ECOGRAPHY

Review

Globally coordinated acoustic aquatic animal tracking reveals unexpected, ecologically important movements across oceans, lakes and rivers

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Acoustic telemetry is a popular approach used to track many different aquatic animal taxa in marine and freshwater systems. However, information derived from focal studies is typically resource- and geography-limited by the extent and placement of acoustic receivers. Even so, animals tagged and tracked in one region or study may be detected unexpectedly at distant locations by other researchers using compatible equipment, who ideally share that information. Synergies through national and global acoustic tracking networks are facilitating significant discoveries and unexpected observations that yield novel insight into the movement ecology and habitat use of wild animals. Here, we present a selection of case studies that highlight unexpected tracking observations or absence of observations where we expected to find animals in aquatic systems around the globe. These examples span freshwater and marine systems across spatiotemporal scales ranging from adjacent watersheds to distant ocean regions. These unexpected movements showcase the power of collaborative telemetry networks and serendipitous observations. Unique and unexpected observations such as those presented here can capture the imagination of both researchers and members of the public, and improve understanding of movement and connectivity within aquatic ecosystems.

Keywords: acoustic telemetry, biologging, biotelemetry, conservation, data sharing, ecology, Ocean Tracking Network

Introduction

Animal movement ecology is undergoing a revolution facilitated by electronic tagging at a global scale (Hussey et al. 2015, Kays et al. 2015). The ability to remotely monitor animals as rapidly as in real time (Klimley et al. 2017), and at very high frequency (Broell et al. 2013), reveals where, when, and how animals move (Nathan et al. 2008). Movement data are making contributions to conservation and are being reflected in management regimes with increasing effectiveness (Lea et al. 2016, Filous et al. 2017, Brooks et al. 2019, Brownscombe et al. 2019, Hays et al. 2019). Early studies using static marks such as anchor tags were inherently biased against the detection of movement. It is telling that a mark–recapture study using (non-electronic) numbered tags led Funk (1957) to conclude that stream fish were sedentary. Unfortunately, the attempts to recapture marked fish to ascertain movement were spatially limited. The finding contributed to freshwater fish ecologists embracing the so-called 'restricted movement paradigm', which was a widely accepted tenet until telemetry studies (using mobile tracking – often with airplanes) conducted over much broader scales began to detect wider-ranging movements (Gowan et al. 1994).

The physical characteristics of water make it difficult to connect most types of tags with global positioning system satellites for real-time monitoring as saltwater rapidly attenuates radio signals, and passive integrated transponder telemetry only works across very short (< 1 m) distances (Lowerre-Barbieri et al. 2019). Animals that never or rarely surface are very difficult to track because positions must be estimated from light levels. However, water is highly conducive to the transmission of sound waves. Acoustic tags coded with unique individual codes (ID) are detected by compatible acoustic receivers placed at strategic locations and animal locations are subsequently inferred from detection data logged on each receiver. This has led to the development of acoustic receiver networks that track animals across aquatic realms (i.e. from freshwater to marine). A limitation of this approach is that the information gained is a function of the detection range of the receivers, which varies based on temperature, depth, wave noise, aquatic vegetation, wind, and other factors (Kessel et al. 2014, Huveneers et al. 2016, Thiemer et al. 2022). This means that receiver arrays must be designed to optimize tracking in a given area of interest and with research questions in mind, with potential loss of information for individuals that are especially vagile or species that are highly mobile or migratory (Heupel et al. 2006).

Popularization of acoustic telemetry methods and accelerating interest in tracking aquatic species to answer both fundamental and applied ecological questions has spurred the development of many individual acoustic telemetry arrays for studying a broad gamut of species around the world. Acoustic telemetry can be found off all continents (Matley et al. 2021), listening for invertebrates, bony and cartilaginous fishes, crustaceans, turtles and more (Hussey et al. 2015, Brodie et al. 2018, Friess et al. 2021). However, many of the highly mobile animals studied cross regional and national boundaries, pass through receiver arrays, and their movements beyond study arrays can remain a mystery. Fortunately, through the use of compatible technologies and the collaborative spirit of animal trackers, acoustic telemetry networks have facilitated surprising, unanticipated, and potentially ecologically important discoveries about animal movements beyond what would be possible from single arrays or researchers working in silos (Welch et al. 2002, Nguyen et al. 2017, Brodie et al. 2018, Iverson et al. 2019, Lowerre-Barbieri et al. 2019). In this paper, we highlight how the network approach to aquatic telemetry has yielded important discoveries about species distributions, niches, movement classes and life spans. We illustrate this through case studies of individually tagged animals making unexpected movements into acoustic arrays hosted by others beyond the original researcher's array, and most often beyond what funding from one individual study could enable. The collection of acoustic telemetry data has its challenges, yet each of the case studies presented here were thoroughly scrutinized for alternative explanations (e.g. predation, false detections) and we believe we present the most likely scenario. In doing so, we develop the thesis that telemetry networks make substantial contributions to ecological understanding and that the existence of digital infrastructure capable of curating hundreds of millions of unique detections, along with compatible software that facilitates data sharing, is crucial to management and conservation agendas.

