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# A multi-scale tracking approach for conserving large migratory fish in an open coastal environment

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ABSTRACT

Coastal habitats serve essential roles in the life cycles of migratory fishes, impacting both local and regional population stability. Conservation efforts for coastal fish often rely on spatial approaches within designated boundaries to mitigate threats and enhance production. However, in open coastal environments, migratory behaviours can extend beyond these protected areas, exposing individuals to potential threats or population bottlenecks elsewhere in their range. To improve conservation outcomes, a comprehensive understanding of movements across the entire migratory range is essential. Aquatic telemetry is a valuable tool for studying these behaviours, but must be adapted to address questions at multiple spatial and temporal scales. In this study we demonstrate how a combination of telemetry techniques can capture both local and regional fish behaviours. We begin by introducing the implications of migratory behaviours for fish conservation in open coastal environments, using the Wadden Sea as an example where additional research and management are needed to address fish declines. We then present a case study which uses the Dutch Wadden Sea to illustrate how a multi-scale telemetry approach can enhance both fundamental knowledge and conservation strategies for migratory fish. Within this case study, we present the general movement strategies exhibited by coastal migrants, alongside an overview of telemetry techniques applicable for open coastal systems. We then apply a size-based assessment using a reference tag to estimate the suitability of common Wadden Sea species for long-term tracking. Drawing from these results, we select four example species to showcase how species-specific understanding of fish life history and abundance can guide tracking studies, accompanied by illustrative examples using telemetry data. Expanding from this case study, we transition to a broader discussion were we provide overarching perspectives on tracking in open coastal ecosystems and offer recommendations to enhance future tracking studies in the Wadden Sea. The integration of telemetry methodologies aligns research and management with fish movement over multiple scales, improving our understanding of fish behaviors and contributing to more effective conservation strategies.

## 1. Background

### 1.1. Fish conservation in open coastal ecosystems

Positioned at the intersection of inland fresh waters and the pelagic marine realm, coastal habitats form an innate link between distinct aquatic ecosystems and are therefore of interest for studies on connectivity and the role of migration in aquatic animal life histories. Coastal marine habitats and estuaries play essential roles for numerous migratory fish species, which typically have life cycles involving use of spatially-discrete habitats at certain life stages or times of year, punctuated by periods of large-scale movement. For migratory fish, coastal habitats serve as seasonal foraging grounds, spawning areas, and nurseries, or as movement corridors (Elliott et al., 2007; Elliott and Hemingway, 2008; Potter et al., 2015). These often shallow, productive waters also face intense disturbance due to anthropogenic factors and rapid climatic changes, posing risks for coastal residents and migratory species alike (Beck et al., 2001; Brown et al., 2018; Jackson et al., 2001).

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Marine conservation and management tools such as those applied in coastal waters and estuaries often rely on spatial approaches designed to protect critical habitats, provide refuge from human activity, and/or prevent overexploitation within a set of jurisdictional boundaries (Edgar et al., 2014). However, in open coastal ecosystems - characterised by high connectivity with adjacent fresh water, estuarine, or marine habitats - spatially-managed areas typically encompass only a portion of the total area used by migratory fish (Breen et al., 2015; Grüss et al., 2011; Palumbi, 2004). The efficacy of coastal management to protect migratory species is therefore influenced by their spatial and temporal distributions, as guided by individual movement behaviors (Elston et al., 2023; Frisk et al., 2019; Heupel and Simpfendorfer, 2005; Santana--Garcon et al., 2014; Speed et al., 2010).

### 1.2. *Fish declines in the Wadden Sea*

Spanning approximately 500 km of coastline across the Netherlands, Germany, and Denmark, the Wadden Sea is the world's largest remaining coastal wetland habitat is recognized as a UNESCO World Heritage Site for it's "Outstanding Universal Value for present and future generations of all humanity" (Common Wadden Sea Secretariat, 2016; UNESCO, 2023). The region plays a vital role for numerous migratory fishes, including diadromous species, occasional visitors, and seasonal residents, all of which require access to multiple aquatic habitats to complete their life cycles. For these species, the Wadden Sea serves both as a movement corridor, facilitating access to adjacent freshwater or marine habitats (Jager et al., 2009; Tulp et al., 2017), while also supporting essential functions such as feeding, growth, and maturation (Hovenkamp, 1991; Rauck and Zijlstra, 1978; van der Veer et al., 2011, 2015, 2022).

Despite harboring approximately 189 fish species, representing a significant portion of the North Sea fish community, the Wadden Sea has witnessed shifts in community composition and alarming declines in overall fish abundance since the 1980s (Berg et al., 1996; Jager et al., 2009; Tulp et al., 2017; Tulp and Bolle, 2009; van der Veer et al., 2011, 2015) (Fig. 1).

While the exact causes of recent fish declines remain unclear, historical changes in the Wadden Sea fish community have likely stemmed from a multitude of anthropogenic and environmental shifts across the broader North Sea region (Tulp et al., 2008; van der Veer et al., 2015). Rising temperatures, including an increase of 1.5 °C over the last 25 years in the Dutch Wadden Sea (van Aken, 2008), have led to altered fish movement patterns, resulting in northward range shifts in marine fishes and potential delays in fish migration (Perry et al., 2005; van Walraven et al., 2017). Simultaneous threats such as coastal habitat destruction, exploitation, and increased predation have also influenced the Wadden Sea's suitability for fish, contributing to the local extinctions of a number of diadromous species (*e.g., Acipenser sturio*, *Salmo salar*, *Coregonus oxyrhynchus*, and *Salmo trutta*) (Brasseur et al., 2015; Camphuysen, 2004; Lotze, 2005, 2007) and degradation of the nursery function for marine juveniles (van der Veer et al., 2011, 2015). Additionally, for migratory fish, persistent barriers to migration success include the obstruction of freshwater routes to the Wadden Sea and destructive practices such as bottom-trawling and sand nourishment in coastal waters (Leewis et al., 2012; Tulp et al., 2020; van der Veer et al., 2015). These multifaceted impacts underscore the broader scale of factors affecting fish communities beyond the Wadden Sea, emphasizing the necessity for comprehensive conservation efforts across larger ecosystems.

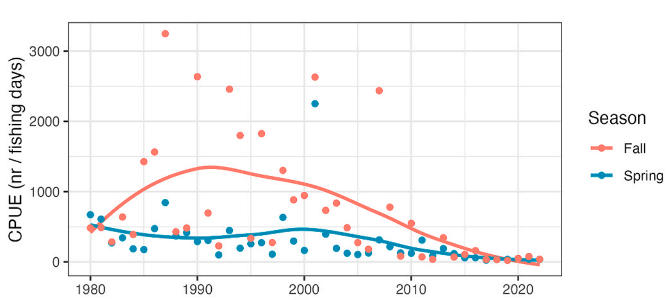


**Fig. 1.** | Historical catch per unit effort (CPUE) for all fish species captured by the NIOZ fyke net survey between the years 1980 and 2021. Line colours are used to distinguish spring and fall catching periods. For a detailed description of methods see: (van der Meer et al., 1995). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

### 1.3. *Conservation needs*

Due to the complex array of factors influencing recent fish declines and the effect of continuously shifting baselines (van der Veer et al., 2015), disentangling the specific causes poses a challenge. This lack of understanding extends to how fish interact with both human activities and the Wadden Sea environment at the individual level, hindering the operationalization of key management and conservation objectives outlined in the 2009 Quality Status Report for the Wadden Sea, known as the five Trilateral Fish Targets (Jager et al., 2009; SWIMWAY, 2019) (Box 1). While local management actions are typically confined to the Wadden Sea, it is important to recognize that the mobile fish they aim to protect exhibit much broader migratory behaviours, resulting in interactions with various environmental, anthropogenic, and ecological factors. Effective implementation and evaluation of spatial protection measures, such as those currently in place in the Wadden Sea within the Natura2000 network and UNESCO World Heritage List (Sieben et al., 2013), rely on knowledge of the spatial characteristics of fish movements both within the Wadden Sea and across adjacent habitats. Scientific evidence elucidating the key processes driving population dynamics and the identification of bottlenecks along the *swimways* of Wadden Sea fishes are essential for making the Fish Targets actionable and quantifying the success of proposed conservation measures.

### 1.4. *A movement ecology approach*

Aquatic telemetry is a field in which electronic tracking devices are affixed, either externally or via internal implantation, to free-ranging organisms to study their *in situ* movements across various spatial and temporal scales (Harcourt et al., 2019; Hussey et al., 2015; Watanabe and Papastamatiou, 2023). These movement data are valuable for understanding the fundamental drivers of fish movement (Elston et al., 2022; Rous et al., 2017; Sims et al., 2006) and have revealed important details of fish home ranges (Pereira et al., 2017), aggregation sites (Daly et al., 2019), and regional connectivity (Corrigan et al., 2018), and illustrated the probability of encountering threats or disturbances (James et al., 2005; Orrell et al., 2023). These insights have proven invaluable for wildlife and fisheries management thus far, guiding approaches for individual species and populations, and informing the delineation of fisheries stocks and protected areas (Brooks et al., 2019; Brownscombe et al., 2022; Crossin et al., 2017; Nathan et al., 2022). As such, telemetry studies are increasingly used to inform adaptive management strategies for fish and fish habitats (Allen and Singh, 2016; Cooke et al., 2016; Crossin et al., 2017; Lennox et al., 2019; Matley et al., 2022a).

