outlook to contribute to food security in an inherently sustainable way (EU 2013). By 2020 at the latest, sustainable exploitation rates (within the MSY definition) had to be ensured for all EU stocks. Within the CFP, a stock was defined as a marine biological resource that occurs in a given management area. The aim was to evolve from single-species fisheries management towards an ecosystem-based fisheries management (EBFM) approach: Fisheries of entire regions were to be managed under multi-annual plans (MAP), entailing long-term policy frameworks for fisheries targeting and catching multiple species. Rather than one threshold for sustainable fishing pressure (F_{MSY}), the total allowable catches (TAC) would now be based on a range ($F_{MSY\ lower}$ to $F_{MSY\ upper}$) to account for the realities of mixed fisheries and interspecies dynamics (EU 2019b). In line with the European objective of good environmental status by 2020 (EU 2017a), the CFP provided the basis of the legal procedure for spatial fisheries management, contributing to the objectives of other environmental policies such as the Marine Strategy Framework Directive (EU 2008). To consolidate socio-economic sustainability, stakeholder engagement was formally made part of the legislative processes, mainly though the Advisory Councils where different players of the commercial and recreational fishing sector were represented, as well as environmental NGOs and representatives of consumers and civil society (EU 2015a, Van Bogaert et al. 2022).

Progress was made since the 2013 CFP reform, but policy makers failed to deliver on legislative targets. The 2020 deadline for fishing pressures below F_{MSY} was not met: For stocks in the Northeast Atlantic, F_{MSY} was exceeded for 44% (35/79) in 2013, whereas this percentage decreased to 26% (21/81) in

2021 (STECF 2023). The CFP listed small-scale fisheries as management priority, but the effective allocation of fishing opportunities remained to be distributed along the lines of neoliberal economic efficiency (Said & Chuenpagdee 2019). The EU was evaluated to be slacking and counteractive in the global commitment to ending overfishing. Although subsidies contributing to overcapacity were to be prohibited by 2020 in line with the sustainable development goals (United Nations 2015), 54% of EU fisheries subsidies (at a value of 2.036 billion USD) were still targeted at enhancing capacity in 2018 (Sumaila et al. 2019). The subsidised overcapacity contributed to fisheries overexploitation outside of EU borders (e.g. in West and Central Africa), where 'Sustainable Fisheries Partnership Agreements' with third countries provided a framework for EU vessels to legally exploit marine wildlife at pressures exceeding F_{MSY} (Okafor-Yarwood & Belhabib 2020). At the time of writing, the next reform of the CFP was being drafted and elaborated (Commission 2023).

Seabass fisheries policy: Emergency measures

After the UK government (Ares & Sutherland 2016) and the European Parliament (EU 2015e) urged for the preservation of seabass stocks, the Commission committed to the protection of this iconic species. The chronology of increasingly drastic measures (Table 9.2) suggested the situation was initially underestimated. In January 2015, the yearly Council Regulation setting the fishing opportunities for 2015 didn't mention seabass (EU 2015c). One week later, the Commission banned pelagic and midwater trawls to fish for the Northern seabass stock (ICES 4b,c, 7a,d-k) from January to April (EU 2015b). For the first time in June 2015, catch limitations for seabass restricted different gear types to monthly catch limits: 1.3 tonnes for hooks and lines, 1 ton for gill nets, 1.8 tonnes for demersal trawls and seines, 3 tonnes for purse seines and 1.5 tonnes for pelagic and mid-water trawls (EU 2015d). In addition, commercial fisheries were prohibited in an entire area around Ireland (7b,c,j,k and 7a,g beyond the 12 nautical mile zone of the UK, Fig. 9.1). From 2016 onwards, seabass was included in the yearly regulation setting fishing opportunities. The 2016 measures (EU 2016) for seabass fisheries were structured similarly as the 2015 regulations, with the addition of a seasonal closure for all gears to protect spawning aggregations of the Northern stock. Seabass fisheries were henceforth prohibited in February and March in the

Northern stock range (ICES 4b,c, 7d-f,h and 7a,g within the 12 nm zone of the UK). The emergency measures taken in 2015 and 2016, including the spatial and seasonal closures, provided the basis of the measures in the following years.

From 2017 until 2022 (EU 2017b, 2018b, 2019a, 2020, 2021a, b, c, 2022a, b), targeted fishing for the Northern seabass stock was only allowed for vessels fishing with hooks and lines. Catch limitations for these vessels were expressed as an amount per vessel per year (PVPY). Apart from the 2017 catch limit of 10 tonnes PVPY, yearly catch limits varied between 5 and 6 tonnes since 2018. Vessels using fixed gillnets, demersal trawls and seines could land seabass as unavoidable by-catch, with the allowable amount per vessel expressed as a yearly, monthly or two-monthly maximum amount per vessel and/or a percentage of the weight of the total catch. For the Bay of Biscay stock, the yearly measures stipulated France and Spain should ensure the fishing mortality would not exceed F_{MSY}. Catch limits per vessel were therefore not specified in EU law, but could still be introduced on other management levels, e.g. measures for French vessels stipulated by the Comité national des pêches (CNPMEM 2023).

An important restriction was added in 2017: vessels using hooks and lines or gill nets could only fish for the Northern seabass stock if they had historical official recorded catches from July 2015 to September 2016 (EU 2017b). These vessel owners were thus awarded exclusive seabass fishing rights, rendering the vessels associated to these licenses, more valuable. Aside from the general issues that so-called 'fishing rights' posed regarding privatization and distributive justice (Pauly 2018), this restriction rewarded those that continued to fish at the time of the stock's most precarious state. Moreover, vessels without registered seabass catches were excluded from seabass fishing in the future, which could render problems for national fisheries policy (as in the Belgian case, see below).

Table 9.2. Chronological overview of EU level fisheries measures (accessible through https://eur-lex.europa.eu/), concerning commercial fisheries of European seabass. The described measures include spatial closures, seasonal closures and catch limitations for distinct gear types in specific areas. Gear types are detailed in caption with FAO alpha 3 fishing gear codes. Areas are identified with the codes of ICES divisions. Seabass catch and unavoidable by-catch (BC) limitations are delineated as tonnes or kilograms per vessel per month (PVPM), per vessel per two months (PVP2M), per vessel per year (PVPY) or as a percentage of the weight of the total catch of marine organisms on board (WTC; since 2017 formulated as: weight of total catch of marine organisms on board caught by that vessel in any single day). When catch restriction units deviated from previous legislation, this was marked in orange. Gear codes mentioned in footnotes complied with the ISSCFG FAO classification (FAO 2016).

Year	Document	Spatial closure[1]	Seasonal closure[2]	Catch limitation[3]	Hooks and lines[4]	Fixed gillnets[5]	Demersal trawls[6]	Seines[7]	Other gears
2015	2015/104	-	-	-					
	2015/111	-	4b,c, 7a,d-k Pelagic trawls[8] *Jan – Apr*	-					
	2015/960*	7b,c,j,k + 7a,g UK >12 nm	-	4b,c, 7d-f,h + 7a,g UK <12nm *Jan (June) – Dec*	1.3 t PVPM	1t PVPM	1.8 t PVPM	1.8 t PVPM	3 t PVPM purse seines[9] 1.5 t PVPM pelagic trawls[10]
2016	2016/72	7b,c,j,k + 7a,g UK >12 nm	4b,c, 7d-f,h + 7a,g UK <12nm *Feb – Mar*	4b,c, 7d-f,h + 7a,g UK <12nm *Jan + Apr – June*	1.3 t PVPM	1.3 t PVPM	1% WTC (incl. Feb – Mar)	1% WTC (incl. Feb – Mar)	Not allowed
				4b,c, 7d-f,h + 7a,g UK <12nm *Jul – Dec*	1.3 t PVPM	1.3 t PVPM	1 t PVPM	1 t PVPM	1 t PVPM
2017	2017/127	7b,c,j,k + 7a,g UK >12 nm	4b,c, 7d-f,h + 7a,g UK <12nm *Feb – Mar*	4b,c, 7d-f,h + 7a,g UK <12nm *Jan + Apr – Dec*	10 t PVPY°	250 kg PVPM BC°	3% WTC BC 400 kg PVPM	3% WTC BC 400 kg PVPM	Not allowed
2018	2018/120	7b,c,j,k + 7a,g UK >12 nm	4b,c, 7d-f,h + 7a,g UK <12nm *Feb – Mar*	4b,c, 7d-f,h + 7a,g UK <12nm *Jan + Apr – Dec*	5 t PVPY°	1.2 t PVPY BC°	1% WTC BC 100 kg PVPM	1% WTC BC 180 kg PVPM	Not allowed

Year	Document	Spatial closure[1]	Seasonal closure[2]	Catch limitation[3]	Hooks and lines[4]	Fixed gillnets[5]	Demersal trawls[6]	Seines[7]	Other gears
2019	2019/124	7b,c,j,k + 7a,g UK >12 nm	4b,c, 7d-f,h + 7a,g UK <12nm *Feb – Mar*	4b,c, 7d-f,h + 7a,g UK <12nm *Jan + Apr – Dec*	5.5 t PVPY°	1.4 t PVPY BC°	1% WTC BC 400 kg PVP2M	1% WTC BC 210 kg PVPM	Not allowed
2020	2020/123	7b,c,j,k + 7a,g UK >12 nm	4b,c, 7d-f,h + 7a,g UK <12nm *Feb – Mar*	4b,c, 7d-f,h + 7a,g UK <12nm *Jan + Apr – Dec*	5.7 t PVPY°	1.4 t PVPY BC°	5% WTC BC 520 kg PVP2M	5% WTC BC 520 kg PVP2M	Not allowed
				8a,b			2,533 t TAC (France + Spain)		
2021	2021/92	*7a-c,g,j,k*	4b,c, 7d-f,h *Feb – Mar*	4b,c, 7d-f,h *Jan*	1.43 t PVPY	0.35 t PVPY	5% WTC BC 520 kg PVP2M	5% WTC BC 520 kg PVP2M	Not allowed
				8a,b			3,108 t TAC (France + Spain)		
	2021/703*			4b,c, 7d-f,h *Jan + Apr - Jul*	3.32 t PVPY	0.82 t PVPY	5% WTC BC 520 kg PVP2M	5% WTC BC 520 kg PVP2M	Not allowed
	2021/1239*			4b,c, 7d-f,h *Jan + Apr - Jul*	5.7 t PVPY	1.4 t PVPY	5% WTC BC 380 kg PVPM	5% WTC BC 380 kg PVPM	Not allowed
2022	2022/109	7a-c,g,j,k	4b,c, 7d-f,h *Feb – Mar*	4b,c, 7d-f,h *Jan*	1.43 t PVPY	0.35 t PVPY	5% WTC BC 520 kg PVP2M	5% WTC BC 520 kg PVP2M	Not allowed
	2022/515*			4b,c, 7d-f,h *Jan + Apr - Dec*	5.95 t PVPY	1.5 t PVPY	5% WTC BC 760 kg PVP2M	5% WTC BC 760 kg PVP2M	Not allowed
				8a,b			3,156 t TAC (France + Spain)		

[1] Prohibited for Union vessels to retain on board, tranship, relocate or land seabass caught in the specified ICES divisions. - [2] Prohibited for Union vessels to retain on board, tranship, relocate or land seabass caught in the specified ICES divisions during the specified period. - [3] Catch limits are not transferable between months or vessels. For vessels using more than one gear in a single calendar month, the lowest catch limit is applied. - [4] All long lines or pole and line or rod and line fisheries, including LHP, LHM, LLD, LL, LTL, LX and LLS. - [5] All fixed gillnets and traps, including GTR, GNS, FYK, FPN and FIX. - [6] All types of demersal trawls, including OTB, OTT, PTB, TBB, TBN, TBS, TB. - [7] All types of seines, including SSC, SDN, SPR, SV, SB, SX. - [8] Mid-water or pelagic trawls, including OTM and PTM, with cod end mesh size of ≥ 70 mm. - [9] Purse seines with gear codes PS and LA. - [10] Mid-water or pelagic trawls, including OTM and PTM. - * Amendment of a legal document within the same year. - ° Fishing for European seabass is only allowed for Union fishing vessels with recorded catches of seabass in the period from July 2015 to September 2016 using hooks and lines or fixed gillnets.

Table 9.3. Chronological overview of EU level measures concerning recreational fishing of European seabass. The described measures include seasonal closures, meaning only catch-and-release is allowed in a specific area during a set period, and catch limitations, delineated as number of seabass that can be retained per day per person (PDPP). Areas are identified with the codes of ICES divisions. When catch restriction units deviated from previous legislation, this was marked in orange.

Year	Document	Seasonal closure: Catch-and-release[1]	Catch limitations Area		Amount
2015	2015/523*	-	4b,c, 7a,d-k		
				Jan (March) – Dec	3 PDPP
2016	2016/72	4b,c, 7a,d-h *Jan – June*	4b,c, 7a,d-h	*Jul – Dec*	1 PDPP
			7j,k	*Jan – Dec*	1 PDPP
2017	2017/127	4b,c, 7a,d-h *Jan – June*	4b,c, 7a,d-h	*Jul – Dec*	1 PDPP
			7j,k	*Jan – Dec*	1 PDPP
			8a,b	*Jan – Dec*	5 PDPP
2018	2018/120	4b,c, 7a-k *Jan – Dec*	8a,b	*Jan – Dec*	3 PDPP
	2018/1308*	4b,c, 7a-k *Jan – Sep*	4b,c, 6a, 7a-k	*Oct – Dec*	1 PDPP
2019	2019/124	4b,c, 6a, 7a-k	4b,c, 6a, 7a-k	*Apr – Oct*	
		Jan – Mar + Nov – Dec			1 PDPP
			8a,b	*Jan – Dec*	3 PDPP
2020	2020/123	4b,c, 6a, 7a-k	4b,c, 6a, 7a-k	*Mar – Nov*	
		Jan – Feb + Dec			2 PDPP
			8a,b	*Jan – Dec*	2 PDPP
			Fixed nets banned		
2021	2021/92	4b,c, 6a, 7a-k *Jan – Feb*	4b,c, 6a, 7a-k	*Mar*	2 PDPP
			8a,b	*Jan – Dec*	2 PDPP
			Fixed nets banned		
	2021/703*		4b,c, 6a, 7a-k	*Mar – July*	2 PDPP
	2021/1239*	4b,c, 6a, 7a-k	4b,c, 6a, 7a-k	*Mar – Nov*	
		Jan – Feb + Dec			2 PDPP
2022	2022/109	4b,c, 6a, 7a-k *Jan – Feb*	4b,c, 6a, 7a-k	*Mar*	2 PDPP
			8a,b	*Jan – Dec*	2 PDPP
			Fixed nets banned		
	2022/515*	4b,c, 6a, 7a-k	4b,c, 6a, 7a-k	*Mar – Nov*	
		Jan – Feb + Dec			2 PDPP

[1] Prohibited to retain on board, relocate, tranship or land European seabass caught in the specified ICES divisions.

* Amendment of a legal document within the same year.

Recreational fisheries

European seabass is a popular species for recreational angling. An estimated two million European anglers yearly spend more than 200 million euro on seabass fishing (EAA 2016). Catch-and-release was considered to be a common practice in seabass angling, resulting in estimated low post-release mortality (Lewin et al. 2018). Nonetheless, recreational fishing could be responsible for over 25% of a country's seabass removals (Hyder et al. 2018, Radford et al. 2018).

The EU emergency measures also considered recreational fishing (Table 9.3). A bag limit was introduced, ranging from five to one depending on the area and year. In the Northern stock and along the West coast of Ireland (4b,c, 7a,d-k), recreational fishing was additionally limited to catch-and-release from January to June 2017 and throughout the entire year in 2018. After intense protest and lobbying of recreational fishers (see below), the yearlong catch-and-release restriction was abandoned and exchanged for a one bag limit. From 2020 onwards, a two bag limit was in place for the Bay of Biscay, the West coast Scotland and Ireland and the Northern stock. For the latter two stocks, the seasonal catch-and-release period was set from December to February. Additionally, recreational fishing with fixed nets was banned since 2020 for all seabass stocks in the Northeast Atlantic.

Over the past decade, recreational fishers called for changing the allocation of seabass fishing opportunities between commercial and recreational fisheries. Although recreational fishers were represented in the Advisory Councils, their involvement in management decisions was considered scarce (Pita et al. 2017, Van Bogaert et al. 2022) and joint policy recommendations with the commercial sector proved to be impossible in some cases (NNWAC & NSAC 2018). When recreational angling was restricted to catch-and-release only in 2018 (whereas commercial vessels could land up to 5 tonnes) (EU 2018b), tension peaked. Recreational fishers took to the streets in Cherbourg and Calais (France) and the European Anglers Alliance (EAA) took the Council of the EU to court (EAA 2018a, EU 2018a). The legal basis of these claims lie in article 17 of the CFP, stating "transparent and objective criteria including those of an environmental, social and economic nature" should be applied for the allocation of fishing opportunities (EU 2013). Arguments to favour recreational

seabass fishing included its high participation rates, the generated economic profits and recreational fishers' welfare (EAA 2018b, Cevenini et al. 2023). The data poverty on recreational fisheries often hamper effective governance, but research on recreational fisheries (including the socio-economic and biological impacts) is rapidly expanding and is set to improve data collection and monitoring (Hyder et al. 2020).

MAP & current stock status

Since 2019, seabass fisheries of all delineated stocks in the Northeast Atlantic were managed under the Western Waters MAP (EU 2019b). Spatiotemporal closures and the quantified fishing opportunities were still outlined in a yearly regulation, but the MAP provided the management framework. The yearly ICES advices provided the estimates of fishing mortality (F) ranges based on this MAP. In case the stock biomass falls below the reference points of B_{lim} or MSY $B_{trigger}$, the MAP states that all appropriate remedial measures should be taken to ensure that the stock rapidly returns to biomass capable of producing MSY. Concerning recreational fishing, the MAP states the Council could set non-discriminatory limits, explicitly taking into account any socio-economic importance.

As a result of the fisheries measures, fishing pressure on the Northern and Biscay stocks decreased and was assessed to have been below F_{MSY} for several years (Fig. 9.2). In 2022, the majority of commercial landings came from nets and lines, followed by bottom trawls (Fig. 9.3) (ICES 2022b, c). Commercial landings of the Northern stock were mainly fished by the UK (613 t, 54%), followed by France (385 t, 34%), the Netherlands (231 t, 21%) and Belgium (45 t, 4%), whereas France was almost entirely responsible for Biscay stock catches. Estimated recreational removals (derived from historical catch records) represented 24% of the total catch for both stocks. At the time of writing, the SSB estimates were below (Northern stock) or just at the limit (Bay of Biscay stock) of B_{MSY}. Using new scientific information, the stock delineation and assessment of the Bay of Biscay and Northern stocks are revised in ICES benchmark workshops in 2023 (ICES 2023). ICES considered the stocks of North Spain and Portugal and of West coast Scotland and Ireland data limited, advising a precautionary approach since 2016 (ICES 2020a, 2021).
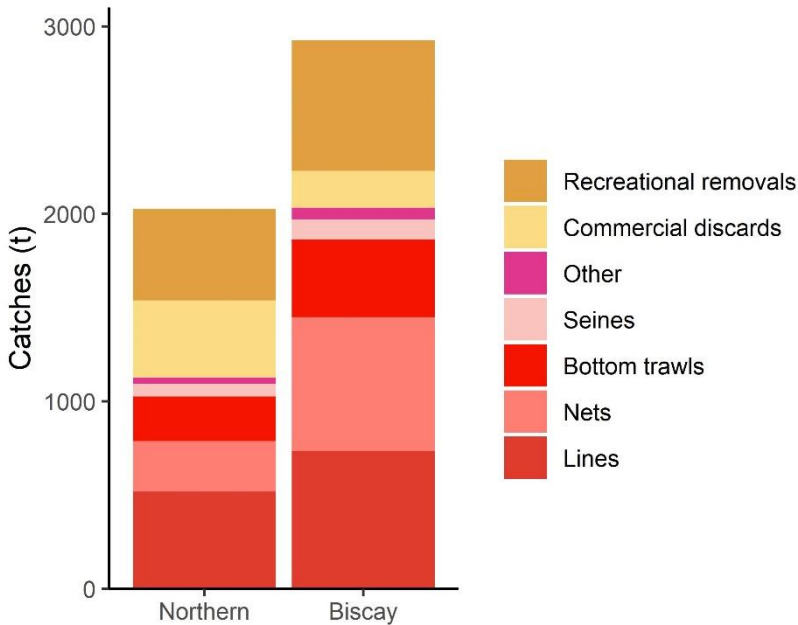
Figure 9.3. Catch shares by gear for commercial landings, in addition to commercial discards and estimated recreational removals for the Northern (left) and Bay of Biscay stock (right), as reported by ICES in 2022 (ICES 2022b, c).

SEABASS FISHERIES MANAGEMENT IN BELGIUM

Belgian fisheries management context

Despite fisheries policy being primarily set out in European regulations, certain aspects were managed by member states, e.g. the allocation of national quota. In Belgium, the use and exploitation of aquatic resources and environments fell under different ministries at different legislative levels (full overview of maritime competences for different institutional bodies in Pecceu et al. (2016)). Whereas activities in the BPNS were under the Belgian federal jurisdiction (Department for the Marine Environment of the Federal Public Service Health, Food chain safety and environment), marine fisheries were under the Flemish government (Department of Agriculture and Fisheries), as well as inland fisheries (Department of Environment). In addition, local governments could put spatial, temporal and/or administrative restrictions to recreational fishing (full overview of local rules available at website Recvis project

). Below, we refer to Belgian fisheries management, but it is important to keep in mind that the mentioned fisheries measures are not regulated at the federal level, but at the Flemish level.

The Belgian fisheries management system was designed to cater for the needs of benthic and demersal multi-species commercial fisheries targeting sole and plaice, which made up the majority of the Belgian commercial fleet (56 out of 63 vessels). In the Belgian system, the yearly allocated TACs to Belgium would be considered as a collective right among the holders of a Belgian fisheries license. Thus, a license provided access to the fishing rights of Belgium, as opposed to management systems where a license would provide the right to fish separately from the actual access to a part of the national quota, e.g. through individual transferable quota. Accessory measures were added to meet the needs of European policy over the past decades, making the collective quota system more complex over time, as reviewed in (Verlé et al. 2020). As national commercial fleets could not exceed the set maximum capacity defined in kW and GT (EC 2002), a vessel would only obtain a fishing license if another vessel exited the fleet. The purchase of a fishing license, inherently coupled with the licensed vessel, was thus subject to market forces and competition, pushing up the price of licensed vessels. As the purchase of vessel was only profitable if you make optimal use of the gained access to the Belgian quota, the system indirectly disfavoured fisheries targeting species that were not managed under TAC (Verlé et al. 2020), such as seabass.

Recreational fisheries

Assessments of Belgian recreational fisheries, under the project Recvis and the national implementation of the Data Collection Framework (EC 2017/1004), resulted in an estimated 1.3 million fish caught over 100,000 fishing hours per year (Verleye et al. 2022). Estimates for the direct economic interest of Belgian recreational marine fishers range between 8.6 (Verleye et al. 2019) and 33 million euro per year (Hyder et al. 2018). More than 800 recreational vessels were identified, of which the majority was used for angling (87 %) (Verlé et al. 2020, Verleye et al. 2022). In addition, anglers targeted seabass from shore on the beach, piers and breakwaters. Seabass was one of the main target species for anglers on boats and on the beach.

Commercial fisheries in inland waters (e.g. rivers and canals) were prohibited, but recreational fishing was allowed with a license (Flemish Government 2013). In light of incessant seabass poaching (Deputter, pers. comm.), specific measures for seabass angling were taken for inland waters in 2017 (Flemish Government 2017). These corresponded the EU measures for recreational seabass angling at the time and included a MCRS of 42 cm, a catch-and-release period of January to June and a daily bag limit of 1 seabass for the rest of the year. Small spatial closures specifically for seabass fishing were installed in the ports of Zeebrugge and Oostende near shipping locks where seabass was targeted whilst presumably predating on prey fish that are flushed with incoming water (Chapter 8). The area in Oostende was restricted to catch-and-release, whereas seabass fishing was prohibited altogether in Zeebrugge (Flemish Government 2017, Cardoen et al. 2023a), with the exception of a mark-recapture research project (see chapter 6).