Unexpected movements

Resource use

Unexpected use of offshore habitat by red drum in the Gulf of Mexico

Red drum *Sciaenops ocellatus* is one of the most important fishery resources of the southeastern US coast and the Gulf of Mexico. Juveniles typically inhabit shallow estuarine waters (Peters and McMichael 1987), moving to deeper sites as they grow, and to adult habitat in the Gulf of Mexico, forming large spawning aggregations in near-shore waters (Lowerre-Barbieri et al. 2016). Federal waters have remained closed or with very limited access to fishers (Porch 2000) ever since the closures of both the commercial (1987) and recreational (1988) sectors, resulting in a lack of landings data to assess the adult stock. To test this hypothesis of red drum remaining on the spawning grounds and to determine the species' availability for capture/recapture for the genetic capture mark recapture model (Lowerre-Barbieri et al. 2016, 2018), receivers were deployed in the spawning grounds and 124 red drum were tagged in 2012–2013. Whereas most of the red drum were detected in the study site during the spawning season (late August to mid-November), surprising data provided by collaborators from the iTag network (itagscience.com; Fig. 1–2, Box 1) showed that all receivers deployed in the area detected red drum, including several small arrays in relatively deep water (~ 50 m) that had been developed to track offshore reef fish. Some fish were even detected outside of the spawning season and up to 120 km northwest of the spawning grounds. Given that red drum were not captured in offshore fishery surveys, the small size of the offshore arrays (< 10 receivers each), and previous hypotheses of overwintering closer to shore or even south in the Everglades (Fig. 2a), this result was completely unexpected. This finding has changed the conceptual models of red drum range size and their annual migratory cycle, suggesting the Tampa Bay spawning site has a large catchment area, and that this species undergoes spawning migrations.

Unexpected use of deep habitat by bluespotted flathead

Bluespotted flathead *Platycephalus caeruleopunctatus* are demersal fish that live on marine sand on the southeast coast of Australia, commonly targeted by the recreational and commercial fisheries (Hall 2015). Because they are ambush