### 1.5. *Applying movement ecology for fish conservation in the Dutch Wadden Sea*

To understand the causes and consequences of local behaviors and migration in fish, individual movements must be tracked and characterized over relevant spatial and temporal scales. Specifically, the scales of fish movements, degrees of habitat connectivity, and frequency of

**Box 1**

Five main management and conservation objectives (Trilateral Fish Targets; Jager et al., 2009; as worded by SWIMWAY, 2019):

1. Viable stocks of populations and a natural reproduction of typical Wadden Sea fish species;
2. Occurrence and abundance of fish species according to the natural dynamics in (a)biotic conditions;
3. Favourable living conditions for endangered fish species;
4. Maintenance of the diversity of natural habitats to provide substratum for spawning and nursery functions for juvenile fish;
5. Maintaining and restoring the possibilities for the passage of migrating fish between the Wadden Sea and inland waters.

transboundary movements all influence population success and must be taken into consideration for effective management at local, regional, and oceanic scales (Barkley et al., 2019; Cooke et al., 2023; Gillanders et al., 2003). Using the Dutch Wadden Sea as a case study, we herby explore the implementation of a multi-scale telemetry approach to acquire fundamental knowledge and inform the conservation of migratory fish in open coastal ecosystems. In doing so, we address general knowledge gaps hindering effective migratory fish management by presenting questions related to large-scale movements, temporal aspects, and fine-scale behaviors, addressing them with the primary telemetry technologies available for marine environments (Box 2).

Our approach begins with an overview of the general migratory strategies observed in the Wadden Sea environment (section 2.1) and an introduction to the primary telemetry approaches available for their study (section 2.2). Subsequently, we use a reference transmitter in combination with a size-based approach to assess the potential suitability of all common and fairly common Wadden Sea fish species for long-term tracking (sections 2.3 & 2.4). Drawing from the selected species and available techniques, we then demonstrate the application of a multi-scale telemetry approach using four example species with differing life history traits and migration strategies (section 2.5). Based on these species-specific details, we propose a combination of telemetry approaches, incorporating novel data where available, to address our original research questions. Finally, we conclude with a discussion of our proposed methods, proposing future directions for implementing long-term tracking approaches in the Wadden Sea, and offer perspectives on how these lessons can be applied in other coastal ecosystems.

## 2. Application of a movement ecology approach for the wadden sea

### 2.1. Migration strategies in open coastal ecosystems

In open coastal environments such as the Wadden Sea, the local and broad-scale movements of migratory fish can occur across three distinct aquatic habitats, simplified here as the offshore marine, coastal, and freshwater realms (Fig. 2). For example, coastal migrants can exhibit wide-ranging movements in coastal or estuarine waters (*e.g. Salmo trutta*) (Degerman et al., 2012). Euryhaline species may move back and forth between marine or brackish coastal waters and freshwater habitats (*e.g., Coregonus oxyrinchus*) (Jensen et al., 2018), while marine fishes may move between coastal areas and deeper pelagic zones (*e.g., Raja clavata*) (Hunter et al., 2005; P. Walker et al., 1997). For diadromous species with large-scale migrations, (*e.g., Anguilla anguilla*) (Verhelst et al., 2018) coastal zones like the Wadden Sea are likely used primarily as movement corridors that link spatially discrete spawning grounds and adult foraging habitats. By generalizing the movement patterns of potential study species, we can help to identify specific research questions that can, in turn, be used to inform spatial management approaches (Box 2). However, to address these questions at the relevant spatial and temporal scales, each question requires its own suitable telemetry technique or combination thereof.

### 2.2. Telemetry approaches for fish conservation

Aquatic movement ecology is dominated by three categories of electronic devices: acoustic and satellite transmitters, and archival (data storage) tags (Hazen et al., 2012; Matley et al., 2022). While additional methods such as radio telemetry and passive integrated transponders (PIT) remain common in fresh waters, the proximities required for

**Box 2**

Movement ecology themes and potential research questions:

1. Temporal aspects of movement
   a. What are the potential long-term (seasonal, annual) environmental/ecological drivers of fish presence?
   b. Is the timing of arrival/departure influenced by external cues?
   c. Do individuals exhibit site fidelity to specific regions/locations and, if so, at what temporal scale?
2. Large-scale movements
   a. Do adult fish move cyclically between distinct habitats on a predictable (seasonal, annual, interannual) basis?
   b. Do specific individuals, populations, or species make use of unique migratory pathways?
   c. Do individual fish movements cross jurisdictional boundaries with varying levels of protection?
3. Fine-scale behaviours and habitat use
   a. How do local environmental/ecological conditions influence the fine-scale movements and habitat use of individual fish?
   b. Do individuals show site-specific resident or transient behaviours?
   c. Are fine-scale individual behaviours consistent over different temporal scales?

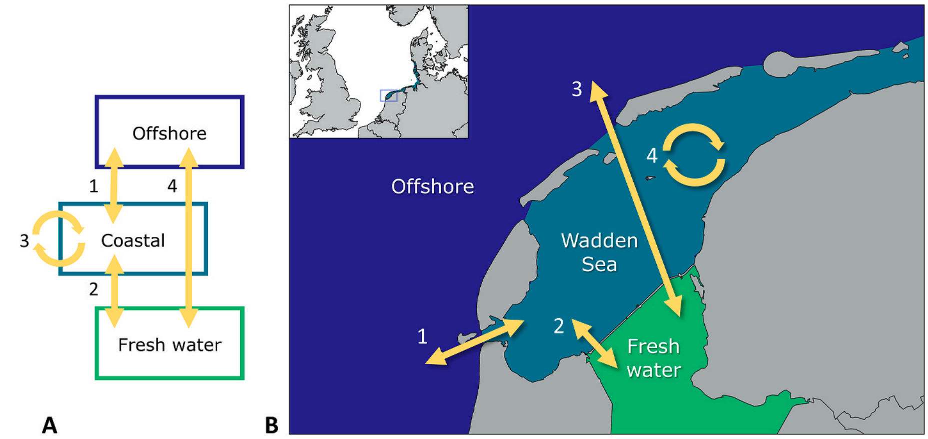


**Fig. 2.** | Generalised movements exhibited by migratory fish species that inhabit (A) coastal waters, and (B) more specifically, in the context of the Dutch Wadden Sea. Arrows depict movement patterns characterised for: 1) coastal/marine migrants, 2) euryhaline species, 3) diadromous species, and 4) coastal/estuarine residents.

detection and ineffectiveness in salt water prohibits their use in coastal environments (Lennox et al., 2017). Despite rapid advancements in this field, technological and logistical constraints continue to affect the spatial and temporal scales addressed by telemetry studies (Harcourt et al., 2019). Tag size, lifespan, and the resolution and recovery of acquired data are all important considerations for selecting appropriate techniques for specific study questions and species. For each of the three dominant tag types (acoustic, satellite, archival), a brief summary of these factors is provided in the following subsections. With these details in mind, we then consider how a combination of these tagging approaches can be used to study the movements of migratory fish both within coastal habitats, and over broader spatial and temporal scales.

### 2.2.1. *Acoustic telemetry*

Acoustic telemetry uses autonomous receivers to detect and decode unique acoustic signals emitted by animal-borne transmitters, enabling tracking of fish movements in both freshwater and marine environments (Donaldson et al., 2014; Heupel and Webber, 2012; Matley et al., 2022b). Acoustic tag lifespans are dictated by transmission settings and battery size, with examples ranging from 100 days for miniature transmitters suitable for juvenile fish (Lingard et al., 2023) and the largest tags lasting for periods of up to 10 years (Edwards et al., 2022a). However, long-term tracking tagged fish requires the maintenance of acoustic receivers over equivalent time periods. Using a network of receivers, known as an acoustic array, researchers can analyse the timing of animal detections to understand fish presence in relation to temporal cues such as diurnal, seasonal, or interannual variations in environmental conditions) (Box 1). Different array configurations can address research questions at various spatial and temporal scales (Heupel et al., 2006). Acoustic positioning methods, employing synchronization tags and positioning models (*e.g.,* using time-difference-of-arrival or time-of-arrival) allow fine-scale positioning in localized areas (Fig. 3d), but require dense arrays of close-proximity receivers and prior knowledge of fine-scale residency by target species (Baktoft et al., 2017; Lennox et al., 2023a; Orrell and Hussey, 2022; van der Knaap et al., 2020). In contrast, courser detection data from receiver gates can indicating fish occurrence, mortality rates, and passage success at key locations along migratory pathways (Fig. 3e) (Chaput et al., 2019; Larocque et al., 2020; Verhelst et al., 2018). Meanwhile other forms of presence-absence arrays (*e.g.,* grids) can effectively illustrate habitat selection, coastal residency, and site fidelity over broader, defined study areas (Fig. 3c) (Able et al., 2014; Novak et al., 2020; Reyier et al., 2023). In each of these approaches, acoustic detections confirm the presence of an individual within the detection range of a receiver, whereas accurate estimates of animal positions remain unknown. Detection ranges are also highly variable over time and space due to the influence of a variety of factors on the transmission and detection of acoustic signals (Kessel et al., 2014). At the largest spatial scales, collaborative telemetry networks, such as the Ocean Tracking Network (OTN) (Iverson et al., 2019), the European Tracking Network (ETN) (Abecasis et al., 2018), the Florida Telemetry network (FACT) (Young et al., 2020), the Integrated Marine Observing System's Animal Tracking Facility in Australia (IMOS ATF) (Hoenner et al., 2018), extend the reach of acoustic studies to regional and international ranges by linking independently managed arrays and facilitating data sharing and collaboration (Fig. 3b) (Abecasis et al., 2018).