Commercial seabass angling with Dutch licenses

As an indirect consequence of the Belgian quota allocation system (indirectly pushing up the price of licensed vessels, that are designed for mixed fisheries, as elaborated in Verlé et al. (2020)), Belgian nationals turned to the Netherlands as a flag state for commercial seabass angling. Because of a different licensing and quota allocation system and a larger fleet capacity (with more available kW and GT), access to fishing rights for smaller boats was easier in The Netherlands than in Belgium. In addition, the Belgian regulations regarding crew and safety on board of a vessel were considered to be more strict (Verlé et al. 2020). The association 'Low impact fishery southern North Sea' (LIFSN, https://www.lifsn.be/) consisted of 20 vessels of Belgian nationals commercially angling for seabass. As this small-scale fishery (vessels < 12 m, trips < 24 hours) were selective for seabass, species managed under TAC weren't targeted. Although these former Belgian recreational anglers fished under the Dutch flag, the majority would land the seabass mainly in Nieuwpoort, Belgium. Small-scale and artisanal fisheries were thus considered a policy priority by the town council of Nieuwpoort, who owned the local fish auction and were a member of LIFSN's management board (Verlé et al. 2020).

After different stakeholders, including the Nieuwpoort council, urged to facilitate small-scale fisheries under Belgian flag, the regulations would be

altered to no longer impede recreational vessels to transition to commercial activities (De Snijder et al. 2014, Verlé et al. 2020). In 2017 however, the EU legislation limited seabass angling to vessels with recorded seabass catches (see above). As previous seabass angling was not licensed under the Belgian flag, creating a small-scale fishery targeting seabass would not be legal.

Stakeholder engagement

Depending on the topic and objective, different stakeholders were involved in Belgian fisheries policy through formal and/or informal consultation (Pecceu et al. 2016). Long-term vision documents, 'covenants', on the future of Belgian fisheries in a sustainability context were agreed upon by different partners: the commercial fisheries producer organisation (Rederscentrale), an association for nature conservation (Natuurpunt) and fisheries scientists (ILVO), as well as political and government representatives of different competencies and policy levels (De Snijder et al. 2014). In addition, the Strategic Advisory Council for Agriculture and Fisheries (SALV, https://www.salv.be/) represents different stakeholders and advises the Flemish government and parliament on agriculture and fisheries topics. For topics involving European seabass, stakeholders might include LIFSN and Sportvisserij Vlaanderen (SVV), the recreational fishers organization.

Some policy procedures involved stakeholder participation, but transparency was far from optimal. For fisheries related topics, Natuurpunt was commonly involved to look after nature's stakes. Considering limited financial means however, the nature organisation chose to focus on nature preservation (e.g. marine protected areas), and decided not to invest in the specific expertise of fisheries impacts (Natuurpunt, pers. comm.). Despite this stance, the authorized minister regularly formulated their participation as the watchful eye over the sustainability of Belgian fisheries in parliament (Tommelein & Crevits 2020, Coudyser & Crevits 2021, Vaneeckhout & Crevits 2023). For the revision of inland seabass fisheries policy (Flemish Government 2017), SVV was informed in order to provide an advice on behalf of recreational fishers and a scientific advice was requested through ILVO. When the authors of this paper enquired about the involvement of environmental stakeholders, they were informed by a government official that law-making procedure required the formal consultation of the 'permanent working commission of riverine

fisheries' (Permanente werkcommissie riviervisserij) (Goossens, pers. comm.). Although this commission, an entity within the Flemish Environmental Council (MINA, https://www.minaraad.be/over-de-minaraad/copy2_of_Samenstelling), still existed on paper, it hadn't been active since years (Wim Van Gils, pers. comm.), and we weren't able to find any documentation on the MINA's website about its history or composition (which was available for other working commissions). Finally, the revision of the inland seabass fisheries measures was legislated through a different procedure in 2023: instead of a ministerial decree, the seabass fisheries measures were administered through a decree of the department head of the Agency for nature and forests (ANB, an entity of the Flemish Government) (Cardoen et al. 2023b, a), for which the legislative procedure didn't require a formal participation of stakeholders (Kristof Vlietinck, pers. comm.).

KEY ISSUES

In the section below, we elaborate on three issues, common to both the European and Belgian national policy, that we consider crucial to tackle in order to improve (seabass) fisheries policy.

Democratic process

The reasoning and decision framework of policy choices need to be transparent to enable democratic evaluation and accountability. On the European level, the lack of transparency in the decision-making process for fishing opportunities was evaluated as 'maladministration' by the European Ombudsman, stating the Council had failed 'to grasp the critical link between democracy and transparency of decision-making' (European Ombudsman 2020). Despite the legislated ambition for sustainable exploitation rates of all EU stocks by 2020, and the specific commitment for seabass recovery since 2015, it remained unclear how the EU would to deal with the failing of these objectives (Clayton 2021). As the involved institutions (Commission, Council or member states) failed to achieve the legislated sustainability targets of F_{MSY} by 2020, they could be held legally accountable before the European Court of Justice (ECJ) (Proelss & Houghton 2012).

A lack of transparency was also applicable to Belgian fisheries management. The complexity of the fisheries management, including the rights based

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system and its indirect issues for access to fishing licenses (Verlé et al. 2020), provided a complex rigidity that wouldn't allow swift adaptation to a changing world. The impediment of democratic accountability was further enhanced by the complexity of Belgian political organization. Clear objectives were set in the 2015 – 2020 covenant, including the making of a recovery plan for seabass and the commitment to have the biomass levels of all stocks above MSY $B_{trigger}$ by 2020 (De Snijder et al. 2014). Yet, the failure to fulfil these commitments was not met with accountability and the 2021 - 2025 covenant makes no mention of these objectives (Crevits et al. 2021).

Stakeholders voicing nature's concerns are key in fisheries governance (Petersson 2022). The right of environmental NGOs to meaningfully participate in environmental decision-making on behalf of the general public was secured under the Aarhus Convention (EU 2003). Although the Advisory Councils provide a formal platform for stakeholder engagement, different impediments for equal participation have been identified: e.g. the skewed member composition of 60 % fishing industry representatives and 40 % other interest groups (including environmental NGOs, small scale and recreational fisheries), budgetary and staff limitations and a decrease in stakeholder involvement due to Brexit (Van Bogaert et al. 2022). In the Belgian context, fisheries decision-making procedures seemingly involved participation of environmental organisations, but didn't always do as such in reality. In this situation, fisheries biologists providing scientific advice sometimes come the closest to the voice for environmental concerns. This can constitute a tricky situation, since the task of fisheries scientists in the procedure consists of advice provision, not of advocacy. Fisheries science itself is deeply entrenched in the framework and terminology of the management that seeks to maximise yield without compromising the resource (Sáenz-Arroyo & Roberts 2008, Hare 2020, Silver et al. 2022). MSY then becomes a conservation target, rather than the theoretical exploitation maximum it was designed for (Earle 2021, Pauly & Froese 2021). Moreover, the same fisheries scientists often collaborate with fishers for their research. Serving as a clear example of the risk in this situation, we recall our own experience where we were told by a recreational fisheries representative that an advice for a fisheries closure would not only be unfortunate news for fishers, but also for their goodwill to collaborate with

scientists (Goossens, pers. comm.). In conclusion, marine wildlife and habitat need a designated spokesperson.

Dealing with uncertainty

A critical aspect of EU environmental policy is the precautionary principle (Commission of the European Communities 2000, EU 2012). The 'better safe than sorry' principle (European Environment Agency 2001) was embedded in the CFP as the precautionary approach to fisheries management, defined as "an approach according to which the absence of adequate scientific information should not justify postponing or failing to take management measures to conserve target species, associated or dependent species and non-target species and their environment" (EU 2013). Other than a guideline for environmental policy makers, the principle was invoked in European case law of the General Court and the Court of Justice of the EU (Garnett & Parsons 2017, Scott 2018). Serving as a rare, but crucial example of reversing the burden of proof, mechanical cockle fishing was banned from a Habitats Directive site in the Dutch Wadden Sea on the basis of the precautionary principle. In this case, the negative impact of the fishery was not proven, but neither was it dismissed (EU 2004). In that light, the failure of the EU to achieve sustainable fisheries could constitute a breach of European and international law (Proelss & Houghton 2012). Precautionary decision-making requires evaluating whether a potential risk (considering scientific uncertainty) is acceptable to society, and is therefore inherently political (Commission of the European Communities 2000, Proelss & Houghton 2012, Scott 2018).

In the case of European seabass, uncertainty manifests on different levels. Considering illegal and unreported fishing of seabass (Pawson 2008, Armstrong et al. 2014, Grilli et al. 2019), fisheries catch estimates are prone to error. High site fidelity and residency put seabass at risk of local depletion (Doyle et al. 2017, de Pontual et al. 2023), with poorly understood consequences for the recovery of exploited populations (Petitgas et al. 2006). Many aspects of seabass biology remain poorly understood, such as spawning locations and timing (López et al. 2015, Dambrine et al. 2021). In times of high and diverse anthropogenic impacts on the marine environment, seabass populations would also be subject to habitat loss (Stamp et al. 2022) and cumulative effects of different stressors (Hodgson & Halpern 2019). On the

other hand, one could argue that warming waters likely expand suitable habitat and thus, increase the carrying capacity for the seabass population. The SSB estimates of the Northern and Bay of Biscay have been overestimated in the past years (ICES 2022b, c). ICES experts account for and report this type of model uncertainty in the estimates of F and SSB, whereby the current SSB confidence intervals cross the thresholds of MSY $B_{trigger}$ (Biscay stock) and B_{lim} (Northern stock) (ICES 2022b, c). In the context of the precautionary framework, we argue that it is a political responsibility to align fisheries policy with the lower part of those confidence intervals.

Marine stewardship

Whereas EU and Belgian policy remain sturdily rusted in protecting the 'fishing rights' of few corporate enterprises, the social contract of the right to fish is forgotten (Lam & Pitcher 2012, Pauly 2018, Said & Chuenpagdee 2019). In contrast, reciprocity is inherent to the concept of environmental stewardship, whereby participants seek to sustain the ecosystems that they are part of (Chapin et al. 2010, Soliman 2014). By default, the limits of overexploitation are not sought within the context of guardianship, which therefore naturally complies with the precautionary principle. Key aspects of such a cooperative framework are the recognition of uncertainty and the flexibility to swiftly adapt to changes (Chapin et al. 2010), as well as accountability at every level of organisation and governance (Ostrom 2000). Considering the "wicked problem" of fisheries with many people involved and many objectives at stake (Hare 2020, Silver et al. 2022), stewardship seems a more promising and realistic avenue than the top-down control framework (Soliman 2014).

Seabass angling could be a prime example of a small-scale fishery with low environmental impact and high socio-economic gains. The fishery as overall characterized by high species selectivity, limited habitat damage and high participation or employment (Williams & Carpenter 2015, Williams et al. 2018). However, some of the current practices contributing to the exhaustion of seabass biomass, such as illegal fishing, high grading or legislated fishing limits to maximise yield (Armstrong et al. 2014, Steadman et al. 2014), would be unacceptable to the stewardship framework. As an addition or alternative to enforcement through deterrence, strategies to achieve compliance could be inspired by fishery cooperative structures with internal enforcement

mechanisms (Bellanger et al. 2019) or nudging approaches (Mackay et al. 2020). The failure of modern fisheries management to ensure sustainable fishing pressures was inherently linked to the lack of explicitly considering the ethical dimension of exploiting marine wildlife for private profit (Lam & Pitcher 2012). This ethical dimension would require to challenge the administrative distinction between professional and recreational seabass anglers, which created a situation where anglers could either keep 2 bass per day versus 5.95 tonnes per year (EU 2022b). Applying the stewardship framework to seabass angling could draw from the lessons learned from the Irish management framework, where drastic measures were taken to protect seabass from collapse and enable a future for seabass fisheries (Colman et al. 2008, Grilli et al. 2019). In the case of Belgium, the current administrative impasse to establish a commercial seabass angling sector could therefore present an opportunity to try out the stewardship framework. The seabass angling fishery would require to stay well within the limits of sustainable fishing pressure, with full transparency, perceived legitimacy and compliance of the management (Chapin et al. 2010, Soliman 2014).

AUTHOR CONTRIBUTIONS

JG led the writing of the manuscript and designed the study. DV analysed and review policy documents. All authors revised the manuscript.

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DISCUSSION

CHAPTER 10

GENERAL DISCUSSION

In this chapter, the findings of my PhD thesis are discussed in relation to the existing body of research. The objective of this thesis was to collect information on movement ecology of European seabass, *Dicentrarchus labrax* L., in the southern North Sea that could contribute to the conservation management of the species. To obtain our goal we applied electronic tags. For elaborating electronic tagging methodologies, investigating seabass biology and for analysing fisheries management, it was of recurrent importance to consider scale and dimension. Since studying movement essentially came down to investigating the whereabouts of an animal at different points in time, the scale of space and time was a quintessential aspect of movement ecology, as well as for the performance of its analysis tools. Likewise, the human activities impacting an animal or exploiting it as a resource could also be managed along these dimensions (e.g. spatiotemporal fisheries closures). In addition to space and time, an extra dimension is that of the individual fish in its relation to a population and species of individuals with varying behaviours. A final reflection on positionality of researchers dealt with how being one scientist investigating one research topic related to the larger scale of the research community and larger society.

SEABASS MOVEMENT ECOLOGY IN THE SOUTHERN NORTH SEA

The main aim of this PhD project was to describe the movement ecology of seabass from the southern North Sea. Seabass habitat use and connectivity were investigated at different spatial scales: large scale seasonal migrations (Chapter 6), habitat use in Belgian waters and the Scheldt Estuary (Chapter 7) and movement behaviour in a port area (Chapter 8). At each of these spatial scales, it was demonstrated that taking into account the individual variability was of great importance.

The general seasonal migration of seabass in the Northeast Atlantic has been described as seabass residing in coastal feeding areas in summer and heading south-westwards to offshore spawning grounds in winter (Vázquez & Muñoz-Cueto 2014, López et al. 2015). Our data confirmed the existence of this

pattern, but we also found high variability in migration patterns. We found different migration 'strategies', whereby seabass migrated to the English Channel, the Celtic Sea and northern areas of the Bay of Biscay, or stayed in the North Sea. Also within the BPNS, different spatial networks were discerned. Seabass tagged offshore were mainly detected offshore and were never observed along the north-eastern coast or in the Scheldt Estuary, whereas seabass tagged along the coast either stayed along the coast (according to detection information) or showed connectivity with offshore areas and not to the south-western coastal stations. These different patterns could mean that different areas were of divergent importance to different groups of seabass. For example, the observation of seabass eggs (stage 1, lasting 24 hours) in the Voordelta (The Netherlands) likely meant that spawning happened in this area (Schnitzler et al. 2011, Tulp et al. 2016), but this might have only been of relevance for seabass residing along the coast, since seabass tagged offshore were never observed in the area around Zeebrugge and the Scheldt Estuary. Likewise, some offshore artificial structures (e.g. the Garden City ship wreck and the radar tower) were considered as seabass hotspots by anglers, but the seabass that seemed to solely migrate along the coast were never detected at these stations. Finally, we also observed that some seabass didn't migrate at all, but instead resided in the warmth of cooling waters or within the port of Zeebrugge throughout the winter or throughout an entire year. In these areas we found the study's temperature extrema of 2.8°C and 32.3°C, demonstrating the species' eurythermy. Although it was possible that these animals were stuck (e.g. that didn't manage to pass through the shipping lock in Zeebrugge) or didn't know where to migrate to (e.g. because no older animals guided younger animals in the migration routes (Petitgas et al. 2006), but it was also likely these animals skipped spawning (Le Luherne et al. 2022).

We found high residency and site fidelity of seabass to the spatial extent of the North Sea, as well as to the areas of few kilometres radius around their release site. Residency, quantifying the presence of an animal in an area, and site fidelity, expressing the return of an animal to that area, indicated that these locations were important to individual seabass (Doyle et al. 2017). In the BPNS, we observed presence in the areas of Zeebrugge and the radar tower throughout the year. In the Scheldt Estuary we only observed long-term residency for two fish, but it was difficult to attribute these findings to fish

behaviour or to failure of detecting the fish, as seabass detections were sometimes missed (i.e. seabass tagged in the estuary were detected offshore without being detected at the receivers in the estuarine mouth between Vlissingen and Breskens). Residency to the Garden City offshore wreck was limited to colder months (mostly November to January) and to the offshore wind farm during the warmer months (mostly June to October). Nonetheless, areas that were only frequented seasonally might fulfil a function of essential fish habitat, likely as feeding grounds (Schmitten 1999, Crossin et al. 2017). Several tagging studies using different tagging techniques (external, acoustic, archival and pop-off satellite tags) demonstrated residency and / or site fidelity of seabass to spawning and / or feeding grounds along the English coast (Pawson et al. 1987, Pawson et al. 2007), in English estuaries (Stamp et al. 2021), in Irish waters (Doyle et al. 2017, O'Neill et al. 2018), in the Iroise Sea (de Pontual et al. 2019) and along the whole of the French coast (Le Luherne et al. 2022, de Pontual et al. 2023). In all these projects (including this PhD project), seabass were captured in collaboration with anglers or at locations where anglers reported high seabass catches. In the future, we could therefore assume that any area with high seabass prevalence is important to a number of seabass (i.e. they are associated to that location and exhibit residency and site fidelity to the area), until proven otherwise.

A generalist species of specialized individuals?

As a species, European seabass has characteristics of a generalist species. Tolerating wide ranges of temperature and salinity, seabass are widely distributed across the Northeast Atlantic Ocean and Mediterranean Sea in rivers, estuaries, ports, inshore and offshore areas (López et al. 2015, Vandeputte et al. 2019). Occupying this range of habitats, seabass is often considered to opportunistically predate on whatever prey type is available (Pickett & Pawson 1994, Spitz et al. 2013). Genetic studies using neutral markers found seabass in the Northeast Atlantic to constitute a genetically homogeneous population (Souche et al. 2015). These characteristics portray seabass as a species that can occur nearly anywhere in a wide variety of abiotic and biotic conditions. However, the movement data demonstrated the high specificity of individuals. Rather than being a species composed of generalist individuals, seabass could be a generalist species composed of specialized individuals (Cobain et al. 2019). Nonetheless, the behavioural specificity of

seabass would not mean they were not able to adapt to a different or changing environment.

The movement behaviours of residency and site fidelity suggested a much more complex population structure than the homogeneity found by genetic studies. In Zeebrugge for example, seabass from the inner and outer port rarely interchanged between these areas even if these locations were only few kilometres apart. Explanations for the lack of genetic differentiation of the Northeast Atlantic seabass population (Souche et al. 2015, Robinet et al. 2020) could be found in hydrodynamic effects on larval drift (Beraud et al. 2018), as well as in the movement patterns themselves: e.g. the expansive dispersion of few individuals (Robinet et al. 2020) and/or shared spawning grounds by seabass that fed in different areas (de Pontual et al. 2019). Genetic research focusing on genes of the adaptive immune system (i.c. the major histocompatibility complex) could identify cryptic population structuring, differentiating between seabass from the Celtic shelf and Portuguese waters (Ratcliffe et al. 2022). Therefore, the lack of genetic differentiation in neutral markers across the Northeast Atlantic was not in opposition of the complex population structuring, as exposed by the movement data.

Zooming in on the individual dimension of movement behaviour, we found indications of a population composed of individuals with a specific habitat use and distinct migration patterns. Likewise, studies investigating stable isotope signatures identified high individual (seasonally varying) trophic specialisation of juvenile seabass (Cobain et al. 2019) and the existence of at least two subpopulations within Welsh waters with little mixing between the seabass groups (Cambiè et al. 2016). On a more anecdotical note, we observed seabass caught in the port of Oostende, where the seabed consisted of razor-sharp oyster beds, were covered in scales much thicker than the scales of conspecifics caught around sandy seabed. Seabass angling techniques (including type of bait, fishing rod and angling method) were notoriously specific for different locations. Anglers knew from practice and experience what type of bait, fishing rod, anchoring technique and angling method to apply in one location, but fishing the exact same way in a different location wouldn't render any seabass captures. These findings suggested that individual seabass were in fact highly adapted to the areas where they resided.

The behavioural specificity we could observe for individuals and locations, should also make us wary of translating our findings to the fish we hardly observed. The fish that had few or no detections were largely ignored in the study for lack of information to convey. We could hypothesize these individuals exhibited residency and site fidelity to another area without receiver coverage, but another possibility consisted of more roaming individuals that would be less likely detected. Considering the existence of different fish personalities and associated movement behaviours (Spiegel et al. 2017, Villegas-Ríos et al. 2018), we should also consider that catching fish by angling might already produce a bias for specific traits (e.g. more bold versus more cautious individuals).

MAXIMIZING THE INFORMATION POTENTIAL OF ELECTRONIC TAGGING

Electronic tagging enables the study of animal movement behaviour at an individual level and at a high spatiotemporal resolution (Lennox et al. 2017, Brownscombe et al. 2022). As with most research methods, gathering these data comes at a financial cost of acquiring scientific equipment, and a substantial time investment for fish tagging and maintenance of receivers. Optimizing tagging technology and analysis methods therefore maximises the amount of information gained from the same effort.

New technologies

By combining acoustic and archival technologies, the acoustic data storage tag (ADST) was a prime example of this information maximization of one tag attached to one fish (Chapter 2). Archival data rendered fine scale information on vertical movement behaviour and temperature experience, as well as reconstructed migration trajectories in horizontal space at a lower spatial resolution. Detections at acoustic receivers corroborated a tagged fish' position and provided information of habitat use at these specific locations. The complementarity of these technologies was all the more relevant because environmental reference fields could not always cover the variability in bathymetry and temperature at depth in inshore areas, where receiver deployment would generally be more convenient than in offshore areas. The acoustic detection data also served to validate the geolocation model. The

analysis potential of the combined technologies was far from limited to the applications in this study. Similarly to the geolocation approach, acoustic detection data could be used to verify behavioural classifications (e.g. active vs less active) from vertical movements (Heerah et al. 2017) and to elucidate the locations where fish perform these specific behaviours (Fig. 10.1). State-space modelling approaches have previously been developed for data from acoustic transmitters (Pedersen & Weng 2013) and data storage tags, e.g. geolocation models (Pedersen et al. 2008, Woillez et al. 2016), and could provide a framework to jointly analyse both data types. The combination of techniques can also aid our understanding and fine-tune previous interpretations of fundamental concepts in movement ecology, such as residency and home range (Kraft et al. 2023).

Another way of maximising the information potential of acoustic telemetry studies consisted of a more stable deployment set-up for acoustic receivers (Chapter 3). Whereas the receiver was in a fixed position in the tripod frame, a commonly used cabled design produced high temporal variability in receiver tilt along a tidal pattern. The tripod therefore rendered a more continuous, as well as a greater detection range, especially at higher environmental noise levels. Since temporal variability in receiver performance could be misinterpreted for ecologically relevant temporal variability in presence (Payne et al. 2010, Brownscombe et al. 2020), a more stable set-up would be essential for acoustic telemetry studies investigating fish movement at fine temporal scales. Moreover, increasing detection range at high environmental noise would also be beneficial for effectively capturing migration through receiver curtains, since some fish use selective tidal stream transport (Verhelst et al. 2018a), thus moving during the highest levels of environmental noise. Although the tripod frame represented a practical and long-term cost-effective deployment mechanism in sandy habitat, we experienced great loss of material when deploying the tripod frame on the fine sediment seabed around Zeebrugge. Receiver deployment should therefore be carefully considered in the targeted habitat type in future studies. To some extent however, loss of equipment remains unavoidable, especially in the extremely challenging circumstances of the southern North Sea.

Over the past decade, electronic tagging was increasingly combined with other techniques (Le Luherne et al. 2022, Matley et al. 2022b). The adapted tripod frame that held both an acoustic receiver and a C-POD made for a more efficient deployment of scientific equipment, but also produced the opportunity to investigate co-occurrence of cetaceans and fish (Chapter 5). Within the context of the seabass research, the initial onset was to investigate potential seabass co-occurrence with cetaceans in the BPNS, since Spitz et al. (2013) had linked high bycatch numbers of dolphins by seabass fisheries to dietary overlap of these species in the Bay of Biscay. However, the study design wasn't targeted at this research question, i.e. the seabass tagged within the context of the PhD weren't released in these specific areas. Nonetheless, we made opportunistic use of the available data to explore how continuous long term data series of passive acoustic monitoring and acoustic telemetry could be combined in co-occurrence research.