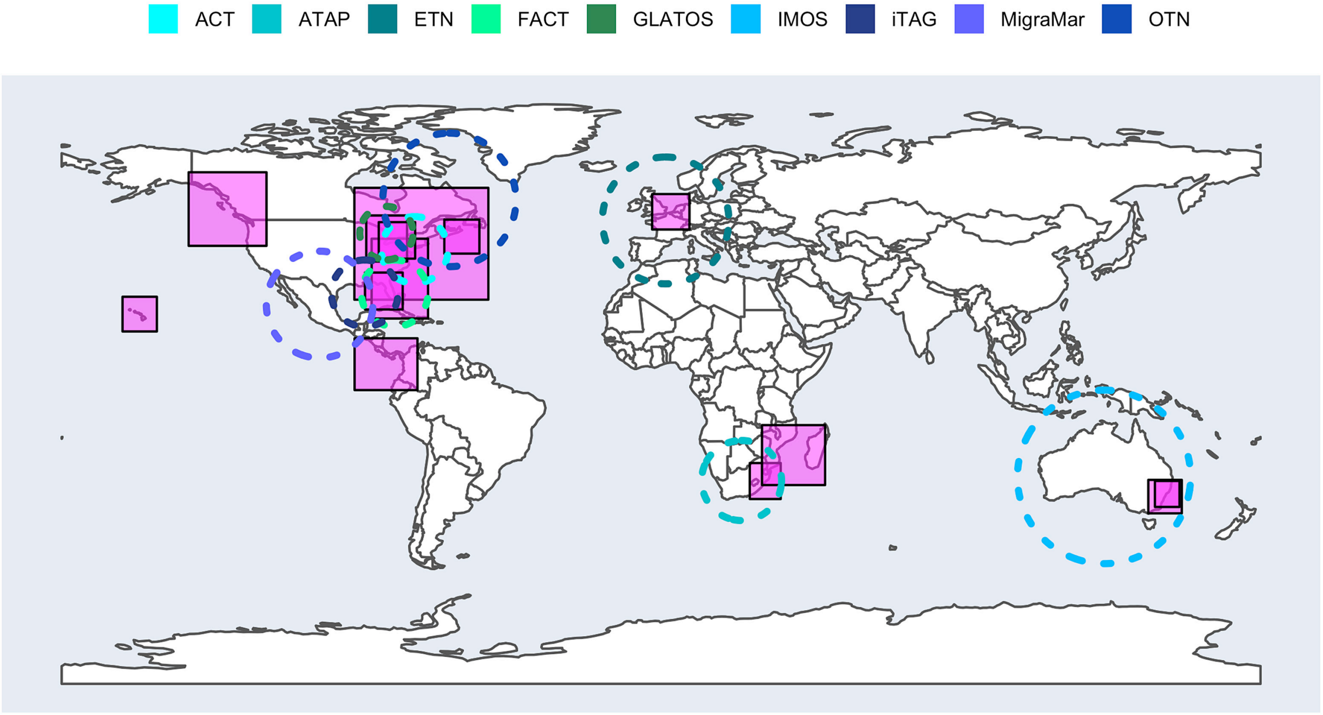

Figure 1. Global distribution of examples of unexpected movements in this study (pink) as well as the approximate ranges of global telemetry networks (Box 1).