### 2.2.2. *Satellite and archival tags*

Satellite transmitters (SAT tags) use platforms such as GPS (Global Positioning System, *e.g.,* GPS and Fasloc GPS tags) and ARGOS (see https://www.argos-system.org/) to remotely transmit stored data and animal positions over vast spatial scales, but are suitable only for animals that spend considerable time at the surface such as marine mammals, sharks, and marine reptiles (Hussey et al., 2015). Tag lifespans are dictated by battery life and attachment success, but are typically programmed for periods of >1 year (Hammerschlag et al., 2011), limiting their application to study migration cycles or repeated movements over longer timespans. By comparison, archival tags – also known as data storage tags or bio-loggers – store information on environmental conditions (*e.g.,* temperature, pressure, light levels) and/or the host's animal's physiological, or biological status (*e.g.,* heart rate, acceleration) to onboard memory, and are ideal for studying smaller, non-surfacing species (Harcourt et al., 2019). Without the energy costs of data transmission, archival tags can be deployed for multi-year periods, but must be physically recovered to access stored data, prompting their preferential use for species with a high likelihood of recapture (*e.g.,* commercially-targeted species or those with predictable distribution patterns) (Watanabe and Papastamatiou, 2023). PSATs (pop-up satellite archival tags) are an exception, wherein summarised or binned subsets of stored data - including depth, temperature, and or light levels - can be transmitted to satellites, along with a GPS position of the tag's location at the surface following pre-programmed release from the host animal (Block et al., 1998; Skomal et al., 2009). Due to difficulties related to tag attachment and premature release from the host animal, PSATs tend to have short deployment periods, typically limited to <1 year (Hammerschlag et al., 2011; Musyl et al., 2011). While lacking continuous positional data, both archival tags and PSATs (if recovered) store high-frequency environmental data useful for revealing individual environmental preferences and retroactively modeling movement trajectories using methods like hidden Markov models (HMMs) (Braun

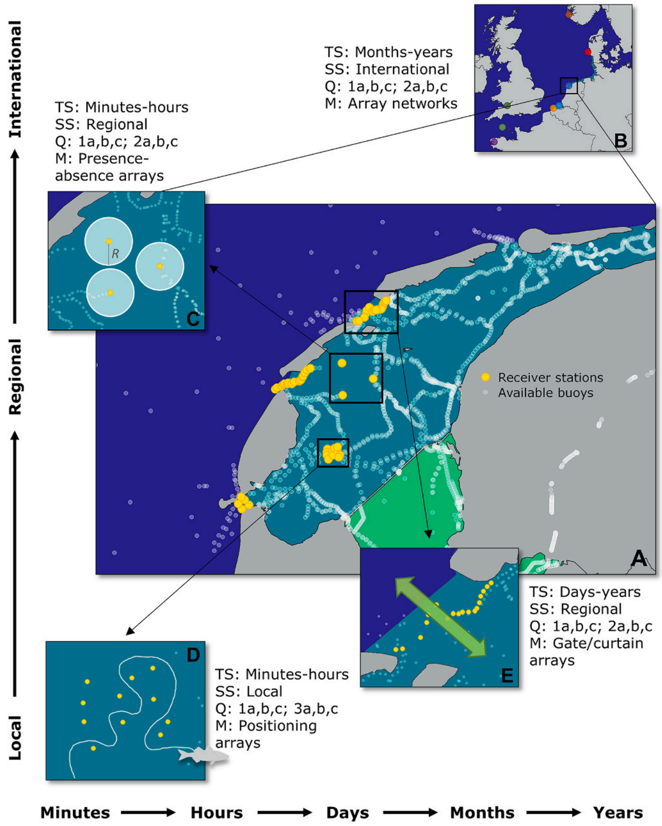


**Fig. 3.** | Spatiotemporal scales and potential applications of acoustic telemetry systems in coastal and offshore marine habitats exemplified for the Dutch Wadden Sea. Panels depict a variety of research techniques available using acoustic telemetry devices, including: A) the selection of receiver attachment locations from available structures (*e.g.,* Rijkswaterstaat navigational buoys – https://www.rijkswaterstaat.nl), B) the incorporation of independently-managed acoustic arrays into an international telemetry network (*e.g.,* the European Tracking Network – https://www.europeantrackingnetwork.org), where coloured circles each represent acoustic arrays comprised of multiple receiver stations, C) a presence-absence array design showing nearby receivers with non-overlapping detection ranges (where *R* indicates detection range), D) a fine-scale acoustic positioning array using receivers in close proximity to track fish trajectories, and E) acoustic receivers in gate/curtain formation. Panel captions describe the temporal scale (TS) and spatial scale (SS) of the illustrated telemetry method (M) and list corresponding research questions (Q) as listed in Box 2.

et al., 2018; Thygesen et al., 2009).

### 2.2.3. Combined approaches for multi-scale tracking

In coastal systems and estuaries, telemetry studies have historically taken place in geographically-constrained locations such as bays, fjords, or lagoons (Grothues, 2009). Access to study animals and receiver deployment sites, alongside a desire to maximize detection or recapture frequencies, have likely contributed to such decisions, but may preclude the consideration of other factors important for migratory fish populations, such as broad-scale connectivity. Conversely, telemetry techniques equipped to study large-scale animal movements may be limited in temporal or spatial resolution, with the use of some tag types further restricted by prohibitive lifespans or sizes. For migratory fish inhabiting open coastal systems, the combination of multiple telemetry approaches will be necessary to capture the complete range of movement behaviours exhibited across various life stages and spatial scales.

Recent advancements in tracking technologies have introduced new capabilities, such as the incorporation of a variety of sensors into acoustic tags to record and, in some cases, transmit information such as animal acceleration, environmental conditions, and predation events (Goossens et al., 2023; Klinard et al., 2019; Lennox et al., 2023b). These innovations are expanding research opportunities to investigate various factors influencing individual fish behavior. Additionally, double-tagging, which involves the attachment of two tags to one individual (*e.g.,* acoustic transmitters and bio-loggers), increases the breadth of data acquired for each tagged animal. While combination tags and double-tagging can increase tag burden and typically require larger individuals, the separate deployment of standard acoustic and archival tags on individuals within a population can also provide valuable insights, particularly for species frequenting both coastal and offshore waters. These complementary approaches are particularly useful in open coastal systems where acoustic receiver coverage is typically distributed close to shore, whereas environmental reference fields and archival tag data can be used to reconstruct movements in more sparsely covered offshore regions.

Modern telemetry techniques can be integrated with conventional methods, such as biological sampling and mark-recapture, to provide a comprehensive understanding of the causes and consequences of fish movement at both individual and population levels. While conventional capture-mark-recapture studies provide insights into movement behaviours at course spatial and temporal scales (Queiroz et al., 2005), the modelling approaches they employ can also be used in combination with electronic tagging to estimate demographic parameters crucial for fisheries management, including survival rates, abundance estimates, and scales of movement (Bacheler et al., 2009; Brooks et al., 2019; Dudgeon et al., 2015; Lees et al., 2021). Furthermore, the integration of telemetry data and non-lethal biological samples collected during tagging (*e.g.,* fin clips, scales, blood) offers additional insights into eco-physiological factors such as ageing, genetics, stable isotopes, microchemistry, and hormone levels (Borcherding et al., 2008; Biton--porsmoguer, 2022; Brownscombe et al., 2022b; Matley et al., 2023). These aggregated datasets contribute to a deeper understanding of fish diets, physiological status, migration histories, and population structure.

### 2.3. Criteria for reference tag selection and species suitability estimates

In the face of multi-species declines, such as those observed in the Wadden Sea, many factors may be used to determine the suitability of a species for tagging. To demonstrate a potential size-based approach, we examined 76 potential study species whose frequency of occurrence in the Wadden Sea was classified as common or fairly common (Jager et al., 2009). To maintain our focus on large-scale connectivity, one strictly freshwater species (*Abramis brama*) was excluded from this list. Scientific names were listed as referred to by (Jager et al., 2009) and common names as they appear in FishBase (Froese and Pauly, 2023).

As a simplified approach, we then used the 2% body weight rule (Jepsen et al., 2005) and the weight of a standard reference tag to estimate the minimum fish body size required for multi-year tracking. Several considerations were used to select a reference tag that would both minimize tag burden on target individuals, while maximizing important factors such as detection range, equipment compatibility, and study duration. Due to the wide-scale adoption of acoustic telemetry, its potential for use across coastal, offshore, and freshwater environments, and the potential to achieve tag lifespans of multiple years, we chose an acoustic transmitter as our reference tag. As a hypothetical approximation of the minimum tag size required to achieve sufficient detection ranges for open coastal areas, equipment compatibility, and study durations of >1 y, we selected a 9 mm 69 kHz acoustic transmitter weighing approximately 3.6 g in air. As many commercially-available DSTs are of comparable size when used without a float, the species suitability estimates listed in Table 1 and Appendix I are deemed applicable to both tag types.

Based on our chosen reference tag, the minimum body weight for fish tagging was 180 g. However, as individual fish weights are often unavailable at capture, we used biological information from FishBase

**Table 1**
Common and fairly common marine Wadden Sea fish species considered to reach suitable (S) or potentially suitable (P) sizes for multi-year tracking with internally implanted acoustic transmitters. Lengths are listed in cm for male/unsexed individuals (M/U) and correspond to total length (TL), standard length (SL), fork length (FL), or disc width (WD). IUCN Red List status includes: Not Evaluated (NE), Data Deficient (DD), Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), and Critically Endangered (CR). For species whose abundance trends for the Dutch Wadden Sea (DWS) have been assessed, recent trends were either stable, decreasing, or uncertain. Wadden Sea guilds are listed as diadromous (D), marine juvenile (MJ), or estuarine resident (ER). Species (potentially) large enough to support tagging with PSATs are denoted by an asterisk.