Sharing of data and knowledge

For every aspect of this research, I benefited from others willing to share their knowledge, skills, code and infrastructure. A first crucial aspect for the tagging research was to be able to catch seabass. As mentioned above, seabass angling required experience and location-specific knowledge. Being nothing of a fishing aficionada myself, I was entirely dependent on the knowledge, skills, gear and willingness of recreational and professional anglers to effectively capture seabass for my research.
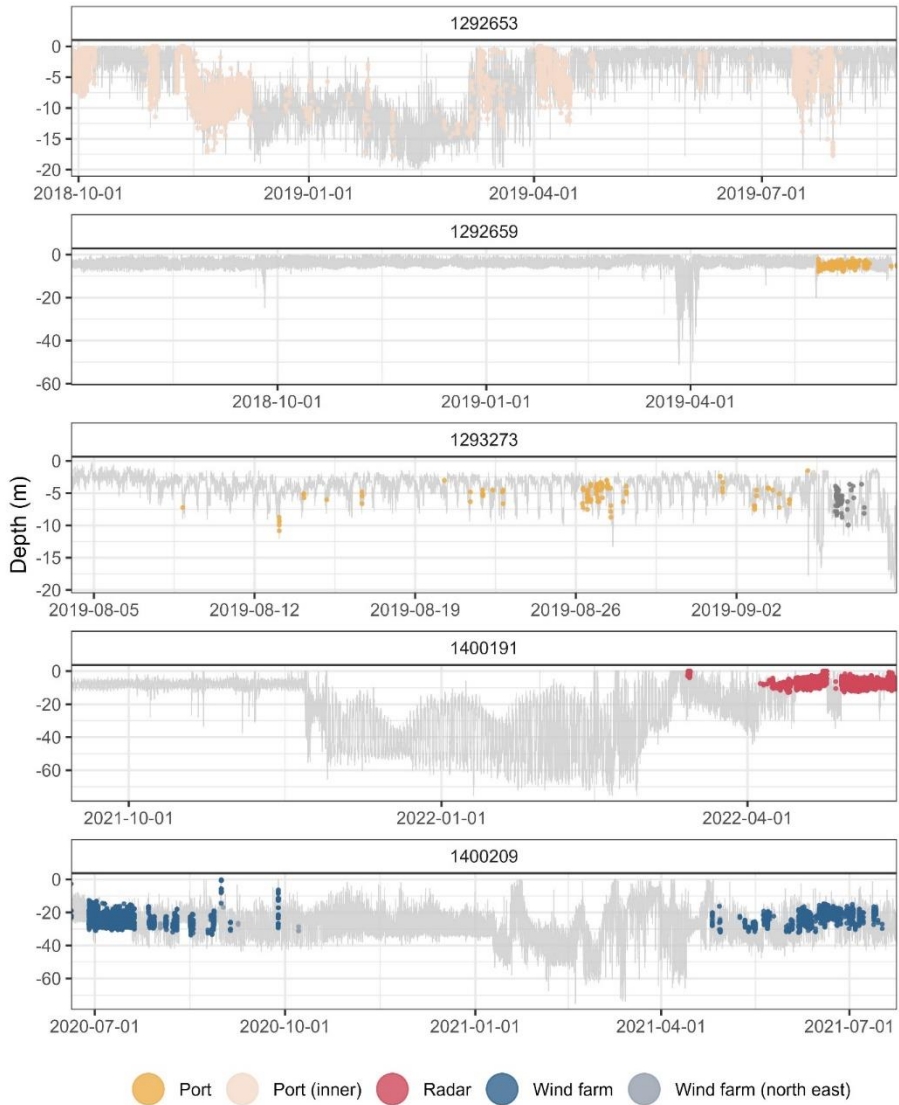
Figure 10.1. Archived depth series (grey line) of five tags with acoustic detections (dots coloured by receiver location).

Within the acoustic telemetry research community, the benefits of sharing data, infrastructure and data infrastructure were recurrently demonstrated over the past decade (Nguyen et al. 2017, Abecasis et al. 2018, Ellis et al. 2019). Within my PhD project I could use acoustic receivers (as well as the infrastructure, ship time, expertise and labour) made available from the LifeWatch project (https://www.lifewatch.be/) to deploy targeted arrays for my research (e.g. in Zeebrugge) or for a combination of research projects (e.g. the array in the Belwind offshore wind farm designed for investigating Atlantic cod, plaice and European seabass). As all the metadata and data of the PhD project were uploaded to the online database of the European tracking network (ETN, https://lifewatch.be/etn/), I could directly access all detection data of animals I tagged. For investigating seabass movements at a greater spatial scale than a local array, I therefore depended on the national infrastructure of the permanent Belgian acoustic receiver network (Reubens et al. 2019b) (Chapter 7) and on data sharing in an international context (Chapter 6), which resulted in the most exciting detections. The expanding national and international receivers networks across the globe (Cooke et al. 2011a, Gazit et al. 2013, Cowley et al. 2017, Hoenner et al. 2018) would benefit from the networking approach even more with interoperability of acoustic telemetry equipment of different manufacturers (Reubens et al. 2021). In the specific case of the ADST, the validation of geolocation model outputs would benefit most from acoustic detection information along the animal's migration trajectory, thus at locations far away from its release position.

For data analysis, I also relied heavily on existing knowledge. For the geolocation modelling approach, I applied a model that was developed for European seabass (Woillez et al. 2016), which itself was derived from open source MATLAB code for a hidden Markov model (HMM) to geolocate Atlantic cod using tidal information (Pedersen et al. 2008, Thygesen et al. 2009). Although open source code for geolocation modelling was available at the time of writing this PhD, e.g. developed by Braun et al. (2018) and Liu et al. (2017), I experienced first-hand that applying geolocation modelling would never be a plug-and-play type of approach and that it was thus highly valuable to collaborate with an expert. The application of the geolocation model relied on the availability of open source software (Gebco and Copernicus), as well as the output of a hydrodynamics model specific to the southern North Sea (Zijl

et al. 2021). Finally, for all analyses I relied on the code made available through open source packages of R (R Core Team 2022) and Python (Van Rossum & Drake Jr 1995), as well as public platforms like GitHub and Stack Overflow. To contribute myself to the principles of findability, accessibility, interoperability and reusability (FAIR data) (Wilkinson et al. 2016), the gathered data of this PhD was made available through DOI and the majority of the developed code was shared and described on GitHub (repositories on https://github.com/JolienGoossens).

RECOMMENDATIONS FOR FUTURE RESEARCH

Seabass research in the North Sea

Two key findings of this thesis research were that seabass tagged offshore might have limited connectivity to coastal areas and that many seabass resided in the North Sea throughout the year. Since seabass fitted with electronic tags in previous research (Quayle et al. 2009, Doyle et al. 2017, O'Neill et al. 2018, de Pontual et al. 2019, Stamp et al. 2021, Le Luherne et al. 2022) were all released from coastal sites, future tagging efforts should include seabass captured at offshore locations. In addition, we identified a key location for an acoustic receiver array off the coast of Norfolk and Suffolk. The reconstructed migration trajectories of multiple seabass residing in the North Sea (tagged in Belgian and English waters) were drawn to this deeper spot. Potentially, seabass aggregated at this location for spawning. A key element of seabass movement behaviour that was not investigated in this dissertation, was the presence of conspecifics. Seabass are known to form shoals (Anras et al. 1997, Quayle et al. 2009), but the dynamics of this shoaling or density-dependent effects on the movement of individual seabass remains unknown. Investigating the relationship between movement behaviour and shoaling could be achieved by combining electronic tags with other techniques as echosounders (David et al. 2022) and video monitoring (Bicknell et al. 2016).

An important knowledge gap in seabass ecology remains the location, timing, triggers and movement behaviour of spawning. Considering the latitudinal gradient of spawning seasons (earlier in southern areas and later in northern areas) (Vinagre et al. 2009), spawning would be highly temperature related, following the presumed 9°C as the threshold for spawning (Pickett & Pawson

1994, Graham et al. 2023). Spawning in the North Sea could therefore be occurring from April onwards, up until May-June. During this period, we observed seabass individuals in the North Sea that resided in the North Sea throughout the year, but also those that returned from southerly migrations. In an aquaculture setting, seabass could spawn multiple times within a year (1 to 5 times for females, 1 to 8 times for males) (Superio et al. 2021). Aquaculture studies also showed spawning to occur at night (Villamizar et al. 2012) and indicated a small effective breeding populations, i.e. only few animals effectively contributed to the next generation (Volckaert et al. 2012, Superio et al. 2021). A modelling approach demonstrated that spawning timing and location determines the nursery destination of an egg (Graham et al. 2023). Factual proof of spawning in the North Sea was limited by the observation of stage 1 eggs at the Dogger bank and at the Voordelta during an egg survey in April and May 2011 (van Damme et al. 2011, Tulp et al. 2016). Considering the importance of spawning for population structure, a targeted study on spawning in the North Sea should be considered a research priority.

A final recommendation would be to make an openly accessible inventory of existing knowledge on European seabass. A good place to start would be the documentation of the local ecological knowledge on the species by anyone who would be willing to share their information. This research benefited greatly from the local ecological knowledge of anglers, who contributed information on seabass hotspots, fishing techniques and ecology. The existence of different groups of seabass in the outer and inner port of Zeebrugge for example, was suggested by anglers who went fishing in the area on a weekly basis. In addition, some scientific documents, e.g. the documentation of a seabass observation in the Scheldt Estuary in 1945 (Vandamme et al. 1994), would have never come to my attention if they hadn't been shared as an anecdote by a more senior researcher. Seabass knowledge gathered in experimental research would also likely contain a multitude of valuable facts on physiology and even ecology, but the body of seabass aquaculture literature would just be too extensive for every seabass ecologist to go through. Moreover, merging information could clarify some contesting numbers on general seabass biology, e.g. the age and size at maturity varied between reports. Knowledge on seabass has been reviewed extensively before (Pickett & Pawson 1994, Vázquez & Muñoz-Cueto 2014, López et al. 2015),

but the format of a book or A1 publication would always be soon outdated. A comprehensive and living encyclopaedic document leaning more towards a more extensive Wikipedia or FishBase page, containing references to research results, relevant legislation and anecdotic observations, would greatly advance general knowledge on European seabass and most likely many other species (similarly to the Atlas of Living Australia https://www.ala.org.au/).

Dimensionality in tagging research

From the methodological side, we repeatedly stumbled on the importance of taking into account the spatiotemporal dimensions of error. Using the verified animal positions from acoustic detection information of the ADST, we evaluated the performance of the geolocation model. Different methods had been developed to evaluate geolocation model performance, as reviewed by Gatti et al. (2021), but – to our knowledge – we were the first to make the important distinction between timed and untimed positional error (Chapter 2). For many studies using archival tags, the exact timing of positions would be less of interest than the route of the track, except for e.g. studies linking the timing of spawning behaviour to a specific location (Aranda et al. 2013). The choice for timed or untimed error estimations should therefore depend on the nature of the research question.

The importance of taking into account the temporal dimension was also shown for the detection range in acoustic telemetry studies (Chapter 4). Although many telemetry studies analyse detection data as animal presence within a time bin (e.g. per day), detection range was generally evaluated as the probability of detecting single transmissions (Huveneers et al. 2016, Reubens et al. 2019a). By developing a method to account for the temporal resolution using a cumulative probability within a time bin, we demonstrated the importance of adapting a range test analysis to the methods and objectives of a telemetry study. This also demonstrated that researchers could optimize the study design in many more aspects than only the distance between receivers. Some aspects would always be beyond a researcher's control, such as environmental factors and animal movement behaviour, but other aspects can be optimized to improve range: receiver attachment (Chapter 3), receiver type (Mourier et al. 2017), removing biofouling to improve receiver performance (Heupel et al. 2008), transmitter power output (Kessel et al. 2015) and

obviously the spacing between receivers. When assessing animal presence within a time bin, researchers can tweak transmitting intervals to improve range and should consider the relevant detection threshold and temporal resolution (Chapter 4).

Whereas we demonstrated the importance of considering the temporal dimension for spatial metrics in the examples above (geolocation model error and detection range), future movement ecology studies could also contemplate the spatial dimension of temporal metrics. Residency and site fidelity are common metrics in tagging research: residency reflects a percentage of time spent in a certain location, and site fidelity reflects the return (or uninterrupted stay) to a certain area after a period of time. Although tagging studies tended to report the temporal resolution and scale rather explicitly, e.g. daily residency or site fidelity as the return after a specific season or period, they are generally more vague about the spatial dimension of those metrics. For example, both Doyle et al. (2017) and de Pontual et al. (2019) reported high residency and site fidelity for European seabass, but the spatial component of that statement would be distinctly different since one study used acoustic telemetry and the other archival tagging (thus resulting in different spatial error). Therefore, study outcomes would be more comparable if residency and site fidelity would be expressed per unit of time and per unit of space (expressed as surface area with an estimated error).

Finally, another important dimension proved to be the individual animal. Rather than averaging out individual variability or considering it as a statistical nuisance, we addressed high ecological importance to the plurality in movement behaviours (Hertel et al. 2020). With our data we could not identify whether different migration strategies would have different selective advantages or individual fitness differences, but the intraspecific and intrapopulation variability in behaviours would likely contribute to the fitness of the population as a whole (Bolnick et al. 2011, Spiegel et al. 2017). Within the context of continuous anthropogenic impacts on the seas, and the high fishing pressures on seabass in past decades, intraspecific behavioural variability might benefit the population as it functions as a risk spreading mechanism. Moreover, the association of individual seabass to specific locations demonstrated habitat selection to be far more complex than mere

habitat suitability. In contrast to recent calls for telemetry scientists to design studies specifically to assess habitat suitability (Rudolfsen et al. 2021, Brownscombe et al. 2022), my viewpoint would oppose that objective for tagging studies using acoustic telemetry and DST. A major disadvantage of tagging is the weakness in numbers: you can only tag a limited number of animals. Tagging is therefore unsuited to make strong conclusions on animal distributions, which require population sampling methods. The great advantage of tagging consists of this individual resolution that is quite rare in ecology studies in the wild. An individual's habitat selection of a habitat, there will be a range of reasons why an individual would be at a certain place in a certain time. The presence of an individual animal at specific place at specific time will have a range of reasons (Nathan et al. 2008), making information on habitat selection on the individual level not entirely suitable for statements of habitat suitability.

RECOMMENDATIONS FOR SEABASS CONSERVATION AND FISHERIES MANAGEMENT

Seabass fisheries policy on the European level and in the Belgian context was reviewed in chapter 9. Here, we added reflections related to seabass movement behaviour.

The existence of different migration strategies and the highly localized behaviour of seabass also have implications for the management of their exploitation. The current EU seasonal closure of seabass fisheries in February and March might not protect all spawning aggregations, since spawning in the North Sea would only take place from April onwards. As a result, fisheries pose a selection mechanism with higher protection of seabass from more southern latitudes and of the northern seabass with migration strategies towards the south. Aside from this artificial selection on certain behaviours and groups of seabass, recruitment would also be spatially affected. Considering the impact of hydrodynamics on egg dispersal, the timing and location of spawning would be defining of the nursery ground destination of an egg (Graham et al. 2023). Failing to protect all spawning aggregations would therefore differentially impact recruitment to different nursery grounds (Beraud et al. 2018). To protect spawning seabass in the North Sea, the seasonal closure would have to be extended to May or June, at least in this area.

The highly localized nature of seabass movements (as demonstrated by residency and site fidelity) shows that local management measures matter. The high residency exhibited in these areas makes these locations as valid candidates for spatial protective measures (McCormick et al. 2021). Under European policy, spatial fisheries closures have to be approved by all member states with fishing rights in the area (EU 2013). Taking spatial conservation measures in marine waters is necessitated by European law, e.g. under the marine strategy framework directive (EU 2008), but it takes a lengthy legislative procedure to administrate fisheries measures (the procedure under article 11 of the CFP), which might deter national policy makers to undertake action. However, the legislative framework for administrating measures for inshore fisheries is different. In the case of Zeebrugge (Chapter 8), we saw that the combination of differing habitat use and different legislative contexts rendered a differential protection of two groups of seabass. The local managers could therefore opt to provide measures for the seabass in that area. In spite of the provided scientific advice, they chose to equate the local measures to European seabass fisheries policy from 2023 onwards (Cardoen et al. 2023b).

Intraspecific variability in (movement) behaviours is key to the fitness of a population (Bolnick et al. 2011, Spiegel et al. 2017) and should be recognized in policy. The behaviours of site fidelity and residency put seabass at risk of local depletion (Doyle et al. 2017). Highly localised seabass fisheries practices, e.g. angling all seabass around a wreck, could therefore erase a seabass group residing at a specific location, and thus erase a specific set of (learned) behaviours and life-cycle patterns (Petitgas et al. 2006). The loss of intraspecific (phenotypical) variation caused by local depletion, could be detrimental for the resilience and recovery of fish populations that experienced excessive fishing pressure (Petitgas et al. 2006, Steadman et al. 2014, Doyle et al. 2017). Although these biological complexities and consequential scientific uncertainties may seem inconvenient to effectively consider in policy, neglecting them wouldn't make them any less real.

A final recommendation for the conservation of seabass would be the most simple one: that is to truly commit to the conservation of seabass. In the words of Hilborn (2007): "Wherever we look at apparent failures in fisheries

management, we can alternatively interpret them as success for other objectives". In my own words: if European and national policy makers would have truly committed to the conservation of European seabass, the populations would have been restored by now. Although I believe my PhD research has resulted in valuable knowledge and has educated me to be a competent scientist, the most meaningful recommendations for fisheries management were well known before doing this research: fish less, protect areas with high seabass abundance, close fisheries during sensitive periods (e.g. times of spawning and migration), increase the minimum landing size to at least - and preferably exceeding - 45 cm (the length at which the majority of females would reach sexual maturity) and be ready and willing to rapidly adapt any necessary management measure in light of the many cumulative impacts of stressors on the marine environment.

POSITIONALITY OF RESEARCHERS

Personally, I hardly contemplated the roles of researchers up until 2021, when I had the rare opportunity to join a research campaign investigating the impacts of deep-sea mining. Three vessels in the middle of the Pacific Ocean made for a fitting metaphor of the societal debate: an industry vessel deploying a prototype mining robot, a research vessel investigating the environmental impacts during the mining test, and Greenpeace's Rainbow Warrior, who came to protest the activity of deep-sea mining. The potential future activity of the novel industry was heavily debated (also among scientists), whereby divergent opinions on deep-sea mining were mostly linked to intrinsically divergent world views. What's more, is that the roles and stances of researchers themselves were put to question: What if researchers would collectively reject the possibility of deep sea mining and refuse to collaborate? Scientists generally self-identifying as objective observers, could suddenly be considered as active, accountable participants of history in the making. I definitely lack a straightforward and universal answer to the complex questions of scientists' societal responsibilities, but the discussions on complicity were educational for me to rethink the relationship between researchers and their research subjects. It enabled me to reflect on how my own research practice - in particular in relation to fisheries management - related to my own values.

Marine scientists are not disconnected from the topics they study (Bearzi 2020) and the messages they propagate on those subjects help shape how societies deal with them: "Language is not just rhetoric and concepts are not just labels. Words determine how we think and how we act, also in a research context." (Jentoft 2022). For example, 'blue growth' and 'ocean grabbing' refer to the same concept (Bennett et al. 2015, Barbesgaard 2018). Likewise, the (translated) statements 'the majority of fish caught by Belgian fishers is caught in a relatively sustainable way' (Verhaeghe & Seys 2020) and 'less than half [of stocks] targeted by Belgian fishers is at a sustainable level in terms of both biomass and fishing pressure' (Goossens 2023) refer to the same numbers. Considering these divergent mind sets, also among researchers (Vigliano Relva & Jung 2021), it is important to consider that dominant narratives remain narratives. Fish are commonly considered as a resource by default, even by biologists (Balcombe 2017). In the case of seabass, several (if not the majority of) A1 papers on the species' ecology mention the financial revenue to be made from selling seabass as a product. "As previous management failures have been largely attributed to data deficiency, a thorough understanding of seabass movement behaviour and exploitation is urgently needed.", thus stated 26-year-old Jolien Goossens in 2018 in the grant application for a PhD project. This type of message is a common one among scientists: *in order to effectively preserve populations, communities and ecosystems, we need to know more*. Five years later, I know slightly more, and I no longer agree with the intent of this statement. We know how to not overfish populations and how to not damage ecosystems. The part where we remain rather clueless, is how to exploit nature for profit maximisation without jeopardising the resource.

Despite fisheries having been shown to be the main cause for the global depletion of fish populations (Pauly 2018), the number of overfished stocks is still increasing (FAO 2022). As an overarching global (United Nations 2015) and European (EU 2013) policy goal to stop overfishing, fishing pressures had to be reduced to the MSY-limit by 2015, at the very latest by 2020. Firstly, the MSY-concept should not go unchallenged. In short, the MSY-concept supposes that density-dependent population growth rate is highest when the population biomass is at ½ carrying capacity, which produces an optimal "yield" (surplus production of biomass). Advanced modelling approaches can

include various complexities, but the approach remains quintessentially reductionist (Pauly & Froese 2021, Silver et al. 2022). As a concept developed for 19th century colonial resource exploitation (Ramesh & Namboothri 2018), MSY has also been criticised for its utilitarian misuse in the capitalist profit framework (Pauly & Froese 2021, Silver et al. 2022). MSY can serve as a theoretical exploitation maximum, but it should not be considered a conservation target. It definitely does not provide a visionary context for equitable fishing access to healthy marine ecosystems. Secondly, even the imperfect MSY targets – despite being legally binding – were not achieved, also not for stocks targeted by Belgian fisheries (Vaneeckhout & Crevits 2023). This – to my opinion Kafkaesque and deeply unsettling – policy framework is the management context to which marine biologists and fisheries scientists are expected to contribute knowledge and expertise.

How, then, can fisheries scientists rethink their relation to the policy framework they operate in? Much like the deep-sea mining discussions, I believe a person's answer to that question will be strongly linked to that person's views on how the world works. One option is a strike: ICES for example, could refuse to fulfil its scientific role to send a clear signal that the social contract they have with society – ICES provides the assessments for policy makers to achieve legislated targets of sustainable fisheries – has been broken by the other party. Another option is to patiently continue the research in line with the ideology of gathering knowledge for the purpose of its prospective utility in the potential sustainable policy framework of an uncertain, distant future. Although the first approach will likely be considered more extreme than the other (or rather: only the first option is considered a narrative), it is worth contemplating which is the more sensible approach. Besides, there are options on the spectrum between them.

I believe the precautionary approach is underutilized as the framework for marine environmental science. The precautionary reversal of the 'burden of proof' (Commission of the European Communities 2000, Scott 2018) could have a direct application in how null hypotheses are formulated. Rather than recurrently validating the importance of diversity, we could assume ecosystems are worth protecting, until proven otherwise. ICES uses the terminology of the precautionary approach in a technocratic setting by

quantifying thresholds for fishing pressure F_{pa} or biomass B_{pa}. This seemingly relieves policy makers from their obligation to apply the precautionary approach in the intrinsically political definition (Commission of the European Communities 2000, Scott 2018). Yet the political application of the concept is what could be most valuable for scientists to frame their findings in a conservation context, as it 1) inherently deals with the inescapable uncertainty of environmental research, and 2) it is already embedded in European law and international policy as the guiding principle for environmental management (European Environment Agency 2001, EU 2013). Therefore, compliance with the precautionary principle is legally binding (Proelss & Houghton 2012). In a precautionary and ecosystem based approach, the MSY calculations can still be of use as a guideline, but conservation policy should take into account model uncertainty, biological interactions within communities of marine animals and the cumulative effects of anthropogenic impacts on marine habitats (Hodgson & Halpern 2019, Pauly & Froese 2021). Potentially, alternatives to MSY could be used, e.g. maximum economic yield (MEY), which targets higher revenue from lower fishing pressure (Dichmont et al. 2010), and maximum sustainable dead biomass (MSDB), departing from biomass sustainability rather than fishing pressure (Rätz et al. 2015). In a truly precautionary framework, the applied metrics would matter less than the true commitment to the conservation of marine wildlife – no matter what it takes-or: "It is simple to stop overfishing, but not necessarily easy." (OCEAN2012)

EPILOGUE

EPILOGUE

SEXISM AND ITS INTERSECTIONS IN (MARINE) SCIENCE

AUTHOR Jolien Goossens

KEYWORDS / CONTENT WARNINGS discrimination, misogyny, sexual violence, rape culture, racism, classism

Although many consider science as if it were operating in a box of objectivity secluded from perturbations in society, (marine) science is not disconnected from 'the world of wounds' in which it operates (Bearzi 2020). Throughout my dissertation on electronic tags and seabass, I have not yet mentioned the topic that has anguished me the most during the PhD process. As a final essay I wish to write about sexism and its intersections in my own work-related experiences of the past five years.

> *And at last you'll know with surpassing certainty that only one thing is more frightening than speaking your truth. And that is not speaking.*
>
> Audre Lorde

DISCLAIMER

The driver for writing this piece is idealism: I believe in the possibility of a marine science environment without sexism (and other –isms and –phobias mentioned below), where people attempting to participate in (marine) science are on equal footing. The difficulty with the topic however, is that many peers seem to think this utopia is our current reality. Talking about incidents and experiences can therefore produce discomforting conversations, as one person's lived reality seemingly jeopardizes another person's perception of it.