| Scientific name | English name | Length at maturity (cm) | Max length (M/U) (cm) | Length unit | Max published weight (kg) | Max reported age (y) | IUCN Red List Status | DWS trend (2011–2020) | WS guild | Suitable for telemetry |
|---|---|---|---|---|---|---|---|---|---|---|
| *Alosa alosa* | Allis shad | 47.8 | 69 | TL | 4 | 10 | LC | | | S* |
| *Alosa fallax* | Twaite shad | 32.5 | 60 | TL | 1.5 | 25 | LC | Decreasing | D | S |
| *Anguilla anguilla* | European eel | 55 | 122 | TL | 6.6 | 23 | CR | Uncertain/ Decreasing[a] | D | S* |
| *Belone belone* | Garfish | U | 104 | TL | 1.4 | | LC | | | P |
| *Chelon labrosus* | Thicklip grey mullet | 29.5 | 75 | SL | 4.5 | 25 | LC | | | S |
| *Cyclopterus lumpus* | Lumpsucker | U | 61 | TL | 9.5 | 13 | | | | P |
| *Dasyatis pastinaca* | Common stingray | U | 69.5 | WD | 10.2 | | VU | | | P |
| *Dicentrarchus labrax* | European sea bass | 36.1 | 103 | TL | 12 | 30 | LC | Decreasing | MJ | S |
| *Gadus morhua* | Atlantic cod | 65.4 | 200 | TL | 96 | 25 | VU | Uncertain | MJ | S* |
| *Gaidropsarus vulgaris* | Three-bearded rockling | U | 60 | TL | | | LC | | | P |
| *Galeorhinus galeus* | Tope shark | 144.1 | 193 | TL | 44.7 | 55 | CR | | | S* |
| *Glyptocephalus cynoglossus* | Witch flounder | 30.4 | 60 | TL | 2.5 | 25 | VU | | | S |
| *Hippoglossoides platessoides* | American plaice | 35 | 82.6 | TL | 6.4 | 30 | EN | | | S |
| *Lampetra fluviatilis* | River lamprey | 34.8 | 50 | TL | 0.15 | 10 | LC | Stable | D | S |
| *Merlangius merlangus* | Whiting | 28.2 | 91.5 | TL | 3.1 | 20 | LC | Stable | MJ | S |
| *Merluccius merluccius* | European hake | 42.3 | 140 | TL | 15 | 20 | LC | | | S |
| *Microstomus kitt* | Lemon sole | 29.3 | 65 | TL | 3 | 23 | LC | | | S |
| *Petromyzon marinus* | Sea lamprey | U | 120 | TL | 2.5 | 11 | LC | Decreasing | D | P |
| *Pleuronectes platessa* | European plaice | 32.7 | 100 | SL | 7 | 50 | LC | Stable | MJ | S |
| *Pollachius pollachius* | Pollack | 41 | 130 | TL | 18.1 | 8 | LC | | | S |
| *Pollachius virens* | Saithe | 39.1 | 130 | TL | 32 | 25 | NE | | | S |
| *Psetta maxima* | Turbot | 40.8 | 100 | SL | 25 | 25 | LC | | | S |
| *Salmo salar* | Atlantic salmon | 73.1 | 150 | TL | 46.8 | 13 | NT | | D | S* |
| *Salmo trutta* | Sea trout | 40.9 | 140 | SL | 50 | 38 | LC | Decreasing | D | S |
| *Scomber scombrus* | Atlantic mackerel | 28.7 | 60 | FL | 3.4 | 17 | LC | | | S |
| *Scophthalmus rhombus* | Brill | 37 | 75 | TL | 8 | 6 | LC | | | S |
| *Solea solea* | Common sole | 30.3 | 70 | SL | 3 | 26 | DD | Stable | MJ | S |
| *Stizostedion lucioperca* | Pike-perch | 37.2 | 100 | SL | 20 | 17 | LC | | | S |

[a] Decreasing trend for juveniles.

(Froese and Pauly, 2023) to convert from a weight-based to a size-based evaluation. Using the length-weight relationship of European sea bass as an example (Froese and Pauly, 2023), we set our length criteria for tagging suitability to a minimum total length of 27 cm. To maintain consistency across species, we then used length at maturity ($L_m$) as a reference for this assessment. Length data for each fish species was obtained from FishBase (Froese and Pauly, 2023) and are listed in Appendix I. For those species where $L_m$ was not available, maximum length was used as the reference value with the minimum criteria being 60 cm (based on the maximum lengths of all other species determined to be suitable). However, due to the level of uncertainty surrounding these length data, species for which the maximum length was used were deemed 'potentially suitable' for tracking. To aid in assessing the priority of potential Wadden Sea species for study, population trends for the Dutch Wadden Sea over the period of 2011–2020 are included in the table, as well as the guild assigned to each species (Tulp et al., 2021).

To determine which species have the potential for study with larger PSAT tags, a minimum length at maturity of ≥47 cm was selected (Table 1). This value was chosen as a cautious estimate as per the results of (Lynch et al., 2017) which found no effect of PSAT tagging on the metabolic rates and swimming kinematics of juvenile sandbar sharks within this size range. It should be noted that a variety of factors may influence the effect of tag burden on short-term swimming performance and long-distance migration (*e.g.,* tag shape and buoyancy as well as the swimming kinematics of the tagged individual) and are, for many species, not well understood (Lynch et al., 2017; Svendsen et al., 2021). For a thorough understanding of species-specific tag effects, similar results must be obtained via additional targeted studies.

### 2.4. Potential target species for long-term tracking

Using our size-based assessment, 28 (fairly) common Wadden Sea fish species were deemed suitable (23 species) or potentially suitable (5 species) for multi-year telemetry studies (Table 1). Only 5 species were of sufficient size (or had sufficient size information available) to be deemed suitable for tagging with PSATs. This included 3 species for which dedicated assessments of the effects of satellite tagging on migratory behaviours and swimming performance have previously been conducted (Atlantic salmon, European eel, and Atlantic cod) (Hedger et al., 2017; Methling et al., 2011; Nielsen et al., 2023; Økland et al., 2013). The majority of species included were classified by the IUCN as being of Least Concern (18 species), while 6 species are classified as Vulnerable (common stingray, Atlantic cod, witch flounder), Endangered (American plaice), or Critically Endangered (tope shark and European eel). Despite their common occurrence in the Dutch Wadden Sea, information on local population status was available for only 10 species in total, of which less than half were classified as stable. Maximum reported ages of these fish also indicated long life spans often exceeding 20 years (14 species) and even reaching 50 years for the tope shark and European plaice.

While this size-based assessment was used to narrow down the list of potential candidate species, additional factors like catchability, vulnerability to capture-induced stress, and protective measures for threatened species are also vital considerations for fish tracking studies. Additionally, local and broadscale population trends, threats, and life history traits affecting population resilience (*e.g.,* long lifespans, low fecundity) are all useful for determining the necessity of tracking studies. Given the potential for long-lived species to exhibit migration cycles extending over multiple years, animal longevity should also be considered in terms of tag selection and programming to prevent mismatches in temporal scale between tracking studies and target behaviours (Edwards et al., 2022b). Furthermore, additional information on species-specific size distributions and capacity for tagging could result in additions to this list. Reductions in tag size and advances in tagging methodologies will also continue to improve survival rates and reduce tag burden in the future, with benefits for animal welfare and data collection (Lennox et al., 2017).

### 2.5. Applying the approach to four example species

Knowledge of a species' life cycle can guide research in movement ecology, particularly for migratory fish that move between various habitats at different life stages. To illustrate the application of a life cycle approach for movement ecology, we selected four fish species from Table 1 that differ in their population trends (Fig. 4) and migration strategies (Fig. 5), as well as in our level of knowledge of each. These example species are: thicklip (or thick-lipped) grey mullet (*Chelon labrosus*), European sea bass (*Dicentrarchus labrax*), sea trout (*Salmo trutta*), and tope shark (*Galeorhinus galeus*). For each of these four species, sufficient knowledge is available to make generalised predictions of where individuals are likely to occur (*i.e.,* in the Wadden Sea or in adjacent freshwater or marine habitats) on a seasonal basis (Fig. 5, Table 2). Furthermore, movement data from the Wadden Sea or adjacent waters are available for each of these four species, highlighting the various telemetry approaches described in this study. Rather than acting as representatives of broader ecological groups, these species were selected as examples with which to demonstrate how species-specific knowledge of fish life histories can be used to inform research questions and telemetry approaches. It should be noted that the multi-year periodicity of migratory behaviours of these species within the described habitats is still poorly understood. Whether migrations between these regions occur annually or interannually, and whether these temporal aspects differ among individuals, are questions that can still be addressed using the telemetry techniques discussed in the following sections. To

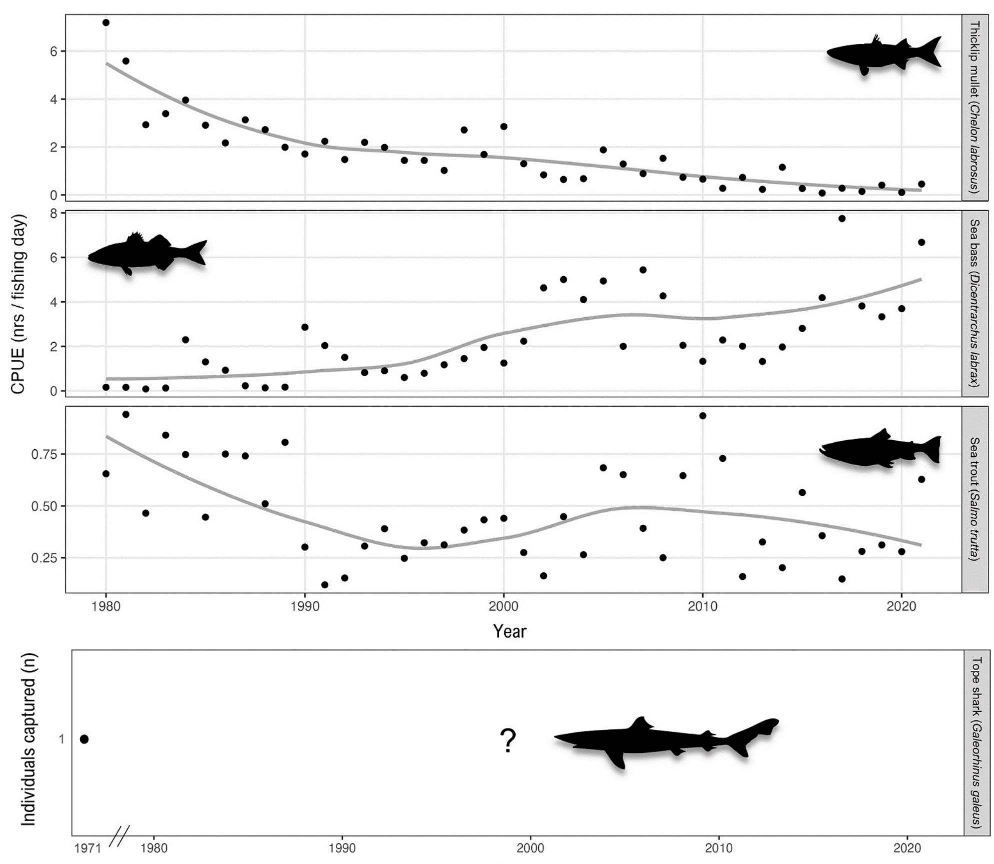


**Fig. 4.** | Historical catch per unit effort (CPUE) and total catches (n) of four large fish species from the NIOZ fyke net survey, which are used in the examples: A) thicklip grey mullet, B) European sea bass, C) sea trout, and D) tope shark. For a detailed description of fishing methodology see: (van der Meer et al., 1995).

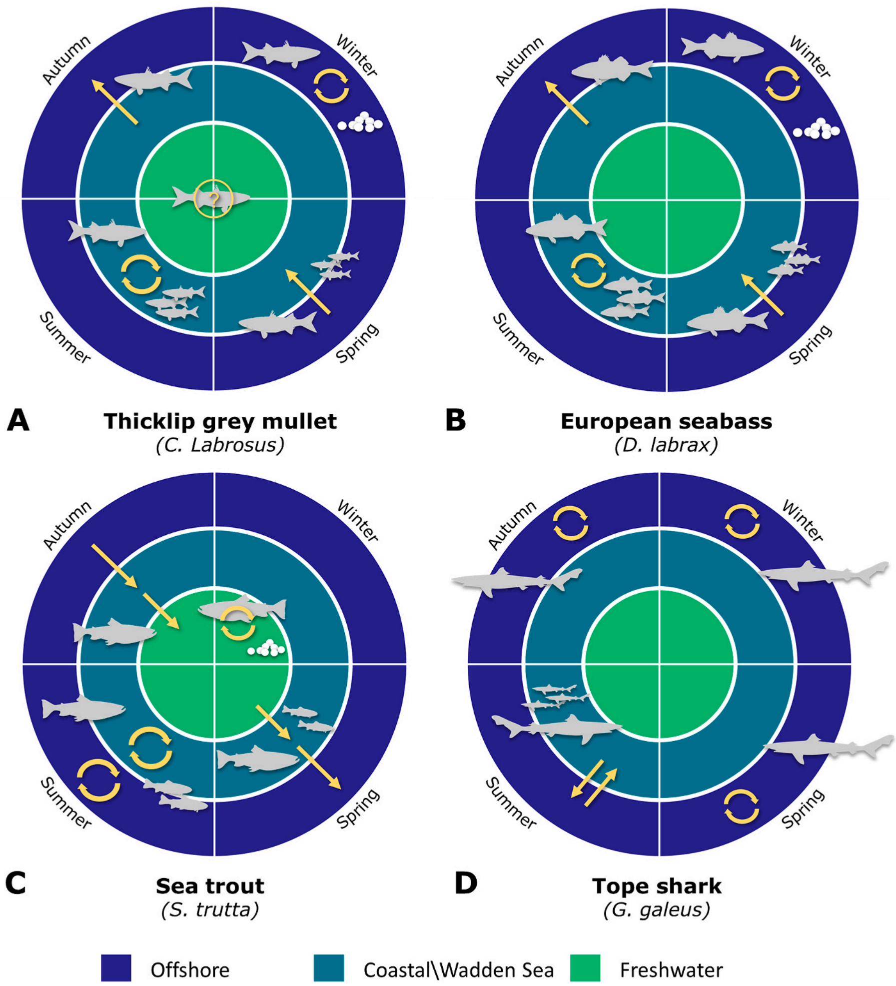


**Fig. 5.** | Generalised movements/migration strategies exhibited by four migratory fish species within and between offshore marine, coastal (*e.g.,* the Wadden Sea), and freshwater habitats. A) thicklip grey mullet, B) European sea bass, C) sea trout, and D) tope shark. The size of the fish indicates the life stage and eggs are shown as white circles.

**Table 2**
| Current knowledge of broad-scale movement behaviours seasonal distributions of adult individuals from four migratory fish species that use the Wadden Sea. Life history information from FishBase (Froese and Pauly, 2023) was used for all species, along with the listed references.

| Species | Winter | Spring | Summer | Autumn | Refs |
|---|---|---|---|---|---|
| *C. labrosus* | Spawning, overwintering | Migrating | Foraging | Migrating | |
| | Offshore; location unknown, timing unknown | Offshore → Wadden Sea | Coastal waters; duration uncertain, spatial scale uncertain | Wadden Sea → Offshore | (Cardona, 2006; Hickling, 1970; Kennedy and Fitzmaurice, 1969, 1972; Walsh et al., 1994) |
| *D. labrax* | Spawning, overwintering | Migrating | Foraging | Migrating | |
| | Offshore; location unknown, timing unknown | Offshore → Wadden Sea | Coastal waters; duration uncertain, spatial scale uncertain | Wadden Sea → Offshore | (de Pontual et al., 2019; Doyle et al., 2017; Holden and Williams, 1974; Kennedy and Fitzmaurice, 1972; Pawson et al., 1987, 2007) |
| *S. trutta* | Spawning, overwintering | Migrating | Foraging | Migrating | |
| | Fresh water | Fresh water → Wadden Sea → Offshore | Coastal waters; duration uncertain, spatial scale uncertain | Offshore → Wadden Sea → Fresh water | (Aldvén et al., 2015; Bendall et al., 2005; Bij De Vaate et al., 2003; Eldøy et al., 2015; Flaten et al., 2016; Jensen et al., 2018; Thorstad et al., 2016) |
| *G. galeus* | Unknown | Unknown | Pupping | Unknown | |
| | Presumed offshore; scale of movements unknown | Presumed offshore; scale of movements unknown | Coastal waters; precise timing and locations unknown | Presumed offshore; scale of movements unknown | (Capapé et al., 2005; Colloca et al., 2019; Fitzmaurice et al., 2003; Holden and Horrod, 1979; Schaber et al., 2022; Stevens, 1990; Thorburn et al., 2019) |

understand the complete life cycles of these and other Wadden Sea fish species, and to unravel the potential causes of local declines in this region, it will be necessary to increase the scope of movement studies to ecologically-relevant scales by combining available telemetry techniques and complementary data sources.

### 2.5.1. Sea bass and thicklip mullet– seasonal residents

*2.5.1.1. Knowledge gaps hindering management.* As adults, both European sea bass and thicklip grey mullet are known as seasonal visitors to the Wadden Sea (Boer, 1971; Cardoso et al., 2015), with juveniles and adults of both species migrating toward coastal waters in spring and adults departing in autumn to spawn and overwinter in offshore waters (Fig. 5a and b) (Hickling, 1970; Pawson et al., 1987). Despite their similar life histories (Fig. 5a and b), historical survey data suggest that sea bass and thicklip mullet populations in the Dutch Wadden Sea have experienced contrasting trends throughout the latter part of the 20th century (Fig. 4a and b). While the cause for this disparity remains unclear, examining differences in the ecological roles of these two seasonal residents may provide insight.

Sea bass and thicklip mullet rely on a distinct set of environmental conditions, including preferred temperatures, substrates, and feeding ecology (Poiesz et al., 2020, 2023). This suggests that local and regional environmental conditions might impact the growth and survival of each species differently, potentially influencing their population trends. However, the precise conditions that individuals encounter and their behavioural responses require further study. For thicklip mullet in particular, whether individuals move between marine and freshwater habitats or represent two distinct populations remains completely unknown (Fig. 5), but could have important implications for population stability. Similarly, anecdotal evidence suggests that a portion of the local sea bass population may remain resident in Dutch coastal waters year-round, however, this has yet to be confirmed by the scientific literature.

For both species, the influence of Wadden Sea conditions (*e.g.,* temperature, substrate type, food availability) and species-specific biology (*e.g.,* thermal and salinity tolerance, diet) on migration timing, residency duration, and home range size are still unknown, but could indicate the suitability of Wadden Sea habitats for fish from distinct ecological guilds, informing local conservation measures. Additionally, little is known about the destinations and migration routes of individuals leaving the Wadden Sea (*e.g.,* spawning or overwintering habitats), obscuring the role of offshore conditions and threats on reproductive success and survival. By addressing these uncertainties, conservation efforts can better target specific threats occurring at both local and regional scales.

*2.5.1.2. Local and large-scale tracking with acoustic and archival telemetry.* Within the boundaries of the Dutch Wadden Sea, acoustic telemetry offers a means to investigate the nature and drivers of local behaviours and migration timing for sea bass and thicklip mullet. As seasonal residents, individuals can be targeted and tagged during the summer feeding period when they are known to be locally present. Presence/absence data from coastal acoustic receivers – such as those in the local Swimway array (https://swimway.nl/hoe-gebruiken-grote-vissen-de-waddenzee/) – can then be used to analyse their space use in relation to potential environmental influences such as depth, temperature, and food availability (Fig. 6). These correlations can provide valuable insights for ecological models that predict how long-term environmental changes might affect the distribution and success of fish populations under future climate and fisheries management scenarios.

Moreover, movement trajectories and departure of tagged fish can be determined by the sequentially arranging individual fish detections within the acoustic network (Fig. 6). These trajectories help define the scales of space use, regional connectivity, and high activity areas at both individual and population levels. Individual movement data can rapidly reveal behavioural responses to changing environmental conditions (Breece et al., 2018; Brownscombe et al., 2022; Lédée et al., 2015), indicating the abilities of sea bass and thicklip mullet to use behavioural flexibility as an adaptive mechanism in the face of climate change.