Moreover, my own feelings of disappointment and anger on the topic of sexism mostly concern people I feel gratitude and respect for on other topics. Considering these divergent and complex perceptions of the same working environment, it is extremely difficult to find the common language to write this piece. Mostly I struggle to be unapologetic about writing it.

Despite its idealist intentions, this essay is in essence a realist piece, covering experiences of one person over the course of one PhD project from application to diploma. Three instances include events from before this time span, but I consider them of ongoing relevance because of the persistent lack of a credible approach to deal with these issues. Although my objective is obviously to get these issues out in the open, I am not blowing any whistles here: nearly all incidents involved a group of people and for the cases that did not involve me personally, I referred to the newspaper articles where I found the information. And yet, by compiling these separate cases into one document, it is my intention to show that these incidents are not mere unfortunate singularities, but recurring symptoms of a systematic disease.

PERSONAL EXPERIENCES

Misogyny, hatred of women, is expressed as prejudice, hostility, disgust and sexual objectification towards women and characteristics perceived as feminine. Misogyny operates through individual attitudes, as well as cultural systems (Ussher 2016, Loewen Walker 2022).

Throughout this PhD project, I was linked to three institutes, attended seven conferences in five countries, boarded three research ships and multiple smaller vessels, and thus collaborated with a lot of people. In these diverse encounters, I came across ample utterances of sexism, but also allyship and support. Examples from either side of that spectrum came from persons with different genders, nationalities, political beliefs, hobbies, educational backgrounds, from people who consider themselves progressive or conservative, from people with or without PhDs. Voicing sexist bigotry therefore definitely does not necessitate a penis and an M on your passport, yet undeniably, the large majority (well within the 95% confidence interval) of my observations involved adult cis men. The overall common denominator in each situation was the reason for my presence: I was there because of work.

The majority of (micro-)aggressions came in the format of small-talk and jokes. While at work I heard women cannot drive, are incapable of cooperating in a group and rapidly get ugly when aging. Personal problems with 'money-grabbing' ex-partners, 'annoying' spouses and 'evil' mothers-in-law were attributed to some inherent female wickedness. As a colleague elaborated how he participated in sex tourism as a holiday activity in a low income country, he explicitly added that he cared less about the likely exploitation of the female sex workers than he did about maxi pads as sources of aquatic pollution. During a scientific outreach event, a presentation of scientific results was followed by an entertainment act that included pictures of women in bikini as laughing stock: either objectified for their perceived desirability or despised for their perceived disposability.

In what I initially perceived as a meritocracy that was selective for few types of merits, my younger self truly believed I could overthrow sexist prejudice by excelling in stereotypically masculine skills, such as coding and intense field work. The naivety of that mindset was demonstrated by the many times an achievement would be complimented, followed by a disclaimer: 'not a lot of women can do this'. On board of some research vessels, the machismo working culture nourished a constant imposter syndrome (for all genders) where you would have to prove your capabilities every single time. Fellow researchers stated 'women get special treatment on board', as I needed help for lifting loads that exceeded assigned thresholds for both men and women. Even in the function of head scientist, I was told I had found my place on board when I was cleaning a dish. While setting up for an 8 March feminist strike, a helping hand from the university union told me he would wait for his male colleague to jointly carry a load that he decided I could not lift (after which I carried it effortlessly with a person half his size). Throughout my PhD, several aspects of my own research were explained to me by men ignorant to the subject. The highlight of mansplaining concerned sexism itself, where I was enlightened which topics feminists should best prioritise or neglect, and how women should behave when confronted with misogyny.

There is no perfect reaction to misogyny, because any incident is a shit situation by default. Calling out someone's behaviour is often considered as more aggressive than the behaviour itself. Personally, I generally feel better

when I speak up, and in most cases I am too pissed off to stay silent. Some situations were less hostile than they were creepy ('it smells like female in here' or someone staring at me for 30 minutes while regularly mumbling 'wow'), for which I had no words in response. Some incidents got so vile that I was too shocked or frightened to defend myself. Once, I was physically hit by a male colleague on the back of my head to the extent that my head was still pounding an hour later. A group of men invited me to join them on their boat for my research - just me though, explicitly no male colleagues - as they joked about gang raping me. During a safety at sea training, I (the only female participant) was effectively bullied by a group of adult men, including one of the teachers, who sang as I performed an exercise ('Another one bites the dust') and called me out as incompetent and fuckable.

The lack of general recognition of the existence of sexism is in stark contrast with the urgency I attribute to the issue. Even just mentioning my own experiences often solicits doubt and denial. When you describe an incident, 'it must have been an exception'. When you talk about multiple incidents, 'you must be doing something wrong'. When it concerns the experiences of multiple people, 'you can still be grateful you live and work in this sexist environment rather than an even more sexist country or institute'. One colleague, when confronted with his own statements in the past, first blamed me for not calling him out earlier (he later apologised for his original statement). Sadly, it doesn't come as a surprise anymore when excellent researchers list sexism as one of the main reasons for never wanting to return to science or academia. Over the course of the past years, people increasingly share their experiences. I find it both healing and deeply upsetting, as there is always a story worse than what you imagined possible.

SEXUAL VIOLENCE IN SCIENCE

Rape culture refers to a cultural framework of beliefs and behaviours that trivialize and normalize widespread sexual violence (Lewis et al. 2018, Seal 2022). Key to rape culture are rape myths, which deny and justify cis male sexual aggression against trans people and cis women. These attitudes include linking sexual violence to the behaviour of the victim (e.g. choice of cloths or lack of resistance), and the perpetuation of the baseless, yet common belief of a high percentage of false testimonies (Lonsway & Fitzgerald 1994, Rollero &

Tartaglia 2019, Seal 2022). Importantly, rape culture is pervasive in colleges and universities worldwide (Lewis et al. 2018, Ahmed 2021). Though I was familiar with verbal sexism at the workplace (see above), I was oblivious to assault and rape as occupational hazards in science. In 2022 however, I learned about different cases of sexual violence in my own working and learning environments.

I learned that a researcher had been the victim of rape on board of the Belgica, one of two Belgian research vessels. Sixteen years ago, her testimony was met with victim blaming and bureaucratic inertia, until she took the case to court and to the press (Barrieux 2009, De Standaard 2011). To this date, I haven't seen a policy in place that effectively informs people on the issue of sexual violence on ships, let alone a policy that tackles sexism on board. For one cruise, we did receive a briefing on sexual conduct, including verbal and physical transgressions, yet the main message was: 'the social situation of a long cruise is a bit peculiar, where signals might be mistaken for an invitation'. The first time I was on the Belgica, I was a 21-year old bachelor student. No one had informed me of what had happened, nor of what to do in case it would happen. Though experiencing sexual violence as a student might sound like the most horrifying thing, it happened at my own university, at my own department.

Multiple students at my university were raped and assaulted by a fellow member of the Biology student organisation (GBK). As the perpetrator was found guilty in court - a rarity in Belgium, since only an estimated 1.3% of sex crimes results in a conviction (Vandekerkhove 2016) - the case was in the news in 2022 (Vermeulen 2022). The only correspondence on the case within the Biology department was an email from a professor who forwarded a statement of the student organisation. The GBK stated they strongly condemned any kind of transgressive behaviour and the professor added it would be a pity if the GBK was associated with the wrongful behaviour of one person. Neither the GBK, nor the professor, apologised or said they would investigate how this could have happened, and how this environment could have been so unsafe. Every few months the GBK prints a newsletter, the *Worm*, featuring fun biology facts and practical information on parties and field excursions, as well as misogynist and homophobic slurs, slut-shaming and rape jokes. Important

side note: some GBK students knew of one of the rape cases in 2017 (Vermeulen 2022). Nonetheless, the perpetrator became the praeses (president) of the student organisation in 2018, after which the violence continued. It reminded me of a field course during my own years as a student: in a group conversation with multiple GBK members, a student was bragging about having had sex without the other person's full consent. Two years later, he became praeses. At the time, I definitely considered this person to be a total creep, but it took me years to understand that rape is not limited to a stranger pushing you against the wall of a dark alley. I don't believe the GBK seeks to create a misogynist environment, but I do think they are oblivious to the pervasiveness of rape culture, just as I was ten years ago. Who then, should make it their mission to create a safe learning environment free of sexual violence? Maybe the professors or the rector?

In 2022, numerous testimonies attested to sexual violence at Belgian universities. Multiple victims who filed complaints through established university protocols, had not seen any consequence or follow-up years after their testimony (Bergmans 2022, Maenhout & Mayda 2022). The universities were hit by a media backlash as institutional procedures were deemed to protect predators in power (Destoop & Goossens 2022, Verschaeve 2022). Anno 2023, a UGent professor who committed sexual assault, was suspended for four months, during which he would receive 80% of his wage (Mayda 2023). Though the university was notified of the case in 2017, the rector only used his capacity as rector to start a procedure after a news article was published five years later (Mayda 2022, Mayda & Maenhout 2022). Rather than protecting employees and students, the hierarchical structures of these institutions facilitated harassment and impunity (Ahmed 2021, Maenhout & Debeuckelaere 2022).

Sexual violence is ubiquitous. In Belgium, 81% of women and 48% of men have experienced sexual violence, with 1 out of 6 women and 1 out of 20 men having been raped (Keygnaert et al. 2021). Calculating the cumulative probability - using the line of R code *1 - pbinom(0, 4, 1/6)* (R Core Team 2022) - shows that it takes four women in a group to have a higher probability that someone in that group has experienced rape than the probability of no one in the group having been raped. I regard this number as educational about the

way we discuss sexual violence. In my experience these conversations are still drenched in denial and victim blaming, whereby it is rarely considered that the conversation likely includes someone who has experienced rape. At work, colleagues laughed with and discredited #MeToo, the hashtag used for the multitude of sexual violence testimonies. One colleague stated that 'in times of #MeToo', he would not want to be alone with a student anymore: not out of fear for sexual violence, but out of fear for false charges. With regard to the Belgica-case, I only heard about it when colleagues were voicing their opinions about the victim's choice of clothing. My own experience of being sexually objectified while wearing an orange survival suit demonstrates that misogyny is dramatically blind for dress code. It will take a lot to create a working and learning environment that effectively tackles the issue of sexual violence (Favaro et al. 2016), but a first step is acknowledging its existence.

INTERSECTIONS

Being a White, cisgender, straight-passing, able-bodied, neurotypical Belgian national with a wage that exceeds the median net income in Belgium, my set of social identities also comes with privilege. Aside from – and mostly along with – sexism, other forms of inequity and discrimination are ubiquitous, also in scientific working environments (Seymour 2017, Miriti 2020, Bourabain 2021, Smith et al. 2023). Incidents of sexism can even be cherry-picked to support racist, classist and transphobic claims (Farris 2017, Canto et al. 2018, Pearce et al. 2020). Limiting this essay to sexism would therefore feel inappropriate, or in the words of Virginie Despentes (2006): "you'd have to be a complete fuckwit, or deeply dishonest, to consider one form of oppression intolerable and another deeply poetic". Although I am certainly not able to fully grasp the complex experiences of oppression that do not concern my demographic, I would like to add observations of how classism and racism persist in marine science and in my own work environment.

Like misogyny, other forms of oppression operate through organisational structures as well as through attitudes and opinions held by individuals (Graves et al. 2022). At Ghent University, the cleaning staff is outsourced (Nieuwsblad 2021). Therefore, the person cleaning a desk and the person typing at that desk are hired under different labour conditions in terms of job security, working hours, pension scheme and wage. In my building (and other

faculties), cleaning staff have separate lunch-rooms, are not included in our mailing list and are not invited to events. During a round of budget cuts, the university announced it would be outsourcing the day care staff, who were told that the projected cost of the potential future pregnancy leaves of the majority female staff was too high for the university (Van Waeyenberghe 2022). Aside from constituting discrimination against persons with a womb, it is particularly cruel to portray day care staff's desire to have children as a budgetary nuisance, considering they accommodate the academic staff's offspring. On one research cruise I participated in, a US company (with majority US staff) subcontracted a Norwegian company to operate the ship (with the positions with higher pay filled by Scandinavians and the ones with lower pay mostly filled by southern and eastern Europeans), who subcontracted a Philippine company for cleaning and cooking on the ship (with all Philippine workers). This resulted in different wages, working hours and periods spent on board of the ship: six weeks for staff of the American and Norwegian company versus eighteen weeks for Philippine workers (who had signed a contract for twelve weeks).

Within biological sciences, colonial power imbalances persist through the inequality of resources for research and the dismissal of different ways of knowing (Livingston et al. 2016, Vigliano Relva & Jung 2021, Datchoua-Tirvaudey et al. 2023). A common example is the practice of 'parachute science' or 'colonial science', whereby ecologists from the Global North make research visits to tropical destinations, with limited agency for the locals who call the 'remote' area home (Baker et al. 2019, de Vos 2020). My own work settings have always been nearly entirely composed of White people. Small-talk and jokes repeatedly featured racism, including the N-word. Ghent University has a diversity commission for all of its eleven faculties, whereby all but one of the 15 coordinators are White (and the designated webpage is only available in Dutch). A marine professional proudly stated he would not care how many refugees he would see drowning, he would never let them enter his boat (a quick reminder: that constitutes a crime under UNCLOS (1982)). Although this type of fascist statements do not reflect the general attitude in marine science environments, neither are they consistently condemned. A politician who has publicly called for not providing food or help to refugees, whom he repeatedly labels as 'illegals' (VRT NWS 2016, 2017), is a regular

invitee to Belgian marine science events, where he gives speeches and hands out awards in his position as governor.

Even when diversity is acknowledged as a legitimate topic, it can still be instrumentalised to serve existing power imbalances. Research institutes publicise #womeninscience and #womeninSTEM as means of self-promotion, but fail to address the sexism that female employees endure in the workplace. Peer-reviewed papers attest to the benefits of diversity in terms of 'competitive advantages' (Arismendi & Penaluna 2016) and 'good performance' (Burdett et al. 2022). When 'diversity benefits everyone' is the message, it makes one wonder who the target audience is. Do we really want a future where we still have meetings among an all-White crowd where cis men do ninety percent of the talking? Answering that question begs another question: who is 'we'? The aim for an 'inclusive' environment still legitimises the power of a certain demographic to choose to 'include' (or worse: 'tolerate') other demographics.

Privilege blinds the privileged for prejudice. Biology has a history of bias, with pseudoscientific arguments for racist (e.g. Georges Cuvier) and sexist (e.g. Charles Darwin) theories still lingering in present time (Imma 2011, Cooke 2022). Sexist bias caused biologists to dismiss the possibility of dominant females (Cooke 2022) and produced a medical health system that is based on the biology of the cis male body (Criado Perez 2019). Cisnormative bias continues to present sexual diversity as though some phenotypes are 'natural' or 'normal', whereas others are pathologized (Seymour 2017, Zemenick et al. 2022). Racist bias caused White environmentalists to dismiss the environmental achievements and concerns of Black, Indigenous and people of colour, even when they are disproportionately impacted by pollution and global change, and when 80% of global biodiversity is protected by Indigenous people (Gilio-Whitaker 2020, Sena 2020, Thomas 2022, Datchoua-Tirvaudey et al. 2023). After centuries of land-grabbing has produced - and continues to produce – the most extreme forms of misogynist, racial and classist violence in a terrestrial context (Federici 2018, Dunlap 2020, Gilio-Whitaker 2020), we are now in an age of privatisation of the ocean (Bennett et al. 2015, Barbesgaard 2018). Marine science too, is often embedded in ideologies that commodify ocean life, as well as the livelihoods of those that

depend on it (Bearzi 2020, Bennett et al. 2021). The necessity of pluralism and equity in the marine science community therefore goes beyond the wellbeing of its practitioners. Tackling scientific, environmental and societal issues will require other lenses than the one currently dominating our belief systems (Seymour 2017, Vigliano Relva & Jung 2021, Datchoua-Tirvaudey et al. 2023).

BECOMING

In an imperfect world, it takes active decisions to create a working and learning environment maximally devoid of the perils of the outside world. In a sexist world, it takes anti-sexism measures to be free of sexism on the job. My workdays will still not be rid of it: some days I get verbally harassed on my way to work, as well as on my way back home. As an individual, I have come to realise that, within my lifetime, I will not live to see a year, probably not even a month, free of sexism. I would not be able to work, to go at sea, to attend an event, to read the news, to go for a run and talk to people without having to endure harassment and bigotry at some point. Since my current alternative is hiding from life itself (Despentes 2006), my individual choice is to face it. Yet, as communities of marine institutes, research groups, colleagues and human beings, we have better options. To name a few: we can listen to each other's experiences, actively seek the voices we never hear, think of different ways to tackle issues, try out strategies, evaluate them, and we can learn how to communicate honestly and constructively. There's a myriad of options that I find infinitely more appealing than stranding in the dull narrative of calling someone woke whenever they tell you you've offended them. I too am a part and a product of this imperfect world and I too reiterate prejudice and hurt people in the process. Yet, I prefer to know, and to contemplate and change my own behaviour, over the option of ignorance.

I believe in the possibility of a science and conservation community that recognizes and transcends omnipresent injustices. That community does not merely operate in a flawed world, but shapes it towards another one. This brings me to another historical legacy: marine biologists who have challenged an existing world order. Rachel Carson's *Silent Spring* (1962) has inspired a global environmental movement for decades to come. Daniel Pauly has shifted the understanding of the impacts of global fisheries (1995). Pia Klemp has saved thousands of lives at sea in resistance to the ongoing criminalisation of

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refugees. In my own surroundings, marine scientists with varying personalities and approaches have inspired me by standing up for one another and for the causes they cared for. The hundreds of people who protested against sexual violence at the university, the feminist strikes, the open letter and podcast *Decolonize UGent*, the movements and lenses of trans and queer ecologies, intersectional environmentalism and ecofeminisms (Seymour 2017, Knott et al. 2021, Thomas 2022), *The Ocean and Us* (Obaidullah 2023) and the heaps of literature I stumbled on while writing this essay, show that we – anyone with whom this message resonates – are not alone.

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BIBLIOGRAPHY

Abecasis D, Steckenreuter A, Reubens J, Aarestrup K, Alós J, Badalamenti F, Bajona L, Boylan P, Deneudt K, Greenberg L, Brevé N, Hernández F, Humphries N, Meyer C, Sims D, Thorstad EB, Walker AM, Whoriskey F, Afonso P (2018) A review of acoustic telemetry in Europe and the need for a regional aquatic telemetry network. Animal Biotelemetry 6:12

Abesamis RA, Green AL, Russ GR, Jadloc CRL (2014) The intrinsic vulnerability to fishing of coral reef fishes and their differential recovery in fishery closures. Reviews in Fish Biology and Fisheries 24:1033–1063

Ahmed S (2021) Complaint! Duke University Press, Durham

Akaike H (1974) A new look at the statistical model identification. IEEE Transactions on Automatic Control 19:716-723

Alfonso S, Zupa W, Manfrin A, Fiocchi E, Dioguardi M, Dara M, Lembo G, Carbonara P, Cammarata M (2020) Surgical implantation of electronic tags does not induce medium-term effect: insights from growth and stress physiological profile in two marine fish species. Animal Biotelemetry 8:21

Alós J, Campos-Candela A, Arlinghaus R (2019) A modelling approach to evaluate the impact of fish spatial behavioural types on fisheries stock assessment. ICES Journal of Marine Science 76:489-500

Alós J, Palmer M, Balle S, Arlinghaus R (2016) Bayesian state-space modelling of conventional acoustic tracking provides accurate descriptors of home range behavior in a small-bodied coastal fish species. PLOS ONE 11:e0154089-e0154089

Anras MLB, Lagardére JP, Lafaye JY (1997) Diel activity rhythm of seabass tracked in a natural environment: group effects on swimming patterns and amplitudes. Canadian Journal of Fisheries and Aquatic Sciences 54:162-168

Aranda G, Abascal FJ, Varela JL, Medina A (2013) Spawning behaviour and post-spawning migration patterns of Atlantic bluefin tuna (*Thunnus thynnus*) ascertained from satellite archival tags. PLOS ONE 8:e76445

Ares E, Sutherland N (2016) Debate pack: conservation of sea bass. In: library HoC (ed), Book 2016/0042

Arismendi I, Penaluna BE (2016) Examining diversity inequities in fisheries science: A call to action. BioScience 66:584-591

Armstrong M, van der Hammen T, Goff R (2014) Assessment of recreational fisheries for seabass. Paper for STECF.

Auger-Méthé M, Newman K, Cole D, Empacher F, Gryba R, King AA, Leos-Barajas V, Mills Flemming J, Nielsen A, Petris G, Thomas L (2021) A guide to state–space modeling of ecological time series. Ecological Monographs 91:e01470

Bagdonas K, Nika N, Bristow G, Jankauskienė R, Salytė A, Kontautas A (2011) First record of *Dicentrarchus labrax* (Linnaeus, 1758) from the southeastern Baltic Sea (Lithuania). Journal of Applied Ichthyology 27:1390-1391

Baker K, Eichhorn MP, Griffiths M (2019) Decolonizing field ecology. Biotropica 51:288-292

Baktoft H, Gjelland KØ, Økland F, Rehage JS, Rodemann JR, Corujo RS, Viadero N, Thygesen UH (2019) Opening the black box of high resolution fish tracking using yaps. bioRxiv:2019.2012.2016.877688

Baktoft H, Zajicek P, Klefoth T, Svendsen JC, Jacobsen L, Pedersen MW, March Morla D, Skov C, Nakayama S, Arlinghaus R (2015) Performance assessment of two whole-lake acoustic positional telemetry systems - Is reality mining of free-ranging aquatic animals technologically possible? PLOS ONE 10:e0126534

Balcombe J (2017) What a fish knows. The inner lives of our underwater cousins. Scientific American, New York, USA

Ballance LT (2018) Cetacean Ecology. In: Würsig B, Thewissen JGM, Kovacs KM (eds) Encyclopedia of Marine Mammals (Third Edition). Academic Press

Barbesgaard M (2018) Blue growth: savior or ocean grabbing? The Journal of Peasant Studies 45:130-149

Barr DJ, Levy R, Scheepers C, Tily HJ (2013) Random effects structure for confirmatory hypothesis testing: Keep it maximal. Journal of Memory and Language 68:255-278

Barrieux Y (2009) Marine ontkent doofpotoperatie na verkrachting studente. Nieuwsblad, 02/11/2009

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1 - 48

Bauer RK, Fromentin J-M, Demarcq H, Brisset B, Bonhommeau S (2015) Co-occurrence and habitat use of fin whales, striped dolphins and Atlantic bluefin tuna in the Northwestern Mediterranean Sea. PLOS ONE 10:e0139218

Bavington D, Grzetic B, Neis B (2004) The feminist political ecology of fishing down: Reflections from Newfoundland and Labrador. Studies in Political Economy 73:159-182

Bearzi G (2020) Marine biology on a violated planet: from science to conscience. Ethics in Science and Environmental Politics 20:1-13

Bégout Anras ML, Covés D, Dutto G, Laffargue P, Lagardère F (2003) Tagging juvenile seabass and sole with telemetry transmitters: medium-term effects on growth. ICES Journal of Marine Science 60:1328-1334

Bégout Anras ML, Lagardère JP, Covès D (2004) Swimming activity of seabass: comparing patterns obtained in natural environment and in re-circulating tanks under high density. Journal of Fish Biology 65:314-315

Belgian Federal Public Service Health FCSaE (2015) Something is moving at sea: the marine spatial plan for 2020-2026. . https://www.health.belgium.be/sites/default/files/uploads/fields/fpshealth_theme_file/brochure_something_is_moving_at_sea_2020.pdf

Bellanger M, Holland DS, Anderson CM, Guyader O (2019) Incentive effect of joint and several liability in fishery cooperatives on regulatory compliance. Fish and Fisheries 20:715-728

Bennett NJ, Blythe J, White CS, Campero C (2021) Blue growth and blue justice: Ten risks and solutions for the ocean economy. Marine Policy 125:104387

Bennett NJ, Govan H, Satterfield T (2015) Ocean grabbing. Marine Policy 57:61-68

Beraud C, van der Molen J, Armstrong M, Hunter E, Fonseca L, Hyder K (2018) The influence of oceanographic conditions and larval behaviour on settlement success—the European sea bass *Dicentrarchus labrax* (L.). ICES Journal of Marine Science 75:455-470

Bergmans E (2022) 'Examenvragen in ruil voor seks': nu ook getuigenissen over grensoverschrijdend gedrag aan UGent. De Morgen, 02/02/2022

Berkes F (2012) Implementing ecosystem-based management: evolution or revolution? Fish and Fisheries 13:465-476