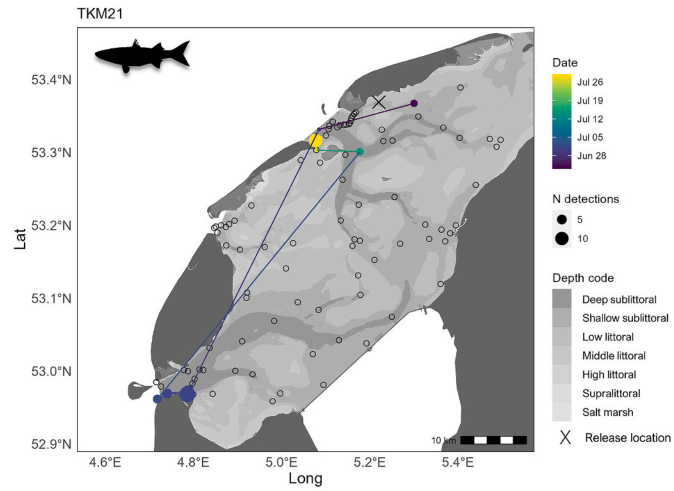


**Fig. 6.** | Local movement trajectory of an individual thicklip grey mullet (animal ID: TKM21) tagged and tracked via acoustic telemetry in the western Dutch Wadden Sea. Hollow circles indicate the locations of all acoustic receiver stations in the Swimway array where the tagged individual was not detected. Filled circles are coloured by date from June 24, 2021 to July 29, 2021 and connected by interpolated shortest-distance paths. Wadden Sea bathymetry data are publicly available via: (Baptist et al., 2019); DOI:10.17632/27-mysx289g.1. Depth codes are classified as follows: deep sublittoral (depth $< -5$ m mean low water spring tide), shallow sublittoral (depth $\geq -5$ m mean low water spring tide, $<4\%$ mean exposure), low littoral ($4\% \leq$ mean exposure $<25\%$), middle littoral ($25\% \leq$ mean exposure $<75\%$), high littoral ($75\% \leq$ mean exposure $<85\%$), supralittoral (mean exposure $\geq 85\%$), salt marsh (vegetated).

Using a combination of acoustic detections from the European Tracking Network and archival data from DSTs, the destinations and migration pathways of sea bass and thicklip mullets can also be addressed. Fish can either be tagged with a single acoustic tag, a single DST or ADST, or - provided that an individual is of adequate size (estimated for sea bass to be $\geq 50$ cm) – internally double-tagged with both an acoustic transmitter and DST. For acoustic-tagged fish that depart the Dutch Wadden Sea (*i.e.,* the Swimway array), data for individuals detected by acoustic arrays in neighbouring regions (*e.g.,* German or Danish Wadden Sea regions to the east, or Belgian waters and the English Channel to the west) can be uploaded to the European Tracking Network by their managing researchers. As a member of the ETN, the tag owner can then access and offload these data to uncover the presence of these tagged fish across a much broader study area (Fig. 7). As knowledge of the distributions of most seasonally migrating Wadden Sea species is limited to only parts of the year when they are locally resident, these data could reveal connectivity between discretely managed stocks as well as highlighting offshore aggregation sites potentially used for spawning, foraging, or overwintering.

### 2.5.2. Sea trout – A diadromous migrant

*2.5.2.1. Knowledge gaps hindering management.* Sea trout are iteroparous, returning to freshwater habitats to spawn multiple times throughout their adult life and exhibiting an array of movement behaviours spanning three habitat types (Fig. 5c). However, reductions in habitat connectivity and the subsequent implications for migrant mortality could jeopardize the stability of local sea trout populations (van Puijenbroek et al., 2019; Wright et al., 2014). Although the Wadden Sea likely acts as a movement corridor or temporary foraging ground for sea trout, the existence and location of common migratory pathways through the system remain unclear. This information is valuable for prioritising or improving fish passages for enhanced migration speed and survival. For instance, in Dutch waters, sea trout catches have

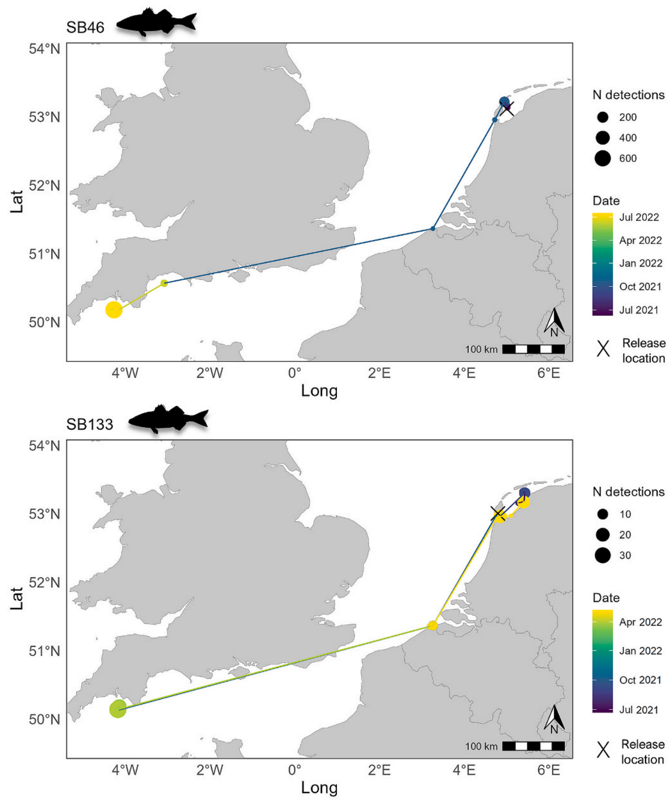


**Fig. 7.** | Large scale movement trajectories outside the Wadden Sea for two adult sea bass (animal IDs: 19840, 19872) tagged with acoustic transmitters in the western Dutch Wadden Sea. Filled circles indicate locations of fish detections and are scaled by the number of detections recorded. Points are connected by interpolated shortest-distance paths which have been curved to prevent overlap. Colours indicate the date of detections ranging from July 9, 2021 to July 17, 2022 (ID: 19840) and July 21, 2021 to May 8, 2022 (ID: 19872), respectively. In the Wadden Sea, detections were recorded by receivers in the SWIMWAY array. Additional data from FISHINTEL (Sheehan et al., 2021) and BPNS (Reubens et al., 2017) receivers were sourced from the European Tracking Network data portal (http://www.lifewatch.be/etn/), developed by the Flanders Marine Institute as part of the Flemish contribution to LifeWatch. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

remained low over the past several decades (Fig. 4), and continued obstruction by the Afsluitdijk dam limits the passage of sea trout entering the Rhine basin from the western Wadden Sea (Bij de Vaate et al., 2003). In contrast, in Danish rivers surrounding the Wadden Sea, measures have been implemented to enhance connectivity for migrating trout, including net fishing restrictions and major river restoration efforts, resulting in positive outcomes such as improved and expanded wild salmonid habitat and increased juvenile production (Tulp et al., 2022).

Despite high mortality rates incurred both at-sea and during migration (Aarestrup et al., 2015), sea trout movements both within and between marine habitats have received limited attention compared to the breadth of fresh water studies (Eldøy et al., 2015; Thorstad et al., 2016). As sea trout are known to use coastal habitats affected by anthropogenic activities, including aquaculture, renewable energy production, and other coastal infrastructure, there is potential for overlap in marine behaviours and a variety of possible threats (Eldøy et al., 2017). The lack of information on sea trout behaviours, survival, and residency in marine habitats are therefore major gaps in our knowledge of when and where population bottlenecks occur, hindering effective conservation and management.

*2.5.2.2. Assessing connectivity and marine movements with acoustic and archival telemetry.* As with the seasonal residents, acoustic telemetry can be used to monitor the movements of diadromous migrants like the sea trout through fresh, transitional, and coastal marine waters (Aldvén et al., 2015; Bendall et al., 2005; Finstad et al., 2005). Strategic placement of single acoustic receivers or receiver gates at marine-freshwater transition points can inform rates of passage on both seaward and return migrations, providing critical insight on migration success and the effectiveness of conservation measures promoting fish passage (Aldvén et al., 2015) (Fig. 2e). In restricted waterways and boundary waters, small acoustic tags with inherently limited transmission ranges can capture the first migrations of the smallest migratory life stages (*e.g.,* post-smolts) (Flaten et al., 2016). In open coastal habitats, receiver gates and grid arrays (Fig. 2c–e) and longer-range transmitters can then be used to identify movement corridors and monitor individual residency to determine the role of coastal regions like the Wadden Sea for growth and survival (Aarestrup et al., 2015; Eldøy et al., 2015). Tags equipped with depth and/or temperature sensors can highlight individual preferences in relation to environmental conditions (Eldøy et al., 2017) or biological factors such as parasite infestation (Gjelland and Hedger, 2017).

For regions with limited coverage by acoustic arrays, including offshore marine habitats, archival data from DSTs can be used alongside hidden Markov models (HMMs) to reconstruct the large-scale movement pathways of adult fish (Braun et al., 2018; Pedersen, 2007; Thygesen et al., 2009). HMMs have already been employed to reconstruct the offshore migrations of two Wadden Sea fish species, the European sea bass and sea trout, which were tagged with data storage tags in coastal European waters (de Pontual et al., 2019; Kristensen et al., 2018, 2019) (Fig. 8). These data highlight the spatial and temporal extent of marine movements, as well as revealing behavioural shifts in response to elevated water temperatures as a means of optimizing growth at sea (Kristensen et al., 2018, 2019). For migrating sea trout in particular, further investigation of the balance between the metabolic costs and benefits of migration could prove useful for understanding the potential consequences of environmental change (Kristensen et al., 2019).