Beukhof E, Dencker TS, Pecuchet L, Lindegren M (2019) Spatio-temporal variation in marine fish traits reveals community-wide responses to environmental change. Marine Ecology Progress Series 610:205-222

Bicknell AWJ, Godley BJ, Sheehan EV, Votier SC, Witt MJ (2016) Camera technology for monitoring marine biodiversity and human impact. Frontiers in Ecology and the Environment 14:424-432

Blanchet FG, Cazelles K, Gravel D (2020) Co-occurrence is not evidence of ecological interactions. Ecology Letters 23:1050-1063

Bolnick DI, Amarasekare P, Araújo MS, Bürger R, Levine JM, Novak M, Rudolf VHW, Schreiber SJ, Urban MC, Vasseur DA (2011) Why intraspecific trait variation matters in community ecology. Trends in Ecology & Evolution 26:183-192

Bourabain D (2021) Everyday sexism and racism in the ivory tower: The experiences of early career researchers on the intersection of gender and ethnicity in the academic workplace. Gender, Work & Organization 28:248-267

Braun CD, Galuardi B, Thorrold SR (2018) HMMoce: An R package for improved geolocation of archival-tagged fishes using a hidden Markov method. Methods in Ecology and Evolution 9:1212-1220

Brier GW (1950) Verification of forecasts expressed in terms of probability. Monthly Weather Review 78:1-3

Brodie S, Lédée EJI, Heupel MR, Babcock RC, Campbell HA, Gledhill DC, Hoenner X, Huveneers C, Jaine FRA, Simpfendorfer CA, Taylor MD, Udyawer V, Harcourt RG (2018) Continental-scale animal tracking reveals functional movement classes across marine taxa. Scientific Reports 8:3717

Brooks JL, Chapman JM, Barkley AN, Kessel ST, Hussey NE, Hinch SG, Patterson DA, Hedges KJ, Cooke SJ, Fisk AT, Gruber SH, Nguyen VM (2018) Biotelemetry informing management: case studies exploring successful integration of biotelemetry data into fisheries and habitat management. Canadian Journal of Fisheries and Aquatic Sciences 76:1238-1252

Brosens D, Breine J, Van Thuyne G, Belpaire C, Desmet P, Verreycken H (2015) VIS - A database on the distribution of fishes in inland and estuarine waters in Flanders, Belgium. Zookeys:119-145

Brown RS, Cooke SJ, Anderson WG, McKinley RS (1999) Evidence to challenge the "2% rule" for biotelemetry. North American Journal of Fisheries Management 19:867-871

Brownscombe JW, Griffin LP, Brooks JL, Danylchuk AJ, Cooke SJ, Midwood JD (2022) Applications of telemetry to fish habitat science and management. Canadian Journal of Fisheries and Aquatic Sciences 79:1347-1359

Brownscombe JW, Griffin LP, Chapman JM, Morley D, Acosta A, Crossin GT, Iverson SJ, Adams AJ, Cooke SJ, Danylchuk AJ (2020) A practical method to account for variation in detection range in acoustic telemetry arrays to accurately quantify the spatial ecology of aquatic animals. Methods in Ecology and Evolution 11:82-94

Brownscombe JW, Lédée EJI, Raby GD, Struthers DP, Gutowsky LFG, Nguyen VM, Young N, Stokesbury MJW, Holbrook CM, Brenden TO, Vandergoot CS, Murchie KJ, Whoriskey K, Mills Flemming J, Kessel ST, Krueger CC, Cooke SJ (2019) Conducting and interpreting fish telemetry studies: considerations for researchers and resource managers. Reviews in Fish Biology and Fisheries 29:369-400

Bruneel S, Verhelst P, Reubens J, Baetens JM, Coeck J, Moens T, Goethals P (2020) Quantifying and reducing epistemic uncertainty of passive acoustic telemetry data from longitudinal aquatic systems. Ecological Informatics 59:101133

Burdett HL, Kelling I, Carrigan M (2022) #TimesUp: tackling gender inequities in marine and fisheries science. Journal of Fish Biology 100:4-9

Buyse J, Hostens K, Degraer S, Reubens J, Goossens J, De Backer A (2023) Hard substrates in offshore wind farms influence spatial movements of plaice *Pleuronectes platessa*. Ecological impacts of offshore wind farms on flatfish with emphasis on plaice *Pleuronectes platessa*, a species of commercial interest in the southern North Sea PhD Thesis. Ghent University, Gent

Cadrin SX (2020) Defining spatial structure for fishery stock assessment. Fisheries Research 221:105397

Calabrese JM, Fagan WF (2004) A comparison-shopper's guide to connectivity metrics. Frontiers in Ecology and the Environment 2:529-536

Cambiè G, Kaiser MJ, Marriott AL, Fox J, Lambert G, Hiddink JG, Overy T, Bennet SA, Leng MJ, McCarthy ID (2016) Stable isotope signatures reveal small-scale spatial separation in populations of European sea bass. Marine Ecology Progress Series 546:213-223

Canto JM, San Martín García J, Novas FP (2018) Exploring the role of aggressor's social class in rape and its relation to right-wing authoritarianism and social dominance. Journal of Interpersonal Violence 36:5635-5658

Cardoen F, Agentschap voor Natuur en Bos, Vlaams Ministerie van Leefmilieu Natuur en Energie, Flemish Government (2023a) Besluit van het afdelingshoofd adviezen, vergunningen, erkenningen en subsidies van het Agentschap voor Natuur en Bos betreffende het instellen van lokale maatregelen voor de bescherming van zeebaars in uitvoering van artikel 14 van de wet van 1 juli 1954 op de riviervisserij.

Cardoen F, Agentschap voor Natuur en Bos, Vlaams Ministerie van Leefmilieu Natuur en Energie, Flemish Government (2023b) Besluit van het afdelingshoofd adviezen, vergunningen, erkenningen en subsidies van het Agentschap voor Natuur en Bos betreffende het instellen van maatregelen in 2023 voor de bescherming van zeebaars in uitvoering van artikel 14 van de wet van 1 juli 1954 op de riviervisserij.

Cardoso JFMF, Freitas V, Quilez I, Jouta J, Witte JI, Van Der Veer HW (2015) The European sea bass *Dicentrarchus labrax* in the Dutch Wadden Sea: from visitor to resident species. Journal of the Marine Biological Association of the United Kingdom 95:839-850

Carlström J (2005) Diel variation in echolocation behavior of wild harbor porpoises. Marine Mammal Science 21:1-12

Carmel Y, Kent R, Bar-Massada A, Blank L, Liberzon J, Nezer O, Sapir G, Federman R (2013) Trends in ecological research during the last three decades – a systematic review. PLOS ONE 8:e59813

Carson R (1962) Silent spring. Houghton Mifflin

Cevenini F, Andrews B, Muench A, Lamb P, Ferrini S, Hyder K (2023) Assessing the welfare impacts of changes in recreational fisheries management: A modelling approach for European sea bass. Marine Policy 148:105408

Chapin FS, III, Carpenter SR, Kofinas GP, Folke C, Abel N, Clark WC, Olsson P, Smith DMS, Walker B, Young OR, Berkes F, Biggs R, Grove JM, Naylor RL, Pinkerton E, Steffen W, Swanson FJ (2010) Ecosystem stewardship: sustainability strategies for a rapidly changing planet. Trends in Ecology & Evolution 25:241-249

Chapman BB, Skov C, Hulthén K, Brodersen J, Nilsson PA, Hansson LA, Brönmark C (2012) Partial migration in fishes: definitions, methodologies and taxonomic distribution. Journal of Fish Biology 81:479-499

Childs AR, Næsje TF, Cowley PD (2011) Long-term effects of different-sized surgically implanted acoustic transmitters on the sciaenid *Arygyrosomus japonicus*: breaking the 2% tag-to-body mass rule. Marine and Freshwater Research 62:432-438

Christensen V, Coll M, Piroddi C, Steenbeek J, Buszowski J, Pauly D (2014) A century of fish biomass decline in the ocean. Marine Ecology Progress Series 512:155-166

Cimino M, Cassen M, Merrifield S, Terrill E (2018) Detection efficiency of acoustic biotelemetry sensors on Wave Gliders. Animal Biotelemetry 6:16

Clausen R, Clark B (2005) The metabolic rift and marine ecology: An analysis of the ocean crisis within capitalist production. Organization & Environment 18:422-444

Clayton A (2021) Lessons from implementation of the EU's Common Fisheries Policy. In: Compart E, Remez M (eds) The Pew Charitable Trusts

Clements S, Jepsen D, Karnowski M, Schreck CB (2005) Optimization of an acoustic telemetry array for detecting transmitter-implanted fish. North American Journal of Fisheries Management 25:429-436

CNPMEM (2023) Comité national des pêches maritimes et des élevages marins (CNPMEM) Délibération du Bureau B2/2023. Délibération relative au régime d'exercice de la pêche du bar (*Dicentrarchus labrax*) dans les divisions CIEM VIII a, b et d (golfe de Gascogne)

pour la campagne de pêche 2023. https://www.comite-peches.fr/wp-content/uploads/2023/03/B2-2023-BAR-GOLFE-CADRE.pdf

Cobain MRD, Steward W, Trueman CN, Jensen A (2019) Individual trophic specialization in juvenile European seabass: implications for the management of a commercially important species. ICES Journal of Marine Science 76:1784-1793

Colman JE, Pawson MG, Holmen J, Haugen TO (2008) European sea bass in the North Sea: Past, present and future status, use and management challenges. Global Challenges in Recreational Fisheries. Blackwell Publishing Ltd

Commission E (2023) COM(2023) Communication from the Commission to the European Parliament and the Council. The common fisheries policy today and tomorrow: a Fisheries and Oceans Pact towards sustainable, science-based, innovative and inclusive fisheries management. Brussels, 21.2.2023:1-21

Commission of the European Communities (2000) COM(2000) Communication from the Commission on the precautionary principle. Brussels, 2.2.2000:1-28

Cooke L (2022) Bitch: on the female of the species. Basic Books, New York, US

Cooke SJ, Iverson SJ, Stokesbury MJW, Hinch SG, Fisk AT, VanderZwaag DL, Apostle R, Whoriskey F (2011a) Ocean tracking network Canada: A network approach to addressing critical issues in fisheries and resource management with implications for ocean governance. Fisheries 36:583-592

Cooke SJ, Woodley CM, Brad Eppard M, Brown RS, Nielsen JL (2011b) Advancing the surgical implantation of electronic tags in fish: a gap analysis and research agenda based on a review of trends in intracoelomic tagging effects studies. Reviews in Fish Biology and Fisheries 21:127-151

Coudyser C, Crevits H (2021) Vraag om uitleg over de derde convenant voor duurzame visserij. Verslag vergadering Commissie voor Landbouw, Visserij en Plattelandsbeleid 23 juni 2021

Cowley PD, Bennett RH, Childs AR, Murray TS (2017) Reflection on the first five years of South Africa's Acoustic Tracking Array Platform (ATAP): status, challenges and opportunities. African Journal of Marine Science 39:363-372

Coyne MS, Godley BJ (2005) Satellite Tracking and Analysis Tool (STAT): an integrated system for archiving, analyzing and mapping animal tracking data. Marine Ecology Progress Series 301:1-7

Crevits H, Department of Agriculture and Fisheries, Institute for Agricultural and Fisheries Research, Province of West-Flanders, Rederscentrale, Natuurpunt (2021) Maatschappelijk Convenant 2021 - 2025: Op koers naar duurzaamheid.

Criado Perez C (2019) Invisible women: Data bias in a world designed for men. Abrams Press, New York, USA

Crook DA, Adair BJ, Hetherington LJ (2018) Low-cost device for retrieval of moorings deployed with underwater remote release systems. Marine and Freshwater Research 69

Crossin GT, Heupel MR, Holbrook CM, Hussey NE, Lowerre-Barbieri SK, Nguyen VM, Raby GD, Cooke SJ (2017) Acoustic telemetry and fisheries management. Ecological Applications 27:1031-1049

Curtin R, Prellezo R (2010) Understanding marine ecosystem based management: A literature review. Marine Policy 34:821-830

Dambrine C (2020) Caractérisation et connectivité des habitats écologiques essentiels des stades adulte et juvénile du bar européen. Biodiversité et Ecologie. Université de Bretagne occidentale -Brest., Français.

Dambrine C, Huret M, Woillez M, Pecquerie L, Allal F, Servili A, de Pontual H (2020) Contribution of a bioenergetics model to investigate the growth and survival of European seabass in the Bay of Biscay – English Channel area. Ecological Modelling 423:109007

Dambrine C, Woillez M, Huret M, de Pontual H (2021) Characterising Essential Fish Habitat using spatio-temporal analysis of fishery data: A case study of the European seabass spawning areas. Fisheries Oceanography 30:413-428

Dance MA, Moulton DL, Furey NB, Rooker JR (2016) Does transmitter placement or species affect detection efficiency of tagged animals in biotelemetry research? Fisheries Research 183:80-85

Datchoua-Tirvaudey A, Martin A, Scott CP (2023) Racial-gender disparities, and the impacts of coloniality in ocean science on BIPOC women. In: Obaidullah F (ed) The Ocean and Us. Springer International Publishing, Cham

David V, Mouget A, Perrot Y, Le Goff L, Thiriet P, Diogoul N, Feunteun E, Acou A, Brehmer P (2022) Insights from a multibeam echosounder to survey pelagic fish shoals and their spatio-temporal distribution in ultra-shallow waters. Estuarine, Coastal and Shelf Science 264:107705

de Pontual H, Heerah K, Goossens J, Garren F, Martin S, Le Ru L, Le Roy D, Woillez M (2023) Seasonal migration, site fidelity and population structure of European seabass: shedding light from large-scale electronic tagging. ICES Journal of Marine Science Accepted

de Pontual H, Lalire M, Fablet R, Laspougeas C, Garren F, Martin S, Drogou M, Woillez M, Grabowski J (2019) New insights into behavioural ecology of European seabass off the West Coast of France: implications at local and population scales. ICES Journal of Marine Science 76:501-515

De Snijder N, Brouckaert E, Hansen K, Heyman J, Polet H, Welvaert M (2014) Vistraject. Duurzaamheidstraject voor de Belgische visserijsector.

De Standaard (2011) Marinier veroordeeld voor aanranding. De Standaard, 25/10/2011

de Vos A (2020) The problem of 'colonial science'. Scientific American, 01/07/2020

Delbare D (2012) Populatiedynamica van zeebaars op het Belgisch continentaal plat. AQUA/2012/01

Desmet P, Oldoni D, Van Hoey S (2022) etn: Access data from the European Tracking Network. https://github.com/inbo/etn

Despentes V (2006) King Kong Theory. Fitzcarraldo Editions, London, Great Britain

Destoop E, Goossens K (2022) Rector Van de Walle, uw verontwaardiging is ongepast en ronduit kwetsend. De Morgen, 07/02/2022

Dichmont CM, Pascoe S, Kompas T, Punt AE, Deng R (2010) On implementing maximum economic yield in commercial fisheries. Proceedings of the National Academy of Sciences 107:16-21

Dingle H, Drake VA (2007) What is migration? BioScience 57:113-121

Doyle TK, Haberlin D, Clohessy J, Bennison A, Jessopp M (2017) Localised residency and inter-annual fidelity to coastal foraging areas may place sea bass at risk to local depletion. Scientific Reports 7:45841

Drake J, Lambin X, Sutherland C (2022) The value of considering demographic contributions to connectivity: a review. Ecography 2022:e05552

Dudgeon CL, Lanyon JM, Semmens JM (2013) Seasonality and site fidelity of the zebra shark, Stegostoma fasciatum, in southeast Queensland, Australia. Animal Behaviour 85:471-481

Dunlap A (2020) Wind, coal, and copper: the politics of land grabbing, counterinsurgency, and the social engineering of extraction. Globalizations 17:661-682

EAA (2016) Sea bass. https://www.eaa-europe.org/topics/sea-bass/

EAA (2018a) Sea bass - Recreational anglers demonstrate in France. Accessed 5 January. https://www.eaa-europe.org/news/12368/sea-bass-recreational-anglers-demonstrate-in-france.html

EAA (2018b) Sea Bass: EAA and EFTTA ask Fisheries Commissioner Vella for a bag-limit now. Accessed 5 January. https://www.eaa-europe.org/news/12641/sea-bass-eaa-and-eftta-ask-fisheries-commissioner-vella-for-a-bag-limit-now.html

Earle M (2021) Maximum sustainable yield in the EU's Common Fisheries Policy - a political history. ICES Journal of Marine Science 78:2173-2181

EC (2002) Council Regulation (EC) No 2371/2002 of 20 December 2002 on the conservation and sustainable exploitation of fisheries resources under the Common Fisheries Policy. Official Journal of the European Communities 358:59-80

Edwards JE, Buijse AD, Winter HV, van Leeuwen A, Bijleveld AI (*in review*) Swimways - A movement ecology framework for tracking fish movements in an open coastal environment. Marine Ecology Progress Series

Edwards JE, Pratt J, Tress N, Hussey NE (2019) Thinking deeper: Uncovering the mysteries of animal movement in the deep sea. Deep Sea Research Part I: Oceanographic Research Papers 146:24-43

Eigaard OR, Bastardie F, Hintzen NT, Buhl-Mortensen L, Buhl-Mortensen P, Catarino R, Dinesen GE, Egekvist J, Fock HO, Geitner K, Gerritsen HD, González MM, Jonsson P, Kavadas S, Laffargue P, Lundy M, Gonzalez-Mirelis G, Nielsen JR, Papadopoulou N, Posen PE, Pulcinella J, Russo T, Sala A, Silva C, Smith CJ, Vanelslander B, Rijnsdorp AD (2017) The footprint of bottom trawling in European waters: distribution, intensity, and seabed integrity. ICES Journal of Marine Science 74:847-865

El Mahrad B, Newton A, Icely JD, Kacimi I, Abalansa S, Snoussi M (2020) Contribution of remote sensing technologies to a holistic coastal and marine environmental management framework: A review. Remote Sensing, Book 12

Ellis RD, Flaherty-Walia KE, Collins AB, Bickford JW, Boucek R, Walters Burnsed SL, Lowerre-Barbieri SK (2019) Acoustic telemetry array evolution: From species- and project-specific designs to large-scale, multispecies, cooperative networks. Fisheries Research 209:186-195

Ellis S, Steyn HS (2003) Practical significance (effect sizes) versus or in combination with statistical significance (p-values). Management Dynamics 12:51-53

Escalle L, Pennino MG, Gaertner D, Chavance P, Delgado de Molina A, Demarcq H, Romanov E, Merigot B (2016) Environmental factors and megafauna spatio-temporal co-occurrence with purse-seine fisheries. Fisheries Oceanography 25:433-447

EU (2003) Directive 2003/4/EC of the European Parliament and of the Council of 28 January 2003 on public access to environmental information and repealing Council Directive 90/313/EEC. Official Journal of the European Union 41:26-32

EU (2004) Judgment of the Court (Grand Chamber) of 7 September 2004 in Case C-127/02 (reference for a preliminary ruling from the Raad van State): Landelijke Vereniging tot Behoud van de Waddenzee, Nederlandse Vereniging tot Bescherming van Vogels v Staatssecretaris van Landbouw, Natuurbeheer en Visserij. Official Journal of the European Union 26:2

EU (2008) Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive). Official Journal of the European Union 164:19-40

EU (2012) Consolidated version of the Treaty on the Functioning of the European Union. Official Journal of the European Union 326:47-390

EU (2013) Regulation (EU) No 1380/2013 of the European Parliament and of the Council of 11 December 2013 on the Common Fisheries Policy, amending Council Regulations (EC) No 1954/2003 and (EC) No 1224/2009 and repealing Council Regulations (EC) No 2371/2002 and (EC) No 639/2004 and Council Decision 2004/585/EC. Official Journal of the European Union 354:22-61

EU (2015a) Commission Delegated Regulation (EU) 2015/242 of 9 October 2014 laying down detailed rules on the functioning of the Advisory Councils under the Common Fisheries Policy. Official Journal of the European Union 41:1-4

EU (2015b) Commission Implementing Regulation (EU) 2015/111 of 26 January 2015 establishing measures to alleviate a serious threat to the conservation of the sea bass (*Dicentrarchus labrax*) stock in the Celtic Sea, Channel, Irish Sea and southern North Sea. Official Journal of the European Union 20:31-33

EU (2015c) Council Regulation (EU) 2015/104 of 19 January 2015 fixing for 2015 the fishing opportunities for certain fish stocks and groups of fish stocks, applicable in Union waters and, for Union vessels, in certain non-Union waters, amending Regulation (EU) No 43/2014 and repealing Regulation (EU) No 779/2014. Official Journal of the European Union 22:1-163

EU (2015d) Council Regulation (EU) 2015/960 of 19 June 2015 amending Regulation (EU) 2015/104 as regards certain fishing opportunities. Official Journal of the European Union 157:1-19

EU (2015e) European Parliament resolution of 12 March 2015 on sustainable exploitation of sea bass (2015/2596(RSP)) Official Journal of the European Union 316:176-177

EU (2016) Council Regulation (EU) 2016/72 of 22 January 2016 fixing for 2016 the fishing opportunities for certain fish stocks and groups of fish stocks, applicable in Union waters and, for Union fishing vessels, in certain non-Union waters, and amending Regulation (EU) 2015/104. Official Journal of the European Union 22:1-165

EU (2017a) Commission Decision (EU) 2017/848 of 17 May 2017 laying down criteria and methodological standards on good environmental status of marine waters and specifications and standardised methods for monitoring and assessment, and repealing Decision 2010/477/EU. Official Journal of the European Union 125:43-74

EU (2017b) Council Regulation (EU) 2017/127 of 20 January 2017 fixing for 2017 the fishing opportunities for certain fish stocks and groups of fish stocks, applicable in Union waters and, for Union fishing vessels, in certain non-Union waters. Official Journal of the European Union 24:1-172

EU (2018a) Action brought on 22 April 2018 - European Anglers Alliance v Council (Case T-252/18) (2018/C 240/55). Official Journal of the European Union 240:48

EU (2018b) Council Regulation (EU) 2018/120 of 23 January 2018 fixing for 2018 the fishing opportunities for certain fish stocks and groups of fish stocks, applicable in Union waters and, for Union fishing vessels, in certain non-Union waters, and amending Regulation (EU) 2017/127. Official Journal of the European Union 27:1-168

EU (2018c) Council Regulation (EU) 2018/1308 of 28 September 2018 amending Regulation (EU) 2018/120 as regards fishing opportunities for European seabass. Official Journal of the European Union 244I

EU (2019a) Council Regulation (EU) 2019/124 of 30 January 2019 fixing for 2019 the fishing opportunities for certain fish stocks and groups of fish stocks, applicable in Union waters and, for Union fishing vessels, in certain non-Union waters. Official Journal of the European Union 29:1-166

EU (2019b) Regulation (EU) 2019/472 of the European Parliament and of the Council of 19 March 2019 establishing a multiannual plan for stocks fished in the Western Waters and adjacent waters, and for fisheries exploiting those stocks, amending Regulations (EU) 2016/1139 and (EU) 2018/973, and repealing Council Regulations (EC) No 811/2004, (EC) No 2166/2005, (EC) No 388/2006, (EC) No 509/2007 and (EC) No 1300/2008. Official Journal of the European Union 83:1-17

EU (2020) Council Regulation (EU) 2020/123 of 27 January 2020 fixing for 2020 the fishing opportunities for certain fish stocks and groups of fish stocks, applicable in Union

waters and, for Union fishing vessels, in certain non-Union waters. Official Journal of the European Union 25:1-156

EU (2021a) Council Regulation (EU) 2021/92 of 28 January 2021 fixing for 2021 the fishing opportunities for certain fish stocks and groups of fish stocks, applicable in Union waters and, for Union fishing vessels, in certain non-Union waters. Official Journal of the European Union 31:31-192

EU (2021b) Council Regulation (EU) 2021/703 of 26 April 2021 amending Regulations (EU) 2021/91 and (EU) 2021/92 as regards certain fishing opportunities for 2021 in Union and non-Union waters. Official Journal of the European Union 146:1-69

EU (2021c) Council Regulation (EU) 2021/1239 of 29 July 2021 amending Regulations (EU) 2019/1919, (EU) 2021/91 and (EU) 2021/92 as regards certain fishing opportunities for 2021 in Union and non-Union waters. Official Journal of the European Union 276:1-60

EU (2022a) Council Regulation (EU) 2022/109 of 27 January 2022 fixing for 2022 the fishing opportunities for certain fish stocks and groups of fish stocks applicable in Union waters and for Union fishing vessels in certain non-Union waters. Official Journal of the European Union 21:1-164

EU (2022b) Council Regulation (EU) 2022/515 of 31 March 2022 amending Regulation (EU) 2022/109 fixing for 2022 the fishing opportunities for certain fish stocks and groups of fish stocks applicable in Union waters and for Union fishing vessels in certain non-Union waters. Official Journal of the European Union 104:1-50

EU (2023) Council Regulation (EU) 2023/194 of 30 January 2023 fixing for 2023 the fishing opportunities for certain fish stocks, applicable in Union waters and, for Union fishing vessels, in certain non-Union waters, as well as fixing for 2023 and 2024 such fishing opportunities for certain deep-sea fish stocks. Official Journal of the European Union 28:1-219

European Environment Agency (2001) Late lessons from early warnings: the precautionary principle 1896–2000. Environmental issue report No 22. Office for Official Publications of the European Communities 22:210

European Ombudsman (2020) Decision in case 640/2019/TE on the transparency of the Council of the EU's decision-making process leading to the adoption of annual regulations setting fishing quotas.

FAO (2016) International standard statistical classification of fishing gear (ISSCFG, 2016). Coordinating Working Party on Fishery Statistics (CWP) Handbook of Fishery Statistics

FAO (2022) The state of world fisheries and aquaculture 2022. Towards blue transformation. Rome

Farris SR (2017) In the name of women's rights: The rise of femonationalism. Duke University Press

Favaro B, Oester S, Cigliano JA, Cornick LA, Hind EJ, Parsons ECM, Woodbury TJ (2016) Your science conference should have a code of conduct. Frontiers in Marine Science 3

Federici S (2018) Witches, witch-hunting, and women. PM Press, New York, USA

Flemish Government (2013) Besluit van de Vlaamse Regering tot uitvoering van de wet van 1 juli 1954 op de riviervisserij. Belgisch Staatsblad 2013035218

Flemish Government (2017) Ministerieel besluit betreffende het instellen van tijdelijke maatregelen voor zeebaars ter uitvoering van artikel 14 van de wet van 1 juli 1954 op de riviervisserij. Belgisch Staatsblad 32051:2194-2196

Folke C, Polasky S, Rockström J, Galaz V, Westley F, Lamont M, Scheffer M, Österblom H, Carpenter SR, Chapin FS, Seto KC, Weber EU, Crona BI, Daily GC, Dasgupta P, Gaffney O, Gordon LJ, Hoff H, Levin SA, Lubchenco J, Steffen W, Walker BH (2021) Our future in the Anthropocene biosphere. Ambio 50:834-869

Fritsch M, Morizur Y, Lambert E, Bonhomme F, Guinand B (2007) Assessment of sea bass (*Dicentrarchus labrax*, L.) stock delimitation in the Bay of Biscay and the English Channel based on mark-recapture and genetic data. Fisheries Research 83:123-132

Froese R, Pauly D (2022) FishBase. Accessed 31/01/2023. www.fishbase.se

Garcia J, Mourier J, Lenfant P (2015) Spatial behavior of two coral reef fishes within a Caribbean marine protected area. Marine Environmental Research 109:41-51

Garnett K, Parsons DJ (2017) Multi-case review of the application of the precautionary principle in European Union law and case Law. Risk Analysis 37:502-516

Gatti P, Fisher JAD, Cyr F, Galbraith PS, Robert D, Le Bris A (2021) A review and tests of validation and sensitivity of geolocation models for marine fish tracking. Fish and Fisheries 22:1041-1066

Gazit T, Apostle R, Branton R (2013) Deployment, tracking, and data management: Technology and science for a global ocean tracking network. Journal of International Wildlife Law & Policy 16:112-127

Georgopoulou DG, Fanouraki E, Voskakis D, Mitrizakis N, Papandroulakis N (2022) European seabass show variable responses in their group swimming features after tag implantation. Frontiers in Animal Science 3

Gilio-Whitaker D (2020) As long as grass grows. The Indigenous fight for environmental justice, from colonization to Standing Rock. Beacon Press, Boston, USA

Giordano F, Mattei G, Parente C, Peluso F, Santamaria R (2016) Integrating sensors into a marine drone for bathymetric 3D surveys in shallow waters. Sensors, Book 16

Glenn H, Tingley D, Sánchez Maroño S, Holm D, Kell L, Padda G, Runar Edvardsson I, Asmundsson J, Conides A, Kapiris K, Bezabih M, Wattage P, Kuikka S (2012) Trust in the fisheries scientific community. Marine Policy 36:54-72

Goossens J (2023) AI dat gepraat over visquota, de minister krijgt er honger van. De Standaard, 03/04/2023

Goossens J, Buyse J, Bruneel S, Verhelst P, Goethals P, Torreele E, Moens T, Reubens J (2022) Taking the time for range testing: an approach to account for temporal resolution in acoustic telemetry detection range assessments. Animal Biotelemetry 10:17

Goossens J, T'Jampens M, Deneudt K, Reubens J (2020) Mooring scientific instruments on the seabed—Design, deployment protocol and performance of a recoverable frame for acoustic receivers. Methods in Ecology and Evolution 11:974-979

Goossens J, Villagra D, De Putter G, Verhelst P, Torreele E, Moens T, Reubens J (*in review*) Not all are equal before the law – fisheries measures protect European seabass groups with distinct habitat use differently. ICES Journal of Marine Science

Goossens J, Woillez M, LeBris A, Verhelst P, Moens T, Torreele E, Reubens J (2023) Acoustic and archival technologies join forces: A combination tag. Methods in Ecology and Evolution 14:860– 866

Gotelli N, Hart E, Ellison A (2015) Null model analysis for ecological data https://cran.microsoft.com/snapshot/2017-03-22/web/packages/EcoSimR/EcoSimR.pdf

Gracanin A, Mikac KM (2022) Camera traps reveal overlap and seasonal variation in the diel activity of arboreal and semi-arboreal mammals. Mammalian Biology 102:341-355

Graham JA, Watson JW, García García LM, Bradley K, Bradley R, Brown M, Ciotti BJ, Goodwin D, Nash RDM, Roche WK, Wogerbauer C, Hyder K (2023) Pelagic connectivity of European sea bass between spawning and nursery grounds. Frontiers in Marine Science 9

Graves JL, Kearney M, Barabino G, Malcom S (2022) Inequality in science and the case for a new agenda. Proceedings of the National Academy of Sciences 119:e2117831119

Griffith DM, Veech JA, Marsh CJ (2016) cooccur: Probabilistic species co-occurrence analysis in R. Journal of Statistical Software, Code Snippets 69:1 - 17

Grilli G, Curtis J, Hynes S, O'Reilly P (2019) Anglers' views on stock conservation: Sea bass angling in Ireland. Marine Policy 99:34-41

Grothues T, Able K, Pravatiner JH (2012) Winter flounder (*Pseudopleuronectes americanus* Walbaum) burial in estuaries: Acoustic telemetry triumph and tribulation. Journal of Experimental Marine Biology and Ecology 438:125-136

Haelters J, Kerckhof F, Toussaint E, Jauniaux T, Degraer S (2012) The diet of harbour porpoises bycaught or washed ashore in Belgium, and relationship with relevant data from the strandings database. .

Hanley JA, McNeil BJ (1982) The meaning and use of the area under a receiver operating characteristic (ROC) curve. Radiology 143:29-36

Hare JA (2020) Ten lessons from the frontlines of science in support of fisheries management. ICES Journal of Marine Science 77:870-877

Hawkins SJ, Bohn K, Sims DW, Ribeiro P, Faria J, Presa P, Pita A, Martins GM, Neto AI, Burrows MT, Genner MJ (2016) Fisheries stocks from an ecological perspective: Disentangling ecological connectivity from genetic interchange. Fisheries Research 179:333-341

Hays GC, Bailey H, Bograd SJ, Bowen WD, Campagna C, Carmichael RH, Casale P, Chiaradia A, Costa DP, Cuevas E, Nico de Bruyn PJ, Dias MP, Duarte CM, Dunn DC, Dutton PH, Esteban N, Friedlaender A, Goetz KT, Godley BJ, Halpin PN, Hamann M, Hammerschlag N, Harcourt R, Harrison A-L, Hazen EL, Heupel MR, Hoyt E, Humphries NE, Kot CY, Lea JSE, Marsh H, Maxwell SM, McMahon CR, Notarbartolo di Sciara G, Palacios DM, Phillips RA, Righton D, Schofield G, Seminoff JA, Simpfendorfer CA, Sims DW, Takahashi A, Tetley MJ, Thums M, Trathan PN, Villegas-Amtmann S, Wells RS, Whiting SD, Wildermann NE, Sequeira AMM (2019) Translating marine animal tracking data into conservation policy and management. Trends in Ecology & Evolution 34:459-473

Hazen EL, Abrahms B, Brodie S, Carroll G, Jacox MG, Savoca MS, Scales KL, Sydeman WJ, Bograd SJ (2019) Marine top predators as climate and ecosystem sentinels. Frontiers in Ecology and the Environment 17:565-574

He Q, Silliman BR (2019) Climate change, human impacts, and coastal ecosystems in the Anthropocene. Current Biology 29:R1021-R1035

Heerah K, Woillez M, Fablet R, Garren F, Martin S, De Pontual H (2017) Coupling spectral analysis and hidden Markov models for the segmentation of behavioural patterns. Movement Ecology 5:20

Hernández F, Dillen N, Fernández-Bejarano S (2023) lwdataexplorer: Access to data from the LifeWatch Data Explorer. R package version 0.0.0.9000. https://lifewatch.github.io/lwdataexplorer/

Hertel AG, Niemelä PT, Dingemanse NJ, Mueller T (2020) A guide for studying among-individual behavioral variation from movement data in the wild. Movement Ecology 8:30

Heupel MR, Reiss KL, Yeiser BG, Simpfendorfer CA (2008) Effects of biofouling on performance of moored data logging acoustic receivers. Limnology and Oceanography: Methods 6:327-335

Heupel MR, Semmens JM, Hobday AJ (2006) Automated acoustic tracking of aquatic animals: scales, design and deployment of listening station arrays. Marine and Freshwater Research 57:1-13

Hilborn R (2007) Defining success in fisheries and conflicts in objectives. Marine Policy 31:153-158

Hind J (2006) Sea bass (*Dicentrarchus labrax*) and a sea change for 21st century fisheries. International Journal of the Society for Underwater Technology 26:3

Hodgson EE, Halpern BS (2019) Investigating cumulative effects across ecological scales. Conservation Biology: the journal of the Society for Conservation Biology 33:22-32

Hoenner X, Huveneers C, Steckenreuter A, Simpfendorfer C, Tattersall K, Jaine F, Atkins N, Babcock R, Brodie S, Burgess J, Campbell H, Heupel M, Pasquer B, Proctor R, Taylor MD, Udyawer V, Harcourt R (2018) Australia's continental-scale acoustic tracking database and its automated quality control process. Sci Data 5:170206

Hornborg S, van Putten I, Novaglio C, Fulton EA, Blanchard JL, Plagányi É, Bulman C, Sainsbury K (2019) Ecosystem-based fisheries management requires broader performance indicators for the human dimension. Marine Policy 108:103639

How JR, de Lestang S (2012) Acoustic tracking: issues affecting design, analysis and interpretation of data from movement studies. Marine and Freshwater Research 63:312–324

Howell D, Schueller AM, Bentley JW, Buchheister A, Chagaris D, Cieri M, Drew K, Lundy MG, Pedreschi D, Reid DG, Townsend H (2021) Combining ecosystem and single-species modeling to provide ecosystem-based fisheries management advice within current management systems. Frontiers in Marine Science 7

Hussey NE, Kessel ST, Aarestrup K, Cooke SJ, Cowley PD, Fisk AT, Harcourt RG, Holland KN, Iverson SJ, Kocik JF, Mills Flemming JE, Whoriskey FG (2015) Aquatic animal telemetry: A panoramic window into the underwater world. Science 348:1255642

Hutchings JA, Minto C, Ricard D, Baum JK, Jensen OP (2010) Trends in the abundance of marine fishes. Canadian Journal of Fisheries and Aquatic Sciences 67:1205-1210

Huusko R, Huusko A, Mäki-Petäys A, Orell P, Erkinaro J (2016) Effects of tagging on migration behaviour, survival and growth of hatchery-reared Atlantic salmon smolts. Fisheries Management and Ecology 23:367-375

Huveneers C, Simpfendorfer CA, Kim S, Semmens JM, Hobday AJ, Pederson H, Stieglitz T, Vallee R, Webber D, Heupel MR, Peddemors V, Harcourt RG, Reynolds J (2016) The influence of environmental parameters on the performance and detection range of acoustic receivers. Methods in Ecology and Evolution 7:825-835

Hyder K, Maravelias CD, Kraan M, Radford Z, Prellezo R (2020) Marine recreational fisheries — current state and future opportunities. ICES Journal of Marine Science 77:2171-2180

Hyder K, Weltersbach MS, Armstrong M, Ferter K, Townhill B, Ahvonen A, Arlinghaus R, Baikov A, Bellanger M, Birzaks J, Borch T, Cambie G, de Graaf M, Diogo HMC, Dziemian Ł, Gordoa A, Grzebielec R, Hartill B, Kagervall A, Kapiris K, Karlsson M, Kleiven AR, Lejk AM, Levrel H, Lovell S, Lyle J, Moilanen P, Monkman G, Morales-Nin B, Mugerza E, Martinez R, O'Reilly P, Olesen HJ, Papadopoulos A, Pita P, Radford Z, Radtke K, Roche W, Rocklin D, Ruiz J, Scougal C, Silvestri R, Skov C, Steinback S, Sundelöf A, Svagzdys A, Turnbull D, van der Hammen T, van Voorhees D, van Winsen F, Verleye T, Veiga P, Vølstad J-H, Zarauz L, Zolubas T, Strehlow HV (2018) Recreational sea fishing in Europe in a global context—Participation rates, fishing effort, expenditure, and implications for monitoring and assessment. Fish and Fisheries 19:225-243

ICES (2012a) Report of the inter-benchmark protocol on new species (turbot and sea bass; IBPNew 2012). 1–5 October 2012, Copenhagen, Denmark. ICES CM 2012/ACOM: 45.

ICES (2012b) Widely distributed and migratory stocks European seabass in the Northeast Atlantic Advice September 2012. ICES advice 2012 Book 9

ICES (2018) Stock annex: Sea bass (*Dicentrarchus labrax*) in division 8ab (Bay of Biscay).71

ICES (2020a) Sea bass (*Dicentrarchus labrax*) in divisions 6.a, 7.b, and 7.j (West of Scotland, West of Ireland, eastern part of southwest of Ireland). Report of the ICES Advisory Committee, 2020 ICES Advice 2020, bss276a7bj

ICES (2020b) Stock annex: Seabass (*Dicentrarchus labrax*) in division 4.b–c, 7.a, and 7.d–h (central and southern North Sea, Irish Sea, English Channel, Bristol Channel, and Celtic Sea).107

ICES (2021) Sea bass (*Dicentrarchus labrax*) in divisions 8.c and 9.a (southern Bay of Biscay and Atlantic Iberian waters). Report of the ICES Advisory Committee, 2020 ICES Advice 2020, bss278c9a

ICES (2022a) Cod (*Gadus morhua*) in Subarea 4, Division 7.d, and Subdivision 20 (North Sea, eastern English Channel, Skagerrak). ICES Advice on fishing opportunities, catch, and effort Greater North Sea ecoregion

ICES (2022b) Sea bass (*Dicentrarchus labrax*) in divisions 4.b–c, 7.a, and 7.d–h (central and southern North Sea, Irish Sea, English Channel, Bristol Channel, and Celtic Sea). Report of the ICES Advisory Committee, 2022 ICES Advice 2022, bss274bc7ad-h

ICES (2022c) Sea bass (*Dicentrarchus labrax*) in divisions 8.a–b (northern and central Bay of Biscay). Report of the ICES Advisory Committee, 2022 ICES Advice 2022, bss278ab

ICES (2023) Benchmark on selected sea bass stocks–stock ID workshop (WKBSEABASS-ID). ICES Scientific Reports 5:31

Imma Zé (2011) "Just ask the scientists": Troubling the "Hottentot" and scientific racism in Bessie Head's Maru and Ama Ata Aidoo's Our Sister Killjoy. In: Gordon-Chipembere N (ed) Representation and Black womanhood: The legacy of Sarah Baartman. Palgrave Macmillan US, New York

Ivanov E, Capet A, Barth A, Delhez EJM, Soetaert K, Grégoire M (2020) Hydrodynamic variability in the Southern Bight of the North Sea in response to typical atmospheric and tidal regimes. Benefit of using a high resolution model. Ocean Modelling 154:101682

Jacoby DMP, Brooks EJ, Croft DP, Sims DW (2012) Developing a deeper understanding of animal movements and spatial dynamics through novel application of network analyses. Methods in Ecology and Evolution 3:574-583

Jeltsch F, Bonte D, Pe'er G, Reineking B, Leimgruber P, Balkenhol N, Schröder B, Buchmann CM, Mueller T, Blaum N, Zurell D, Böhning-Gaese K, Wiegand T, Eccard JA, Hofer H, Reeg J, Eggers U, Bauer S (2013) Integrating movement ecology with biodiversity research - exploring new avenues to address spatiotemporal biodiversity dynamics. Movement Ecology 1:6

Jennings S, Pawson MG (1992) The origin and recruitment of bass, *Dicentrarchus labrax*, larvae to nursery areas. Journal of the Marine Biological Association of the United Kingdom 72:199-212

Jentoft S (2022) Small-Scale Fisheries in the Blue Economy. In: Jentoft S, Chuenpagdee R, Bugeja Said A, Isaacs M (eds) Blue justice: Small-scale fisheries in a sustainable ocean economy. Springer International Publishing, Cham

Jepsen N, Koed A, Thorstad EB, Baras E (2002) Surgical implantation of telemetry transmitters in fish: how much have we learned? Hydrobiologia 483:239-248

Jones KR, Klein CJ, Halpern BS, Venter O, Grantham H, Kuempel CD, Shumway N, Friedlander AM, Possingham HP, Watson JEM (2018) The location and protection status of earth's diminishing marine wilderness. Current Biology 28:2506-2512.e2503

Kamilar JM, Ledogar JA (2011) Species co-occurrence patterns and dietary resource competition in primates. Am J Phys Anthropol 144:131-139

Kastelein RA, Helder-Hoek L, Jennings N (2018) Seasonal changes in food consumption, respiration rate, and body condition of a male harbor porpoise (*Phocoena phocoena*). . Aquatic Mammals 44:76-91

Kendall MS, Siceloff L, Winship A, Monaco ME (2017) Determining conservation potential of an opportunistically defined MPA boundary using fish telemetry. Biological Conservation 211:37-46

Kendall MS, Williams BL, Ellis RD, Flaherty-Walia KE, Collins AB, Roberson KW (2021) Measuring and understanding receiver efficiency in your acoustic telemetry array. Fisheries Research 234:105802

Kennedy M, Fitzmaurice P (1972) The biology of the bass, *Dicentrarchus labrax*, in Irish water. Journal of the Marine Biological Association of the United Kingdom 52:557-597

Kerr LA, Hintzen NT, Cadrin SX, Clausen LW, Dickey-Collas M, Goethel DR, Hatfield EMC, Kritzer JP, Nash RDM (2017) Lessons learned from practical approaches to reconcile mismatches between biological population structure and stock units of marine fish. ICES Journal of Marine Science 74:1708-1722

Kessel ST, Cooke SJ, Heupel MR, Hussey NE, Simpfendorfer CA, Vagle S, Fisk AT (2014) A review of detection range testing in aquatic passive acoustic telemetry studies. Reviews in Fish Biology and Fisheries 24:199-218

Kessel ST, Hussey NE, Webber DM, Gruber SH, Young JM, Smale MJ, Fisk AT (2015) Close proximity detection interference with acoustic telemetry: the importance of considering tag power output in low ambient noise environments. Animal Biotelemetry 3:5

Keygnaert I, De Schrijver L, Cismaru Inescu A, Schapansky E, Nobels A, Hahaut B, Stappers C, De Bauw Z, Lemonne A, Renard B, Weewauters M, Nisen L, Vander Beken T, Vandeviver C (2021) UN-MENAMAIS - Understanding the mechanisms, nature, magnitude and impact of sexual violence in Belgium. Belgian Science Policy Office

Klinard NV, Halfyard EA, Matley JK, Fisk AT, Johnson TB (2019) The influence of dynamic environmental interactions on detection efficiency of acoustic transmitters in a large, deep, freshwater lake. Animal Biotelemetry 7:17

Knott C, Power N, Neis B, Frangoudes K (2021) North Atlantic fishy feminists and the more-than-human approach: a conversation. Gender, Place & Culture:1-19

Kraak SBM, Kelly CJ, Codling EA, Rogan E (2010) On scientists' discomfort in fisheries advisory science: the example of simulation-based fisheries management-strategy evaluations. Fish and Fisheries 11:119-132

Kraft S, Gandra M, Lennox RJ, Mourier J, Winkler AC, Abecasis D (2023) Residency and space use estimation methods based on passive acoustic telemetry data. Movement Ecology 11:12

Kraus RT, Holbrook CM, Vandergoot CS, Stewart TR, Faust MD, Watkinson DA, Charles C, Pegg M, Enders EC, Krueger CC (2018) Evaluation of acoustic telemetry grids for determining aquatic animal movement and survival. Methods in Ecology and Evolution 9:1489-1502

Kruskal WH, Wallis WA (1952) Use of ranks in one-criterion variance analysis. Journal of the American Statistical Association 47:583-621

Ku H (1966) Notes on the Use of Propagation of Error Formulas. Journal of Research of the National Bureau of Standards C, Engineering and Instrumentation 70C:263-273

Kwiatkowski L, Torres O, Bopp L, Aumont O, Chamberlain M, Christian JR, Dunne JP, Gehlen M, Ilyina T, John JG, Lenton A, Li H, Lovenduski NS, Orr JC, Palmieri J, Santana-Falcón Y, Schwinger J, Séférian R, Stock CA, Tagliabue A, Takano Y, Tjiputra J, Toyama K, Tsujino H, Watanabe M, Yamamoto A, Yool A, Ziehn T (2020) Twenty-first century ocean warming, acidification, deoxygenation, and upper-ocean nutrient and primary production decline from CMIP6 model projections. Biogeosciences 17:3439-3470

Lam ME, Pitcher TJ (2012) The ethical dimensions of fisheries. Current Opinion in Environmental Sustainability 4:364-373

Lamothe KA, Dextrase AJ, Drake DAR (2019) Aggregation of two imperfectly detected imperilled freshwater fishes: understanding community structure and co-occurrence for multispecies conservation. Endangered Species Research 40:123-132

Landrigan PJ, Stegeman JJ, Fleming LE, Allemand D, Anderson DM, Backer LC, Brucker-Davis F, Chevalier N, Corra L, Czerucka D, Bottein MD, Demeneix B, Depledge M, Deheyn DD, Dorman CJ, Fénichel P, Fisher S, Gaill F, Galgani F, Gaze WH, Giuliano L, Grandjean P, Hahn ME, Hamdoun A, Hess P, Judson B, Laborde A, McGlade J, Mu J, Mustapha A, Neira M, Noble RT, Pedrotti ML, Reddy C, Rocklöv J, Scharler UM, Shanmugam H, Taghian G, van de Water J, Vezzulli L, Weihe P, Zeka A, Raps H, Rampal P (2020) Human health and ocean pollution. Ann Glob Health 86:151

Langhans SD, Jähnig SC, Lago M, Schmidt-Kloiber A, Hein T (2019) The potential of ecosystem-based management to integrate biodiversity conservation and ecosystem service provision in aquatic ecosystems. Science of The Total Environment 672:1017-1020

Le Luherne E, Daverat F, Woillez M, Pécheyran C, de Pontual H (2022) Coupling natural and electronic tags to explore spawning site fidelity and natal homing in northeast Atlantic European seabass. Estuarine, Coastal and Shelf Science 278:108118

Lê S, Josse J, Husson F (2008) FactoMineR: An R Package for Multivariate Analysis. Journal of Statistical Software 25:1 - 18

Lea JSE, Humphries NE, von Brandis RG, Clarke CR, Sims DW (2016) Acoustic telemetry and network analysis reveal the space use of multiple reef predators and enhance marine protected area design. Proceedings of the Royal Society B: Biological Sciences 283:20160717

Legrand S, Baetens K (2021) Hydrodynamic forecast for the Belgian Coastal Zone. Physical State of the Sea - Belgian Coastal Zone - COHERENS UKMO. Royal Belgian Institute of Natural Sciences