### *2.5.3. Tope shark – an occasional visitor*

*2.5.3.1. Knowledge gaps hindering management.* Tope sharks are capable of conducting extensive migrations across deep pelagic waters in the northeast Atlantic, occasionally moving into the western Mediterranean (Colloca et al., 2019; Fitzmaurice et al., 2003; Holden and Horrod, 1979) or as far west as Iceland (Stevens, 1990; Thorburn et al., 2019). However, whether these broad-scale movements represent repeated migratory behaviours or occasional dispersion is still the subject of speculation (Colloca et al., 2019). Incidental catches of adult females and neonates from within the Wadden Sea and along the northern Dutch coastline suggest that pupping occurs in these areas in mid-summer (Batsleer et al., 2020) (Fig. 5d). However, the use of these coastal waters by gravid females and their potential nursery function for pups have yet to be determined. Due to a lack of directed angling for tope sharks and their absence from standard fish monitoring programs, their presence can easily remain undetected, leaving insufficient data to indicate local abundance (Fig. 4). Importantly, northeast Atlantic tope sharks have been deemed Critically Endangered by the IUCN's Red List (T. I. Walker et al., 2020), but are still vulnerable to capture by French and English fishing fleets in coastal waters of the English Channel (Biton-porsmoguer, 2022). Given the scale of horizontal movements exhibited by this species, tope sharks may act as indicators of regional connectivity at an ocean basin scale. Furthermore, if specific biological needs are met by discrete locations throughout its vast range (*e.g.,* pupping in shallow coastal waters), broad-scale connectivity between juvenile and adult habitats may be critical for their population success.

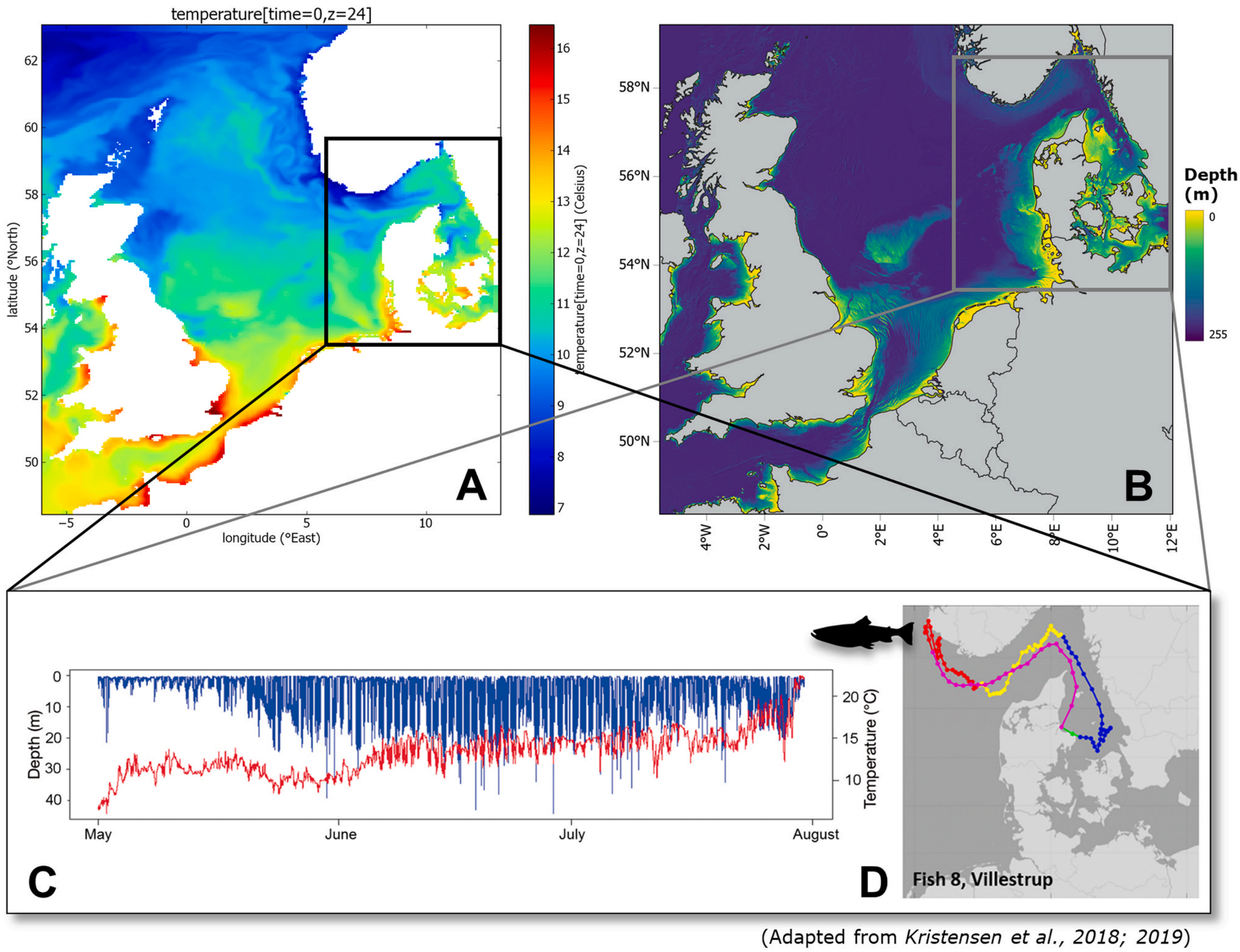


**Fig. 8.** | Data types required for the reconstruction of fish trajectories from archival tags (*i.e.*, data storage tags, bio-loggers): A) Sea surface temperatures representing a single timepoint for the North Sea and Baltic Sea region: data from (Van der Molen et al., 2021), B) bathymetry of the North Sea and Baltic Sea region: data from (Perluka et al., 2006), C) From Kristensen et al. (2018): example of marine behaviour with depth (blue) and temperature (red) time series recorded by a data storage tag (DST) deployed on an adult sea trout, D) From: Kristensen et al. (2019): reconstructed track of the most probable movements of an adult sea trout (Fish 8). Line colour refers to the month of tracking as follows: April (green), May (blue), June (yellow), July (red), August (pink). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

*2.5.3.2. Acoustic telemetry networks and PSATs to capture long-range movements.* Acoustic telemetry can provide insight into the nursery function of coastal and estuarine habitats and indicate the efficacy of spatial protections such as Shark Refuge Areas and fisheries closures (McAllister et al., 2015). In place of catch data, long-term acoustic monitoring can provide estimates of juvenile mortality for improved population modeling as well as demonstrating population recovery (Heupel and Simpfendorfer, 2002; McAllister et al., 2015). Receiver gates positioned across the tidal inlets could also indicate the timing of emigration toward offshore waters for juveniles tagged in the Wadden Sea (Heupel, 2007; Wada et al., 2017). However, as juveniles begin emigrating from nursery areas as early as 1–2 y of age with low rates of return (McAllister et al., 2015), fixed coastal receiver arrays will likely capture only glimpses of adult behaviours. Gravid females have also been shown to demonstrate partial migration, with some individuals using offshore migration routes where they may bypass protected coastal areas and face higher fishing pressures (McMillan et al., 2019). Strategic use of acoustic networks can thereby help elucidate connectivity between protected and unprotected coastal and offshore waters for both juveniles and adults, allowing the evaluation and refinement of spatial management boundaries (Espinoza et al., 2021; McAllister et al., 2015).

Due to their large body size, adult tope sharks can also be equipped with large devices such as PSATs that record high-resolution data for track reconstruction and examination of vertical movement behaviours (Schaber et al., 2022; Thorburn et al., 2019) (Table 1, Fig. 9). Similarly, this species is potentially suitable for double tagging with PSATs and long-lifespan acoustic transmitters, combining the benefits of short-term high-resolution data with the potential for opportunistic detections over longer time spans. Further evidence of large-scale regional connectivity in the north Atlantic could have implications for tope shark population structure and resilience, signifying a need for broad-scale cooperation among European fisheries managers to prevent further declines in this Critically Endangered species.

## 3. Synthesis

### 3.1. Summary of findings

The interconnected nature of open coastal systems means that fish tagged in these regions are not necessarily restricted to a defined study area. The timing and duration of fish presence in coastal waters, as well as the scale of local movements, environmental drivers, and habitat associations, can all influence the effectiveness of local management actions and are relevant for identifying potential causes of fish declines and informing conservation approaches. In this research, we considered