Lennox RJ, Aarestrup K, Cooke SJ, Cowley PD, Deng ZD, Fisk AT, Harcourt RG, Heupel M, Hinch SG, Holland KN, Hussey NE, Iverson SJ, Kessel ST, Kocik JF, Lucas MC, Flemming JM, Nguyen VM, Stokesbury MJW, Vagle S, VanderZwaag DL, Whoriskey FG, Young N (2017) Envisioning the future of aquatic animal tracking: Technology, science, and application. BioScience 67:884-896

Lennox RJ, Paukert CP, Aarestrup K, Auger-Méthé M, Baumgartner L, Birnie-Gauvin K, Bøe K, Brink K, Brownscombe JW, Chen Y, Davidsen JG, Eliason EJ, Filous A, Gillanders BM, Helland IP, Horodysky AZ, Januchowski-Hartley SR, Lowerre-Barbieri SK, Lucas MC, Martins EG, Murchie KJ, Pompeu PS, Power M, Raghavan R, Rahel FJ, Secor D, Thiem JD, Thorstad EB, Ueda H, Whoriskey FG, Cooke SJ (2019) One hundred pressing questions on the future of global fish migration science, conservation, and policy. Frontiers in Ecology and Evolution 7:286

Lewin W-C, Strehlow HV, Ferter K, Hyder K, Niemax J, Herrmann J-P, Weltersbach MS (2018) Estimating post-release mortality of European sea bass based on experimental angling. ICES Journal of Marine Science 75:1483-1495

Lewis R, Marine S, Kenney K (2018) 'I get together with my friends and try to change it'. Young feminist students resist 'laddism', 'rape culture' and 'everyday sexism'. Journal of Gender Studies 27:56-72

Lewison RL, Crowder LB, Read AJ, Freeman SA (2004) Understanding impacts of fisheries bycatch on marine megafauna. Trends in Ecology & Evolution 19:598-604

Li X, Bellerby R, Craft C, Widney SE (2018) Coastal wetland loss, consequences, and challenges for restoration. Anthropocene Coasts 1:1-15

Link J, S. , Garrison LP (2002) Trophic ecology of Atlantic cod *Gadus morhua* on the northeast US continental shelf. Marine Ecology Progress Series 227:109-123

Liu C, Cowles GW, Zemeckis DR, Cadrin SX, Dean MJ (2017) Validation of a hidden Markov model for the geolocation of Atlantic cod. Canadian Journal of Fisheries and Aquatic Sciences 74:1862-1877

Liu C, Cowles GW, Zemeckis DR, Fay G, Le Bris A, Cadrin SX (2019) A hardware-accelerated particle filter for the geolocation of demersal fishes. Fisheries Research 213:160-171

Livingston G, Waring B, Pacheco LF, Buchori D, Jiang Y, Gilbert L, Jha S (2016) Perspectives on the global disparity in ecological science. BioScience 66:147-155

Loewen Walker R (2022) Call it misogyny. Feminist Theory:14647001221119995

Loher T, Webster RA, Carlile D (2017) A test of the detection range of acoustic transmitters and receivers deployed in deep waters of Southeast Alaska, USA. Animal Biotelemetry 5:27

Lohmann KJ, Putman NF, Lohmann CMF (2008) Geomagnetic imprinting: A unifying hypothesis of long-distance natal homing in salmon and sea turtles. Proceedings of the National Academy of Sciences 105:19096-19101

Lonsway KA, Fitzgerald LF (1994) Rape myths: In review. Psychology of Women Quarterly 18:133-164

López R, de Pontual H, Bertignac M, Mahévas S (2015) What can exploratory modelling tell us about the ecobiology of European sea bass (*Dicentrarchus labrax*): a comprehensive overview. Aquatic Living Resources 28:61-79

Lowerre-Barbieri SK, Catalán IA, Frugård Opdal A, Jørgensen C (2019a) Preparing for the future: integrating spatial ecology into ecosystem-based management. ICES Journal of Marine Science 76:467-476

Lowerre-Barbieri SK, Kays R, Thorson JT, Wikelski M (2019b) The ocean's movescape: fisheries management in the bio-logging decade (2018–2028). ICES Journal of Marine Science 76:477-488

MacGregor HEA, Ioannou CC (2021) Collective motion diminishes, but variation between groups emerges, through time in fish shoals. Royal Society Open Science 8:210655

Mackay M, Yamazaki S, Jennings S, Sibly H, van Putten IE, Emery TJ (2020) The influence of nudges on compliance behaviour in recreational fisheries: a laboratory experiment. ICES Journal of Marine Science 77:2319-2332

MacKenzie DI, Bailey LL, Nichols JD (2004) Investigating species co-occurrence patterns when species are detected imperfectly. Journal of Animal Ecology 73:546-555

Maenhout K, Debeuckelaere H (2022) De onwankelbare prof en de kwetsbare doctorandus. De Standaard, 29/10/2022

Maenhout K, Mayda K (2022) Na de melding volgt al te vaak de stilte. De Standaard, 04/02/2022

Malone MA, Polivka CM (2022) The behavioural ecology toolkit for fish management and conservation. Fish and Fisheries 23:1485-1506

Marandel F, Lorance P, Andrello M, Charrier G, Le Cam S, Lehuta S, Trenkel VM (2017) Insights from genetic and demographic connectivity for the management of rays and skates. Canadian Journal of Fisheries and Aquatic Sciences 75:1291-1302

Marshall RC, Fisher JAD, Gatti P, Carruthers EH, Robert D, Le Bris A (2023) Combining electronic tag data and fish harvesters' knowledge to identify ocean management concerns. Marine Policy 147:105393

Martino S, Riebler A (2019) Integrated Nested Laplace Approximations (INLA). arXiv 1907.01248

Mathies NH, Ogburn MB, McFall G, Fangman S (2014) Environmental interference factors affecting detection range in acoustic telemetry studies using fixed receiver arrays. Marine Ecology Progress Series 495:27-38

Matley JK, Klinard NV, Barbosa Martins AP, Aarestrup K, Aspillaga E, Cooke SJ, Cowley PD, Heupel MR, Lowe CG, Lowerre-Barbieri SK, Mitamura H, Moore J-S, Simpfendorfer CA, Stokesbury MJW, Taylor MD, Thorstad EB, Vandergoot CS, Fisk AT (2022a) Global trends in aquatic animal tracking with acoustic telemetry. Trends in Ecology & Evolution 37:79-94

Matley JK, Klinard NV, Larocque SM, McLean MF, Brownscombe JW, Raby GD, Nguyen VM, Barbosa Martins AP (2022b) Making the most of aquatic animal tracking: a review of complementary methods to bolster acoustic telemetry. Reviews in Fish Biology and Fisheries 33:35-54

Matuschek H, Kliegl R, Vasishth S, Baayen H, Bates D (2017) Balancing Type I error and power in linear mixed models. Journal of Memory and Language 94:305-315

Maxwell SM, Hazen EL, Bograd SJ, Halpern BS, Breed GA, Nickel B, Teutschel NM, Crowder LB, Benson S, Dutton PH, Bailey H, Kappes MA, Kuhn CE, Weise MJ, Mate B, Shaffer SA, Hassrick JL, Henry RW, Irvine L, McDonald BI, Robinson PW, Block BA, Costa DP (2013) Cumulative human impacts on marine predators. Nature Communications 4:2688

Mayda K (2022) 'Ik werd niet geholpen door de UGent zoals het moest'. De Standaard, 11/02/2022

Mayda K (2023) 'UGent geeft signaal dat aanranding getolereerd wordt'. De Standaard, 20/01/2023

Mayda K, Maenhout K (2022) UGent begint tuchtprocedure tegen hoogleraar. De Standaard, 22/02/2022

McCormick H, Salguero-Gómez R, Mills M, Davis K (2021) Using a residency index to estimate the economic value of coastal habitat provisioning services for commercially important fish species. Conservation Science and Practice 3:e363

McInturf AG, Pollack L, Yang LH, Spiegel O (2019) Vectors with autonomy: what distinguishes animal-mediated nutrient transport from abiotic vectors? Biological Reviews 94:1761-1773

Mellinger DK, Stafford KM, Moore SE, Dziak RP, Matsumoto H (2007) An overview of fixed passive acoustic observation methods for cetaceans. Oceanography 20:36-45

Melnychuk M (2012) Detection efficiency in telemetry studies: Definitions and evaluation methods. In: Adams N, Beeman J, Eiler J (eds) Telemetry techniques: a user guide for fisheries research. American Fisheries Society Books, Bethesda, Maryland

Melnychuk M, Walters C (2010) Estimating detection probabilities of tagged fish migrating past fixed receiver stations using only local information. Canadian Journal of Fisheries and Aquatic Sciences 67:641-658

Meredith M, Ridout M (2021) overlap: Estimates of coefficient of overlapping for animal activity patterns https://cran.r-project.org/web/packages/overlap/overlap.pdf

Metcalfe JD, Arnold GP (1997) Tracking fish with electronic tags. Nature 387:665-666

Methot RD, Wetzel CR (2013) Stock synthesis: A biological and statistical framework for fish stock assessment and fishery management. Fisheries Research 142:86-99

Meyer CG (2017) Electronic tags reveal the hidden lives of fishes. Bulletin of Marine Science 93:301-318

Michener WK, Jones MB (2012) Ecoinformatics: supporting ecology as a data-intensive science. Trends in Ecology & Evolution 27:85-93

Millar C, Large S, Magnusson A, Pinto C (2022) icesSAG: Stock Assessment Graphs Database Web Services.

Minister for the Marine (1990) Bass (Conservation of Stocks) Order (SI 128/1990). https://www.irishstatutebook.ie/eli/1990/si/128/made/en/print#

Ministry of Agriculture Fisheries and Food, Welsh Office Agriculture Department (1990) Nursery areas and other conservation measures.

Miriti MN (2020) The elephant in the room: race and STEM diversity. BioScience 70:237-242

Mourier J, Bass NC, Guttridge TL, Day J, Brown C (2017) Does detection range matter for inferring social networks in a benthic shark using acoustic telemetry? Royal Society Open Science 4:170485

Myers RA, Worm B (2003) Rapid worldwide depletion of predatory fish communities. Nature 423:280-283

Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE (2008) A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences 105:19052-19059

Nguyen VM, Brooks JL, Young N, Lennox RJ, Haddaway N, Whoriskey FG, Harcourt R, Cooke SJ (2017) To share or not to share in the emerging era of big data: perspectives from fish telemetry researchers on data sharing. Canadian Journal of Fisheries and Aquatic Sciences 74:1260-1274

Nieuwsblad (2021) Schoonmaakpersoneel UGent krijgt opslag, maar blijft in dienst van ISS. Nieuwsblad, 21/02/2021

NNWAC, NSAC (2018) Management measures for sea bass for 2019. Accessed 5 January. https://www.nwwac.org/_fileupload/Opinions%20and%20Advice/Year%2013/FINAL_NWWAC-NSAC_Advice_Seabass_EN.pdf

Noor A, Mir ZR, Govindan GV, Habib B (2017) Activity patterns and spatial co-occurrence of sympatric mammals in the moist temperate forest of the Kashmir Himalaya, India. Folia Zoologica 66:231-241

Novak AJ, Becker SL, Finn JT, Danylchuk AJ, Pollock CG, Hillis-Starr Z, Jordaan A (2020) Inferring residency and movement patterns of horse-eye jack *Caranx latus* in relation to a Caribbean marine protected area acoustic telemetry array. Animal Biotelemetry 8:12

Nuuttila HK, Courtene-Jones W, Baulch S, Simon M, Evans PGH (2017) Don't forget the porpoise: acoustic monitoring reveals fine scale temporal variation between bottlenose dolphin and harbour porpoise in Cardigan Bay SAC. Mar Biol 164:50

Nuuttila HK, Meier R, Evans PGH, Turner JR, Bennell JD, Hiddink JG (2013) Identifying foraging behaviour of wild bottlenose dolphins (*Tursiops truncatus*) and harbour porpoises (*Phocoena phocoena*) with static acoustic dataloggers. Aquatic Mammals 39:147-161

O'Donnell MS, Edmunds DR, Aldridge CL, Heinrichs JA, Monroe AP, Coates PS, Prochazka BG, Hanser SE, Wiechman LA (2022) Defining fine-scaled population structure among continuously distributed populations. Methods in Ecology and Evolution 13:2222-2235

O'Neill R, Ó Maoiléidigh N, McGinnity P, Bond N, Culloty S (2018) The novel use of pop-off satellite tags (PSATs) to investigate the migratory behaviour of European sea bass *Dicentrarchus labrax*. Journal of Fish Biology 92:1404-1421

O'Brien MHP, Secor DH (2021) Influence of thermal stratification and storms on acoustic telemetry detection efficiency: a year-long test in the US Southern Mid-Atlantic Bight. Animal Biotelemetry 9:8

Obaidullah F (2023) The Ocean and Us. Springer International Publishing, Cham

OCEAN2012 (2012) MSY - Maximum Sustainable Yield. https://www.pewtrusts.org/-/media/assets/2015/03/turning_the_tide_msy_explained.pdf

Okafor-Yarwood I, Belhabib D (2020) The duplicity of the European Union Common Fisheries Policy in third countries: Evidence from the Gulf of Guinea. Ocean & Coastal Management 184:104953

Ostrom E (2000) Reformulating the Commons. Swiss Political Science Review 6:29-52

Oyanedel R, Gelcich S, Milner-Gulland EJ (2020) A synthesis of (non-)compliance theories with applications to small-scale fisheries research and practice. Fish and Fisheries 21:1120-1134

Pauly D (1995) Anecdotes and the shifting baseline syndrome of fisheries. Trends in Ecology & Evolution 10:430

Pauly D (2018) Vanishing fish: Shifting baselines and the future of global fisheries, Vol ISBN: 978-1-77164-398-6. Greystone Books, Vancouver, BC

Pauly D, Froese R (2021) MSY needs no epitaph—but it was abused. ICES Journal of Marine Science 78:2204-2210

Pawson M (2008) The contribution of science to management of the North Sea cod (*Gadus morhua*) and UK sea bass (*Dicentrarchus labrax*) fisheries: Can we do better? Advances in Fisheries Science

Pawson MG, Brown M, Leballeur J, Pickett GD (2008) Will philopatry in sea bass, *Dicentrarchus labrax*, facilitate the use of catch-restricted areas for management of recreational fisheries? Fisheries Research 93:240-243

Pawson MG, Pickett GD (1996) The annual pattern of condition and maturity in bass, *Dicentrarchus Labrax*, in waters around England and Wales. Journal of the Marine Biological Association of the United Kingdom 76:107-125

Pawson MG, Pickett GD, Kelley DF (1987) The distribution and migrations of bass, *Dicentrarchus labrax* L., in waters around England and Wales as shown by tagging. Journal of the Marine Biological Association of the United Kingdom 67:183-217

Pawson MG, Pickett GD, Leballeur J, Brown M, Fritsch M (2007) Migrations, fishery interactions, and management units of sea bass (*Dicentrarchus labrax*) in Northwest Europe. ICES Journal of Marine Science 64:332-345

Payne NL, Gillanders BM, Webber DM, Semmens JM (2010) Interpreting diel activity patterns from acoustic telemetry: the need for controls. Marine Ecology Progress Series 419:295-301

Pearce R, Erikainen S, Vincent B (2020) TERF wars: An introduction. The Sociological Review 68:677-698

Pecceu E, Hostens K, Maes F (2016) Governance analysis of MPAs in the Belgian part of the North Sea. Marine Policy 71:265-274

Pedersen MW, Burgess G, Weng KC (2014) A quantitative approach to static sensor network design. Methods in Ecology and Evolution 5:1043-1051

Pedersen MW, Weng KC (2013) Estimating individual animal movement from observation networks. Methods in Ecology and Evolution 4:920-929

Pedersen MWPW, Righton DR, Thygesen UHTH, Andersen KHAH, Madsen HM (2008) Geolocation of North Sea cod (*Gadus morhua*) using hidden Markov models and behavioural switching. Canadian Journal of Fisheries and Aquatic Sciences 65:2367-2377

Peltier H, Authier M, Caurant F, Dabin W, Daniel P, Dars C, Demaret F, Meheust E, Van Canneyt O, Spitz J, Ridoux V (2021) In the wrong place at the wrong time: Identifying spatiotemporal co-occurrence of bycaught common dolphins and fisheries in the Bay of Biscay (NE Atlantic) From 2010 to 2019. Frontiers in Marine Science 8:617342

Peng C-YJ, Lee KL, Ingersoll GM (2002) An introduction to logistic regression analysis and reporting. The Journal of Educational Research 96:3-14

Petersson MT (2022) Transparency in global fisheries governance: The role of non-governmental organizations. Marine Policy 136:104128

Petitgas P, Reid D, Planque B, Nogueira E, O'Hea B, Cotano U (2006) The entrainment hypothesis: an explanation for the persistence and innovation in spawning migrations and life cycle spatial patterns. In: ICES (ed), Book ICES CM2006/B:07

Petitgas P, Rijnsdorp AD, Dickey-Collas M, Engelhard GH, Peck MA, Pinnegar JK, Drinkwater K, Huret M, Nash RDM (2013) Impacts of climate change on the complex life cycles of fish. Fisheries Oceanography 22:121-139

Pickett GD, Pawson MG (1994) Sea bass. Biology, exploitation and conservation. Chapman & Hall, London

Pita P, Artetxe I, Diogo H, Gomes P, Gordoa A, Hyder K, Pereira J, Pita C, Rangel M, Garcia-Rodrigues J, Sagué O, Veiga P, Vingada J, Villasante S (2017) Research and management priorities for Atlantic marine recreational fisheries in Southern Europe. Marine Policy 86:1-8

Pita P, Freire J (2011) Movements of three large coastal predatory fishes in the northeast Atlantic: a preliminary telemetry study. Scientia Marina 75:759-770

Proelss A, Houghton K (2012) The EU Common Fisheries Policy in light of the precautionary principle. Ocean & Coastal Management 70:22-30

Pulver JR, Liu H, Scott-Denton E (2016) Modelling community structure and species co-occurrence using fishery observer data. ICES Journal of Marine Science 73:1750-1763

Quayle VA, Righton D, Hetherington S, Pickett G (2009) Observations of the behaviour of European sea bass (*Dicentrarchus labrax*) in the North Sea. In: Nielsen JL, Arrizabalaga H, Fragoso N, Hobday A, Lutcavage M, Sibert J (eds) Tagging and tracking of marine animals with electronic devices. Springer Netherlands, Dordrecht

R Core Team (2022) R: A language and environment for statistical computing. R Foundation for Statistical Computing

Radford Z, Hyder K, Zarauz L, Mugerza E, Ferter K, Prellezo R, Strehlow HV, Townhill B, Lewin W-C, Weltersbach MS (2018) The impact of marine recreational fishing on key fish stocks in European waters. PLOS ONE 13:e0201666

Ramesh M, Namboothri N (2018) Maximum sustainable yield: A myth and its manifold effects. Economic and Political Weekly 53:58-63

Ramos LF, Solar RRC, Santos HT, Fagundes M (2019) Variation in community structure of gall-inducing insects associated with a tropical plant supports the hypothesis of competition in stressful habitats. Ecol Evol 9:13919-13930

Ramsden S, Cotton C, Curran M (2017) Using acoustic telemetry to assess patterns in the seasonal residency of the Atlantic stingray *Dasyatis sabina*. Environmental Biology of Fishes 100:89–98

Ratcliffe FC, Garcia de Leaniz C, Consuegra S (2022) MHC class I-α population differentiation in a commercial fish, the European sea bass (*Dicentrarchus labrax*). Animal Genetics 53:340-351

Rätz H-J, Casey J, Holmes SJ, Lloret J, Dörner H, Mitrakis N, Charef A (2015) An alternative reference point in the context of ecosystem-based fisheries management: maximum sustainable dead biomass. ICES Journal of Marine Science 72:2257-2268

Reebs SG (2002) Plasticity of diel and circadian activity rhythms in fishes. Reviews in Fish Biology and Fisheries 12:349-371

Reid AJ, Eckert LE, Lane J-F, Young N, Hinch SG, Darimont CT, Cooke SJ, Ban NC, Marshall A (2021) "Two-Eyed Seeing": An Indigenous framework to transform fisheries research and management. Fish and Fisheries 22:243-261

Reubens J, Aarestrup K, Meyer C, Moore A, Okland F, Afonso P (2021) Compatibility in acoustic telemetry. Animal Biotelemetry 9:33

Reubens J, Verhelst P, van der Knaap I, Deneudt K, Moens T, Hernandez F (2019a) Environmental factors influence the detection probability in acoustic telemetry in a marine environment: results from a new setup. Hydrobiologia 845:81-94

Reubens J, Verhelst P, van der Knaap I, Wydooghe B, Milotic T, Deneudt K, Hernandez F, Pauwels I (2019b) The need for aquatic tracking networks: the permanent Belgian acoustic receiver network. Animal Biotelemetry 7

Reubens JT, Braeckman U, Vanaverbeke J, Van Colen C, Degraer S, Vincx M (2013a) Aggregation at windmill artificial reefs: CPUE of Atlantic cod (*Gadus morhua*) and pouting (*Trisopterus luscus*) at different habitats in the Belgian part of the North Sea. Fisheries Research 139:28-34

Reubens JT, De Rijcke M, Degraer S, Vincx M (2014) Diel variation in feeding and movement patterns of juvenile Atlantic cod at offshore wind farms. Journal of Sea Research 85:214-221

Reubens JT, Pasotti F, Degraer S, Vincx M (2013b) Residency, site fidelity and habitat use of Atlantic cod (*Gadus morhua*) at an offshore wind farm using acoustic telemetry. Marine Environmental Research 90:128-135

Righton DA, Andersen KH, Neat F, Thorsteinsson V, Steingrund P, Svedäng H, Michalsen K, Hinrichsen HH, Bendall V, Neuenfeldt S, Wright P, Jonsson P, Huse G, van der Kooij J, Mosegaard H, Hüssy K, Metcalfe J (2010) Thermal niche of Atlantic cod *Gadus morhua*: limits, tolerance and optima. Marine Ecology Progress Series 420:1-13

Risch D, Castellote M, Clark CW, Davis GE, Dugan PJ, Hodge LEW, Kumar A, Lucke K, Mellinger DK, Nieukirk SL, Popescu CM, Ramp C, Read AJ, Rice AN, Silva MA, Siebert U, Stafford KM, Verdaat H, Van Parijs SM (2014) Seasonal migrations of North Atlantic minke whales:

novel insights from large-scale passive acoustic monitoring networks. Movement Ecology 2:24

Roberts BL, Read AJ (2015) Field assessment of C-POD performance in detecting echolocation click trains of bottlenose dolphins (*Tursiops truncatus*). Marine Mammal Science 31:169-190

Robinet T, Roussel V, Cheze K, Gagnaire P-A (2020) Spatial gradients of introgressed ancestry reveal cryptic connectivity patterns in a high gene flow marine fish. Molecular Ecology 29:3857-3871

Rockström J, Steffen W, Noone K, Persson Å, Chapin FS, Lambin EF, Lenton TM, Scheffer M, Folke C, Schellnhuber HJ, Nykvist B, de Wit CA, Hughes T, van der Leeuw S, Rodhe H, Sörlin S, Snyder PK, Costanza R, Svedin U, Falkenmark M, Karlberg L, Corell RW, Fabry VJ, Hansen J, Walker B, Liverman D, Richardson K, Crutzen P, Foley JA (2009) A safe operating space for humanity. Nature 461:472-475

Rogdakis Y, Ramfos A, Koukou K, Dimitriou E, Katselis G (2010) Feeding habits and trophic level of sea bass (*Dicentrarchus labrax*) in the Messolonghi-Etoliko lagoons complex (Western Greece). Journal of Biological Research 13:13-26

Rojano-Doñate L, McDonald BI, Wisniewska DM, Johnson M, Teilmann J, Wahlberg M, Højer-Kristensen J, Madsen PT (2018) High field metabolic rates of wild harbour porpoises. Journal of Experimental Biology 221:jeb185827

Rollero C, Tartaglia S (2019) The effect of sexism and rape myths on victim blame. Sexuality & Culture 23:209-219

Rönkkö M, Aalto E, Tenhunen H, Aguirre-Urreta MI (2021) Eight simple guidelines for improved understanding of transformations and nonlinear effects. Organizational Research Methods 25:48-87

Rosenberg A (2005) Implementing ecosystem-based approaches to management for the conservation of ecosystem services. Marine Ecology Progress Series 300:270-274

Rudolfsen TA, Watkinson DA, Charles C, Kovachik C, Enders EC (2021) Developing habitat associations for fishes in Lake Winnipeg by linking large scale bathymetric and substrate data with fish telemetry detections. Journal of Great Lakes Research 47:635-647

Sáenz-Arroyo A, Roberts CM (2008) Consilience in fisheries science. Fish and Fisheries 9:316-327