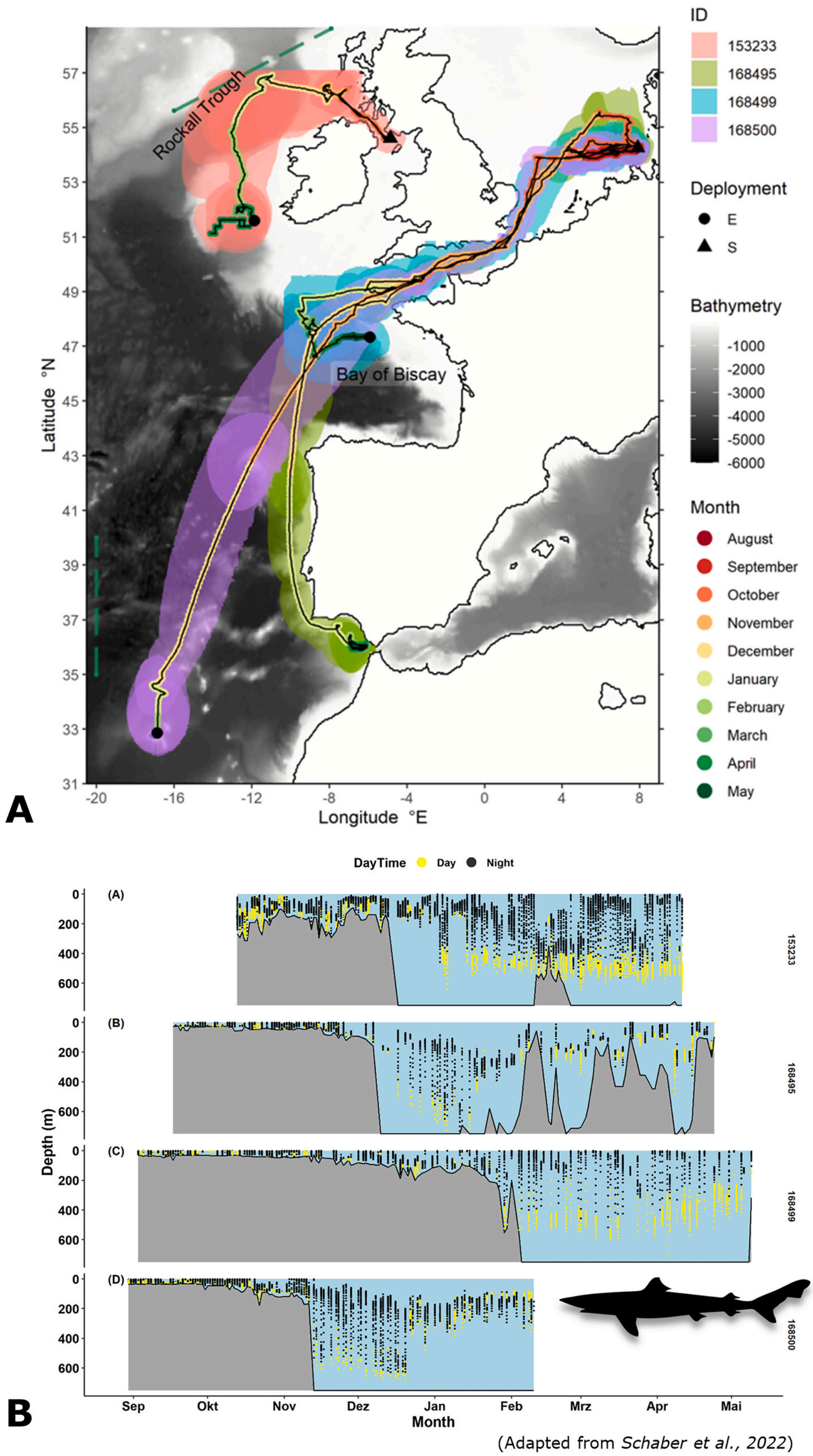


**Fig. 9.** | Data on the large-scale movements of four tope sharks (IDs: 153233, 168495, 168499, 168500) in the North Sea and Northeast Atlantic from (Schaber et al., 2022) (both panels). A) Most likely movement trajectories-geolocation from GPE3 state-space model between deployment start (S) and end (E) locations (black paths). Shaded zones around the most likely tracks indicate the 95% location probabilities and are colour-coded by tag ID/Ptt. B) Time series of tope shark depth measurements from four PSAT deployments with corresponding bathymetry along migration path. For complete details on both figures, please refer to the original manuscript. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

the importance of studying fish behaviours and developing management strategies at ecologically-relevant spatial and temporal scales. Given the variety of movement behaviours exhibited by coastal migrants, and the potential for threats and bottlenecks to be encountered at any point within a species' migratory range, we propose that movement studies will ultimately require a combination of telemetry approaches designed to match these behavioural scales to the data resolution provided by commercially available tags.

Using the Dutch Wadden Sea as an example study environment, we suggested a size-based approach as a first means of evaluating the suitability of fish species for long-term tracking, and illustrated how telemetry approaches can be selected and combined to address questions relating to species-specific knowledge gaps and migratory strategies. Specifically, acoustic telemetry provides options for fish tracking at various spatial and temporal scales (Fig. 2), but is limited by the spatial coverage of receivers in offshore marine waters and cooperation among telemetry researchers. While lacking positional information, sensor data from acoustic and archival tags and PSATs can be used to understand the environmental drivers of movement within and beyond coastal waters, and provide opportunities to model movement trajectories beyond the extent of acoustic arrays (Figs. 8 and 9).

While each of these methods are already available for use, they are not always employed to their full potential. We here discuss some of the limitations that should be considered and addressed for open coastal ecosystems in general and propose future directions for research in the Dutch Wadden Sea.

### 3.2. Perspectives for long-term tracking in open coastal ecosystems

For many migratory species, current knowledge of coastal behaviours may be insufficient to combat locally-observed declines. Despite more holistic efforts to monitor fish behaviours across broader spatial scales, acoustic receiver arrays are typically geographically-limited and rarely extend beyond national borders (Abecasis et al., 2018). Acoustic telemetry networks expand the scope of animal tracking studies to ecologically-relevant scales, but require commitment from independent researchers to ensure equipment compatibility, prompt and regular inputs of data to online databases, and coordinated placement of acoustic arrays (Reubens et al., 2021). At the ETN, these issues are addressed via annual meetings that foster collaborations, promote equipment and data compatibility, such as via the introduction of Open Protocols (Reubens et al., 2021) (https://www.europeantrackingnetwork.org/en/open-protocol), and outreach activities, including workshops for telemetry researchers and online tutorials (https://www.youtube.com/@europeantrackingnetwork). Researchers tagging migratory fish in the Wadden Sea can benefit from existing platforms such as this to prioritise collaborations at regional, national, and international levels.

In an era of rapid environmental change, long-term datasets may act as valuable indicators of shifts in fish communities, including species replacements, modified behaviours, or altered distributions (Daufresne et al., 2004; Hoegh-Guldberg and Bruno, 2010; Perry et al., 2005; Rodriguez-Dominguez et al., 2019). However, most fish tracking studies are conducted over a period of only a few years, limiting their practicality for long-term monitoring. For example, acoustic receiver arrays managed by independent research institutes are often deployed temporarily, resulting in changes to receiver coverage within or across coastal regions between years, and potentially obscuring infrequent or unexpected fish behaviours that may be of high ecological importance (Lennox et al., 2024). Acoustic arrays are both costly and time consuming to establish and maintain, prohibiting extensive coverage, and should therefore be designed with the aim of maximizing data output and applicability (Lennox et al., 2024). As such, array managers should coordinate across at least, regional, and at best, international scales to maximize the potential for animal detection and address relevant study questions. Recent studies have already proposed the deployment of receiver gates at important transition points and jurisdictional borders (Abecasis et al., 2018; Lennox et al., 2024), a task which is currently being undertaken by a pan-European network covering four key locations in Europe: 1) the Danish Straits, 2) the North Channel, 3) the Strait of Gibraltar, and 4) the Strait of Bosphorus and Dardanelles (https://www.europeantrackingnetwork.org/en/straits). Networks of permanent or semi-permanent arrays will be critical for identifying long-term trends in population- or community-level responses to environmental change.

Limited study durations are also problematic for methods such as archival tagging in which tag recovery rates may be low - particularly for non-commercial species - and in which significant delays between tag deployment and recovery may prolong the collection of sufficient data for statistical analyses (Domeier et al., 2018). By comparison, PSATs provide more predictable data returns over shorter time periods (Hussey et al., 2015), but are more cost-prohibitive and unsuitable for animals below a threshold body size. Furthermore, archived data are binned prior to transmission to satellites, leading to lower resolutions compared to the data records available upon tag recovery (Edwards et al., 2019). As such, the potential value of archival tag recoveries should not be overlooked. Instead, the time periods predicted for sufficient data recovery should be factored into project proposals and funding schemes.

### 3.3. Recommendations for future tracking in the Wadden Sea

The Dutch Wadden Sea was selected as a prime example of an open coastal system requiring enhanced understanding of local and regional fish mobility to manage severe population declines. Using this system as a case study, highlighted the importance of existing knowledge of population trends, species-specific life histories, biological parameters (*e.g.,* size and morphology) for defining research questions and identifying appropriate telemetry techniques. We identified 28 fish species that commonly occur in the Wadden Sea as being potentially suitable for tagging (Table 1), and suggest this as a starting point for future telemetry studies. We also recommend the consideration of aspects such as population status, catchability – including availability of skilled and knowledgeable fisherman -, and vulnerability to capture and handling when selecting potential study species and associated telemetry devices.

In this study, we aimed to showcase the application of acoustic, archival, and PSAT technologies to examine the full range of migratory fish behaviours and identify population bottlenecks across coastal, marine, and fresh waters. Specific guidelines for where and when these techniques should be employed, and for which species, are highly dependant on individual research questions and are therefore difficult to provide. Instead we hope that this work will aid in selecting appropriate telemetry techniques for a predetermined research question and/or species. Furthermore, we advocate for the selection of management-driven research objectives, particularly in the face of significant population declines (Matley et al., 2022). For example, the importance of coastal environments for occasional visitors might be difficult to discern due to low observation rates or unpredictability, but could be crucial for overall population success. Large-scale acoustic telemetry networks and environmental data recorded by archival tags and PSATs could thereby be essential for revealing broad migration pathways and highlighting interregional connectivity between adult and juvenile habitats and subpopulations (McMillan et al., 2019). For seasonal residents, acoustic receiver arrays and long-lifespan tags can be used to define periods and individual fish occurrence over seasonal and multi-year periods and illustrate fine-scale behaviours within coastal waters, informing the delineation and refinement of local protections and area closures (Kohler et al., 2023; Nemeth et al., 2023). Meanwhile, tracks reconstructed using archival data from double-tagged fish or other individuals within a population, alongside acoustic telemetry networks, can fill in knowledge gaps in offshore marine regions, other coastal habitats, or adjacent freshwaters (Goossens et al., 2023; Thorburn et al., 2019). For diadromous species that are often required pass through a variety of anthropogenic barriers *en* route between freshwater to offshore marine environments, acoustic receivers deployed strategically at habitat boundaries and transition zones can pinpoint barriers to regional connectivity and direct restoration efforts (Verhelst et al., 2018). Acoustic detection data can be supplemented by environmental records derived from animal-borne data storage tags, sensors, or data repositories to infer the factors driving fine-scale behaviours and habitat use across a spatially and temporally variable environment. Ultimately, the management of migratory fish populations will require a thorough understanding of the ecological role of coastal habitats in fish life cycles to determine when and where spatial management actions can be applied most effectively.

## Declaration of generative Ai in scientific Writing

During the preparation of this work the author(s) used ChatGPT, a language generation tool developed by OpenAI, in order to assist in diversifying word choice and grammar. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

## CRediT authorship contribution statement

**J.E. Edwards:** Conceptualization, Data curation, Investigation, Visualization, Writing – original draft, Writing – review & editing. **A.D. Buijse:** Conceptualization, Supervision, Writing – review & editing. **H. V. Winter:** Conceptualization, Data curation, Supervision, Writing – review & editing. **A. van Leeuwen:** Data curation, Investigation, Supervision, Writing – review & editing. **A.I. Bijleveld:** Conceptualization, Data curation, Supervision, Writing – review & editing.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2024.108737.

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