Said A, Chuenpagdee R (2019) Aligning the sustainable development goals to the small-scale fisheries guidelines: A case for EU fisheries governance. Marine Policy 107:103599

Said A, Pascual-Fernández J, Amorim VI, Autzen MH, Hegland TJ, Pita C, Ferretti J, Penca J (2020) Small-scale fisheries access to fishing opportunities in the European Union: Is the Common Fisheries Policy the right step to SDG14b? Marine Policy 118:104009

Santos MB, Pierce GJ, Learmonth JA, Reid RJ, Ross HM, Patterson IAP, Reid DG, Beare D (2004) Variability in the diet of harbor porpoises (*Phocoena phocoena*) in Scottish waters 1992–2003. Marine Mammal Science 20:1-27

Schaffeld T, Bräger S, Gallus A, Dähne M, Krügel K, Herrmann A, Jabbusch M, Ruf T, Verfuß UK, Benke H, Koblitz JC (2016) Diel and seasonal patterns in acoustic presence and foraging behaviour of free-ranging harbour porpoises. Marine Ecology Progress Series 547:257-272

Scherrer SR, Rideout BP, Giorli G, Nosal EM, Weng KC (2018) Depth- and range-dependent variation in the performance of aquatic telemetry systems: understanding and predicting the susceptibility of acoustic tag-receiver pairs to close proximity detection interference. PeerJ 6:e4249

Schmitten RA (1999) Essential fish habitat: Opportunities and challenges for the next millennium. American Fisheries Society Symposium 22:3-10

Schnitzler JG, Thomé JP, Lepage M, Das K (2011) Organochlorine pesticides, polychlorinated biphenyls and trace elements in wild European sea bass (*Dicentrarchus labrax*) off European estuaries. Science of the Total Environment 409:3680-3686

Scott J (2018) Legal aspects of the precautionary principle: a British Academy Brexit briefing. In: Academy TB (ed), London

Seal L (2022) Sexual violence. In: Seal L (ed) Gender, crime and justice. Springer International Publishing, Cham

Sebastián-González E, Sánchez-Zapata JA, Botella F, Ovaskainen O (2010) Testing the heterospecific attraction hypothesis with time-series data on species co-occurrence. Proceedings of the Royal Society B: Biological Sciences 277:2983-2990

Secor D (2015) Migration ecology of marine fishes. Johns Hopkins University Press, Baltimore, USA

Selby TH, Hart KM, Fujisaki I, Smith BJ, Pollock CJ, Hillis-Starr Z, Lundgren I, Oli MK (2016) Can you hear me now? Range-testing a submerged passive acoustic receiver array in a Caribbean coral reef habitat. Ecol Evol 6:4823-4835

Sena K (2020) Recognizing Indigenous Peoples' land interests is critical for people and nature. Accessed 16 April 2023. https://www.worldwildlife.org/stories/recognizing-indigenous-peoples-land-interests-is-critical-for-people-and-nature

Seymour N (2017) Transgender environments. Routledge Handbook of Gender and Environment. Routledge

Shaw AK, Levin SA (2011) To breed or not to breed: a model of partial migration. Oikos 120:1871-1879

Silver JJ, Okamoto DK, Armitage D, Alexander SM, Atleo C, Burt JM, Jones R, Lee LC, Muhl E-K, Salomon AK, Stoll JS (2022) Fish, people, and systems of power: Understanding and disrupting feedback between colonialism and fisheries science. The American Naturalist 200:168-180

Simpfendorfer CA, Heupel MR, Collins AB (2008) Variation in the performance of acoustic receivers and its implication for positioning algorithms in a riverine setting. Canadian Journal of Fisheries and Aquatic Sciences 65:482-492

Singleton P, McRae B (2013) Assessing habitat connectivity. In: Craighead LF, Convis CL (eds) Conservation Planning: Shaping the Future. Esri Press

Singmann H, Bolker B, Westfall J, Aust F, Ben-Shachar MS (2022) afex: Analysis of factorial experiments. R package version 11-1

Slabbekoorn H (2019) Population level consequences of seismic surveys on fish: Final Progress Report, Phase II. Joint Industry Programme on E&P Sound and Marine Life.

Smircich MG, Kelly JT (2014) Extending the 2% rule: the effects of heavy internal tags on stress physiology, swimming performance, and growth in brook trout. Animal Biotelemetry 2:16

Smith OM, Davis KL, Pizza RB, Waterman R, Dobson KC, Foster B, Jarvey JC, Jones LN, Leuenberger W, Nourn N, Conway EE, Fiser CM, Hansen ZA, Hristova A, Mack C, Saunders AN, Utley OJ, Young ML, Davis CL (2023) Peer review perpetuates barriers for historically excluded groups. Nature Ecology & Evolution 7:512-523

Snijders T, Bosker R (1999) Multilevel analysis: An introduction to basic and advanced multilevel modeling. In: Publications S (ed)

Soliman A (2014) Duty of stewardship and fisheries governance: a proposed framework. Maritime Studies 13:11

Solorio-Rivera JL, Segura-Correa JC, Sánchez-Gil LG (2007) Seroprevalence of and risk factors for brucellosis of goats in herds of Michoacan, Mexico. Prev Vet Med 82:282-290

Souche EL, Hellemans B, Babbucci M, MacAoidh E, Guinand B, Bargelloni L, Chistiakov DA, Patarnello T, Bonhomme F, Martinsohn JT, Volckaert FAM (2015) Range-wide

population structure of European sea bass *Dicentrarchus labrax*. Biological Journal of the Linnean Society 116:86-105

Spiegel O, Leu ST, Bull CM, Sih A (2017) What's your move? Movement as a link between personality and spatial dynamics in animal populations. Ecology Letters 20:3-18

Spitz J, Chouvelon T, Cardinaud M, Kostecki C, Lorance P (2013) Prey preferences of adult sea bass *Dicentrarchus labrax* in the northeastern Atlantic: implications for bycatch of common dolphin *Delphinus delphis*. ICES Journal of Marine Science 70:452-461

Stamp T, Clarke D, Plenty S, Robbins T, Stewart JE, West E, Sheehan E (2021) Identifying juvenile and sub-adult movements to inform recovery strategies for a high value fishery—European bass (*Dicentrarchus labrax*). ICES Journal of Marine Science 78:3121-3134

Stamp T, West E, Robbins T, Plenty S, Sheehan E (2022) Large-scale historic habitat loss in estuaries and its implications for commercial and recreational fin fisheries. ICES Journal of Marine Science 79:1981-1991

Steadman D, Appleby T, Hawkins JP (2014) Minimising unsustainable yield: Ten failing European fisheries. Marine Policy 48:192-201

STECF (2014) 46th Plenary Meeting Report (PLEN-14-02). In: Union POotE (ed), Luxembourg

STECF (2023) Monitoring of the performance of the Common Fisheries Policy (STECF-adhoc-23-01). In: Union POotE (ed), Luxembourg

Stehfest KM, Patterson TA, Barnett A, Semmens JM (2015) Markov models and network analysis reveal sex-specific differences in the space-use of a coastal apex predator. Oikos 124:307-318

Stone L, Roberts A (1990) The checkerboard score and species distributions. Oecologia 85:74-79

Stott ND, Faust MD, Vandergoot CS, Miner JG (2021) Acoustic telemetry detection probability and location accuracy in a freshwater wetland embayment. Animal Biotelemetry 9:19

Strøm JF, Thorstad EB, Chafe G, Sørbye SH, Righton D, Rikardsen AH, Carr J (2017) Ocean migration of pop-up satellite archival tagged Atlantic salmon from the Miramichi River in Canada. ICES Journal of Marine Science 74:1356-1370

Sullivan GM, Feinn R (2012) Using effect size—or why the p value is not enough. Journal of Graduate Medical Education 4:279-282

Sumaila UR, Ebrahim N, Schuhbauer A, Skerritt D, Li Y, Kim HS, Mallory TG, Lam VWL, Pauly D (2019) Updated estimates and analysis of global fisheries subsidies. Marine Policy 109:103695

Superio J, Fakriadis I, Tsigenopoulos CS, Lancerotto SA, Rodriguez AV, Vervelakis E, Mylonas CC (2021) Spawning kinetics and parentage contribution of European sea bass (*Dicentrarchus labrax*) broodstocks, and influence of GnRHa-induced spawning. Aquaculture Reports 21:100766

Swadling DS, Knott NA, Rees MJ, Pederson H, Adams KR, Taylor MD, Davis AR (2020) Seagrass canopies and the performance of acoustic telemetry: implications for the interpretation of fish movements. Animal Biotelemetry 8:8

Taylor MD, Babcock RC, Simpfendorfer CA, Crook DA (2017) Where technology meets ecology: acoustic telemetry in contemporary Australian aquatic research and management. Marine and Freshwater Research 68

Telesca JE (2017) Accounting for loss in fish stocks: A word on life as biological asset. Environment and Society 8:144-160

Thieurmel B, Elmarhraoui A (2022) suncalc: Compute sun position, sunlight phases, moon position and lunar phase. R package version 051

Thomas L (2022) The intersectional environmentalist. How to dismantle systems of oppression to protect people + planet Voracious, New York, USA

Thorstad EB, Rikardsen AH, Alp A, Økland F (2013) The use of electronic tags in fish research – An overview of fish telemetry methods. Turkish Journal of Fisheries and Aquatic Sciences 13:881-896

Thygesen U, Pedersen M, Madsen H (2009) Geolocating fish using hidden Markov models and data storage tags. In: Nielsen JL, Arrizabalaga H, Fragoso N, Hobday A, Lutcavage M, Sibert J (eds) Tagging and tracking of marine animals with electronic devices, Book 9

Titzler PS, McMichael GA, Carter JA (2010) Autonomous acoustic receiver deployment and mooring techniques for use in large rivers and estuaries. North American Journal of Fisheries Management 30:853-859

Todd NRE, Jessopp M, Rogan E, Kavanagh AS (2022) Extracting foraging behavior from passive acoustic monitoring data to better understand harbor porpoise (*Phocoena phocoena*) foraging habitat use. Marine Mammal Science 38:1623-1642

Tommelein B, Crevits H (2020) Vraag om uitleg over de evaluatie en de toekomst van het project Vistraject. Verslag vergadering Commissie voor Landbouw, Visserij en Plattelandsbeleid 8 juli 2020

Tulloch AIT, Chadès I, Lindenmayer DB (2018) Species co-occurrence analysis predicts management outcomes for multiple threats. Nature Ecology & Evolution 2:465-474

Tulp I, van Hal R, van Damme CJG, Smith S (2016) Zeebaars paaigebieden en opgroeigebieden in Nederlandse wateren.

Tyler JA, Rose KA (1994) Individual variability and spatial heterogeneity in fish population models. Reviews in Fish Biology and Fisheries 4:91-123

Udyawer V, Dwyer RG, Hoenner X, Babcock RC, Brodie S, Campbell HA, Harcourt RG, Huveneers C, Jaine FRA, Simpfendorfer CA, Taylor MD, Heupel MR (2018) A standardised framework for analysing animal detections from automated tracking arrays. Animal Biotelemetry 6:17

UN Convention for Biological Diversity (2000) From policy to implementation. In: Diversity SotCoB (ed) Decisions from the fifth meeting of the conference of the parties to the convention on biological diversity, Nairobi, Kenya,Montreal, Canada

UN General assembly (1982) United Nations Convention on the Law of the Sea.

UNEP (2011) Taking steps toward marine and coastal ecosystem-based management - an introductory guide. UNEP Regional Seas Reports and Studies, Book 189

United Nations (1995) Agreement for the implementation of the provisions of the United Nations on the Law of the Sea of 10 December 1982 relating to the conservation and management of straddling fish stocks and highly migratory fish stocks. A/CONF.164/37

United Nations (2015) Sustainable Development Goals. https://www.un.org/sustainabledevelopment/oceans/

Ussher JM (2016) Misogyny. The Wiley Blackwell encyclopedia of gender and sexuality studies

Van Bogaert Nm, Lemey L, De Peuter S, Kraan M, Giesbers E, Sanderse J, Steins NA, Ustups D, Pliks's Mr, Hansson M, Valentinsson D, Ringdahl K, Rakowski M, Mytlewski A, Panayotova M, Galatchi M, Tiganov G, Mangi Chai S, Abreu S, Metz Sb, Aranda M, Perales C, Triantaphyllidis G, Strbenac A, Hayes D, Alhaija R, Gugnali A, Mravlje E, Vandamme S, Hintzen N, Wakeford R (2022) CFP regionalisation: final report. Publications Office of the European Union, Luxemburg

van Dam A, Dekker M, Morales-Castilla I, Rodríguez MÁ, Wichmann D, Baudena M (2021) Correspondence analysis, spectral clustering and graph embedding: applications to ecology and economic complexity. Scientific Reports 11:8926

van Damme CJG, Hoek R, Beare D, Bolle LJ, Bakker C, van Barneveld E, Lohman M, Os-Koomen E, Nijssen P, Pennock I, Tribuhl S (2011) Shortlist Master plan Wind Monitoring fish eggs and larvae in the Southern North Sea. Report C098/11.

van der Knaap I, Slabbekoorn H, Winter HV, Moens T, Reubens J (2021) Evaluating receiver contributions to acoustic positional telemetry: a case study on Atlantic cod around wind turbines in the North Sea. Animal Biotelemetry 9:14

Van Rossum G, Drake Jr F (1995) Python reference manual. Centrum voor Wiskunde en Informatica Amsterdam

Van Waeyenberghe S (2022) Opnieuw heibel over mogelijke besparingen bij kinderdagverblijven UGent: "Zwanger worden, dat kost veel". PZC, 21/02/2022

Vandamme P, Hostens K, Ollevier F (1994) Fish species of the Lower Zeeschelde (Belgium) - A comparison with historical checklists. Belgian Journal of Zoology 124:93-103

Vandekerkhove S (2016) Acht verkrachtingen per dag, amper veroordelingen: VN legt België op de rooster. De Morgen, 20/01/2016

Vandeputte M, Gagnaire PA, Allal F (2019) The European sea bass: a key marine fish model in the wild and in aquaculture. Animal Genetics 50:195-206

Vandeputte M, Quillet E, Chatain B (2012) Are sex ratios in wild European sea bass (*Dicentrarchus labrax*) populations biased? Aquat Living Resour 25:77-81

Vaneeckhout J, Crevits H (2023) Vraag om uitleg over de visquota en de duurzaamheid van onze visgronden. Verslag vergadering Commissie voor Landbouw, Visserij en Plattelandsbeleid 29 maart 2023

Vázquez FJS, Muñoz-Cueto JA (2014) Biology of European Sea Bass. CRC Press

Veech JA (2013) A probabilistic model for analysing species co-occurrence. Global Ecology and Biogeography 22:252-260

Vergeynst J, Baktoft H, Mouton A, De Mulder T, Nopens I, Pauwels I (2020a) The influence of system settings on positioning accuracy in acoustic telemetry, using the YAPS algorithm. Animal Biotelemetry 8:25

Vergeynst J, Vanwyck T, Baeyens R, De Mulder T, Nopens I, Mouton A, Pauwels I (2020b) Acoustic positioning in a reflective environment: going beyond point-by-point algorithms. Animal Biotelemetry 8:16

Verhaeghe K (2020) Hengelen om vissenlevens te redden. https://www.eoswetenschap.eu/natuur-milieu/hengelen-om-vissenlevens-te-redden

Verhaeghe K, Seys J (2020) Hoe fit is onze Noordzee? EOS, 09/03/2020

Verhelst P, Aarestrup K, Hellström G, Jepsen N, Koed A, Reubens J, Sjöberg N, Svendsen JC, Kristensen ML (2022) The effect of externally attached archival data loggers on the short-term dispersal behaviour and migration speed of European eel (*Anguilla anguilla* L.). Animal Biotelemetry 10:9

Verhelst P, Bruneel S, Reubens J, Coeck J, Goethals P, Oldoni D, Moens T, Mouton A (2018a) Selective tidal stream transport in silver European eel (*Anguilla anguilla* L.) – Migration behaviour in a dynamic estuary. Estuarine, Coastal and Shelf Science 213:260-268

Verhelst P, Brys R, Cooke SJ, Pauwels I, Rohtla M, Reubens J (2023) Enhancing our understanding of fish movement ecology through interdisciplinary and cross-boundary research. Reviews in Fish Biology and Fisheries 33:111-135

Verhelst P, Buysse D, Reubens J, Pauwels I, Aelterman B, Van Hoey S, Goethals P, Coeck J, Moens T, Mouton A (2018b) Downstream migration of European eel (*Anguilla anguilla* L.) in an anthropogenically regulated freshwater system: Implications for management. Fisheries Research 199:252-262

Verlé K, Sys K, Pecceu E, Verleye T, van Winsen F, Lescrauwaet A-K (2020) The re-emergence of small-scale fisheries in Belgium? – An enquiry. In: Pascual-Fernández JJ, Pita C, Bavinck M (eds) Small-scale fisheries in Europe: Status, resilience and governance. Springer International Publishing, Cham

Verleye TJ, Dauwe S, van Winsen F, Torreele E (2019) Beleidsinformerende Nota: Recreatieve zeevisserij in België anno 2018 - Feiten en cijfers. . In: VLIZ (ed) Beleidsinformerende nota's BIN 2019_002, Oostende

Verleye TJ, Lanssens T, Dauwe S, Torreele E (2022) Beleidsinformerende Nota: Recreatieve zeevisserij in het Belgisch deel van de Noordzee: Een continue meerjaarlijkse datareeks van 2017 tot 2021. . In: VLIZ (ed) Beleidsinformerende nota's BIN 2022_002, Oostende

Vermeulen D (2022) Ex-preses Gentse studentenvereniging schuldig aan verkrachting twee studentes: 'Ik ben gestopt toen ze 'stop' zeiden'. De Standaard, 21/02/2022

Verschaeve I (2022) Zolang universiteiten grensoverschrijdend gedrag niet als een institutioneel probleem beschouwen, blijft echte verandering uit. De Morgen, 04/02/2022

Vigliano Relva J, Jung J (2021) Through the eyes of another: Using a narrative lens to navigate complex social-ecological systems and to embrace multiple ways of knowing. Frontiers in Marine Science 8:678796

Villamizar N, Herlin M, López MD, Sánchez-Vázquez FJ (2012) Daily spawning and locomotor activity rhythms of European sea bass broodstock (*Dicentrarchus labrax*). Aquaculture 354-355:117-120

Villegas-Ríos D, Freitas C, Moland E, Thorbjørnsen SH, Olsen EM (2020) Inferring individual fate from aquatic acoustic telemetry data. Methods in Ecology and Evolution 11:1186-1198

Villegas-Ríos D, Réale D, Freitas C, Moland E, Olsen EM (2018) Personalities influence spatial responses to environmental fluctuations in wild fish. Journal of Animal Ecology 87:1309-1319

Vinagre C, Ferreira T, Matos L, Costa MJ, Cabral HN (2009) Latitudinal gradients in growth and spawning of sea bass, Dicentrarchus labrax, and their relationship with temperature and photoperiod. Estuarine, Coastal and Shelf Science 81:375-380

Volckaert FAM, Hellemans B, Batargias C, Louro B, Massault C, Van Houdt JKJ, Haley C, de Koning D-J, Canario AVM (2012) Heritability of cortisol response to confinement stress in European sea bass *Dicentrarchus labrax*. Genetics Selection Evolution 44:15

VRT NWS (2016) "Deel geen voedsel uit aan illegale vluchtelingen". VRT NWS, 01/02/2016

VRT NWS (2017) Decaluwé: "Al 3.000 illegalen onderschept in West-Vlaanderen". VRT NWS, 02/08/2017

Walker ND, Boyd R, Watson J, Kotz M, Radford Z, Readdy L, Sibly R, Roy S, Hyder K (2020) A spatially explicit individual-based model to support management of commercial and recreational fisheries for European sea bass Dicentrarchus labrax. Ecological Modelling 431:109179

Walker RW, Ashton NK, Brown RS, Liss SA, Colotelo AH, Beirão BV, Townsend RL, Deng ZD, Eppard MB (2016) Effects of a novel acoustic transmitter on swimming performance and predator avoidance of juvenile Chinook Salmon: Determination of a size threshold. Fisheries Research 176:48-54

Ward EJ, Jannot JE, Lee Y-W, Ono K, Shelton AO, Thorson JT (2015) Using spatiotemporal species distribution models to identify temporally evolving hotspots of species co-occurrence. Ecological Applications 25:2198-2209

Weinz AA, Matley JK, Klinard NV, Fisk AT, Colborne SF (2020) Identification of predation events in wild fish using novel acoustic transmitters. Animal Biotelemetry 8:28

Welsh J, Fox R, Webber D, Bellwood D (2012) Performance of remote acoustic receivers within a coral reef habitat: Implications for array design. Coral Reefs 31:693-702

Whoriskey K, Martins EG, Auger-Méthé M, Gutowsky LFG, Lennox RJ, Cooke SJ, Power M, Mills Flemming J (2019) Current and emerging statistical techniques for aquatic telemetry data: A guide to analysing spatially discrete animal detections. Methods in Ecology and Evolution 10:935-948

Wilcoxon F (1945) Individual Comparisons by Ranking Methods. Biometrics Bulletin 1:80-83

Wilkinson MD, Dumontier M, Aalbersberg IJ, Appleton G, Axton M, Baak A, Blomberg N, Boiten J-W, da Silva Santos LB, Bourne PE, Bouwman J, Brookes AJ, Clark T, Crosas M, Dillo I, Dumon O, Edmunds S, Evelo CT, Finkers R, Gonzalez-Beltran A, Gray AJG, Groth P, Goble C, Grethe JS, Heringa J, 't Hoen PAC, Hooft R, Kuhn T, Kok R, Kok J, Lusher SJ, Martone ME, Mons A, Packer AL, Persson B, Rocca-Serra P, Roos M, van Schaik R, Sansone S-A, Schultes E, Sengstag T, Slater T, Strawn G, Swertz MA, Thompson M, van der Lei J, van Mulligen E, Velterop J, Waagmeester A, Wittenburg P, Wolstencroft K, Zhao J, Mons B (2016) The FAIR guiding principles for scientific data management and stewardship. Scientific Data 3:160018

Williams C, Carpenter G (2015) European seabass in the UK: A test case for implementing Article 17 of the reformed CFP. In: Foundation NE (ed)

Williams C, Carpenter G, Clark R, O'Leary BC (2018) Who gets to fish for sea bass? Using social, economic, and environmental criteria to determine access to the English sea bass fishery. Marine Policy 95:199-208

Williamson LD, Scott BE, Laxton MR, Bachl FE, Illian JB, Brookes KL, Thompson PM (2022) Spatiotemporal variation in harbor porpoise distribution and foraging across a landscape of fear. Marine Mammal Science 38:42-57

Winter ER, Hindes AM, Lane S, Britton JR (2020) Predicting the factors influencing the inter- and intraspecific survival rates of riverine fishes implanted with acoustic transmitters. Journal of Fish Biology 97:1209-1219

Winter ER, Hindes AM, Lane S, Britton JR (2021a) Acoustic telemetry reveals strong spatial preferences and mixing during successive spawning periods in a partially migratory common bream population. Aquatic Sciences 83:52

Winter ER, Hindes AM, Lane S, Britton JR (2021b) Detection range and efficiency of acoustic telemetry receivers in a connected wetland system. Hydrobiologia 848:1825-1836

Winton MV, Kneebone J, Zemeckis DR, Fay G (2018) A spatial point process model to estimate individual centres of activity from passive acoustic telemetry data. Methods in Ecology and Evolution 9:2262-2272

Woillez M, Fablet R, Ngo T-T, Lalire M, Lazure P, de Pontual H (2016) A HMM-based model to geolocate pelagic fish from high-resolution individual temperature and depth histories: European sea bass as a case study. Ecological Modelling 321:10-22

Wright SR, Lynam CP, Righton DA, Metcalfe J, Hunter E, Riley A, Garcia L, Posen P, Hyder K (2020) Structure in a sea of sand: fish abundance in relation to man-made structures in the North Sea. ICES Journal of Marine Science 77:1206-1218

Zemenick AT, Turney S, Webster AJ, Jones SC, Weber MG (2022) Six principles for embracing gender and sexual diversity in postsecondary biology classrooms. BioScience 72:481-492

Zijl F, Laan S, Groenenboon J (2021) Development of a 3D model for the NW European Shelf (3D DCSM-FM). Deltares

Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer Science & Business Media

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1:3-14

Zuur AF, Ieno EN, Saveliev AA (2017) Beginner's guide to spatial, temporal, and spatial-temporal ecological data analysis with R-INLA. Volume 1: Using GLM and GLMM, Vol 1. Highland Statistics Ltd., Newburgh, UK