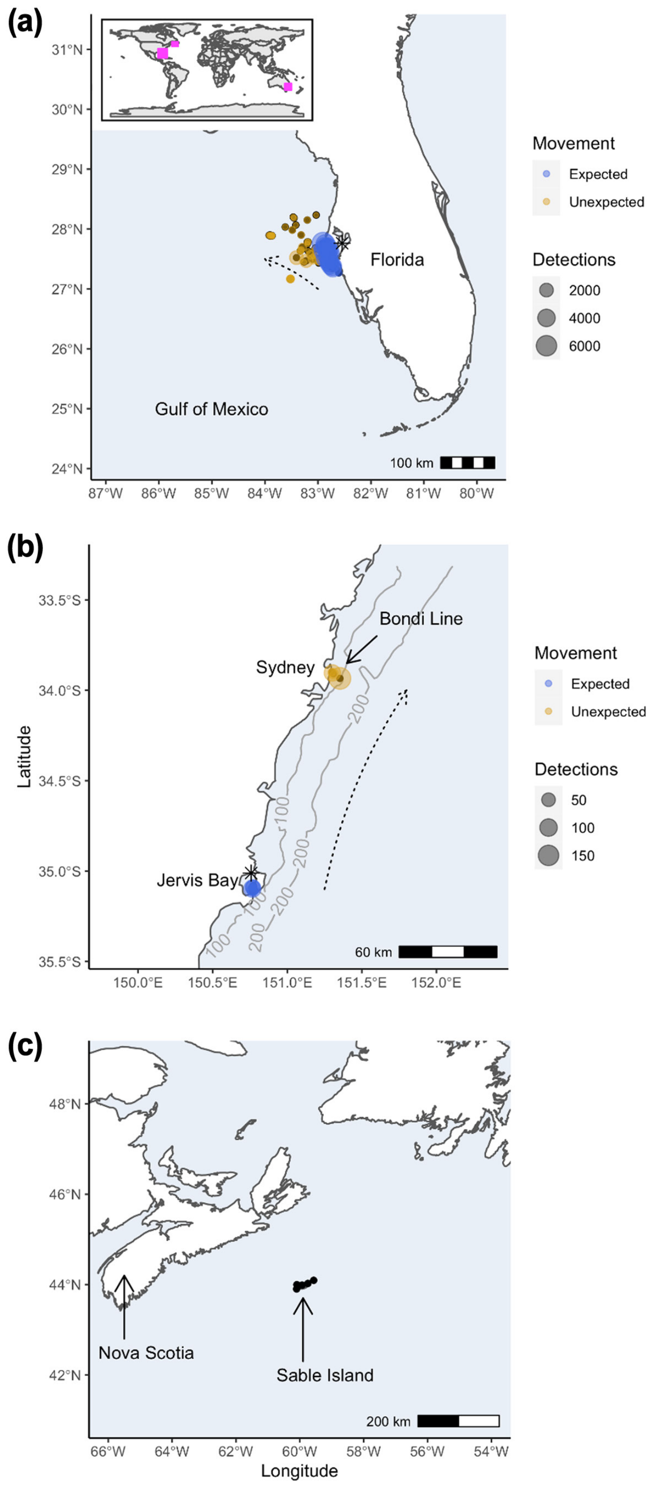

Figure 2. Movement data showing unexpected resource use (or lack thereof) by red drum (a), bluespotted flathead (b), and white sharks (c). Inset panel depicts global location of each illustration.

predators (Barnes et al. 2011), relatively sedentary behaviour was expected, with few obvious drivers for movements across long distances. Recent evidence from Jervis Bay on the south coast of New South Wales, eastern Australia, confirmed that bluespotted flathead exhibit strong long-term residency of up to 600 days at relatively small areas (Fetterplace et al. 2016, Fetterplace 2018). However, a significant proportion of these fish (24%) also made relatively fast, long-distance northward movements, after spending many months moving within small areas (sensu Brodie et al. 2018). Twenty-four percent of fish tagged in Jervis Bay were detected 155 km away (straight-line distance) off the coast of Sydney (Fetterplace 2018, Fig. 2b) predominantly between late May and July, suggesting that they may be related to spawning (spawning begins in late winter; Hall 2015). These detections were unexpected because, despite being a common, highly targeted fisheries species, there were no data on the movement patterns of this species nor any commercial catch patterns that suggested long-distance or spawning-related migrations. Telemetry findings suggested that spatial management is potentially appropriate for this species, but is complicated by the large-scale movements. Research is still needed to determine whether these fish are heading on their northern travels to specific spawning areas, as these would then become high priority areas for management and conservation.

White sharks are not being found in numbers where they surely ought to be at prime seal colonies in the northwest Atlantic

The absence of detections of tagged animals can also be very informative, notably when this provides surprises about how animals are not where they are predicted to be. A good example is the case of the wide-ranging white shark *Carcharodon carcharias* whose populations appear to be rebounding in the northwest Atlantic Ocean (Curtis et al. 2014). Recolonization of grey seals *Halichoerus grypus* in parts of Cape Cod in the late 1990s quickly attracted large numbers of white sharks to that region (due to them being an important prey), initiating a white shark tracking program by the Massachusetts Department of Marine Fisheries and the Massachusetts White Shark Conservancy to provide information about the movements and residency patterns of these animals (www.atlanticwhiteshark.org). Northwest Atlantic white sharks appear to be wide-ranging, and have been detected at multiple sites in Canadian waters by Ocean Tracking Network (OTN, Box 1) receivers. In Canadian waters, the largest population of grey seals occurs at Sable Island (380 300 individuals; Hammill et al. 2017) (Fig. 2c). Based on the rapid arrival of white sharks off Cape Cod following the establishment of a seal colony there, it was anticipated that Sable Island would surely provide irresistible and important feeding grounds for white sharks. Despite many detections of the approximately 150 total acoustically tagged white sharks detected by OTN receivers, only two individuals have been detected at the Sable Island grey seal breeding hotspot (Fig. 2), and only in 2020. It seems unlikely that the sharks could not find the site (due to the odor plume), which suggests that a majority of the sharks avoid the area, potentially because of seals working together to drive off sharks, as evidenced for both Cape fur seal (*Arctocephalus pusillus pusillus*, Stewardson and Brett 2000, Johnson et al. 2009) and Australian fur seal

Box 1. Examples of telemetry networks that span regional to worldwide coverage and provide infrastructure (including e-infrastructure) and infrastructure services to animal trackers.

Ocean Tracking Network (OTN)

The Ocean Tracking Network is an international aquatic tracking information facility headquartered in Canada. OTN provides infrastructure and infrastructure services to researchers including hardware for tracking (e.g. receiver loans), operation of key arrays to detect local and long-distance movements from other research groups, data analysis and visualization training, and e-infrastructure for archiving tag detections compatible with international frameworks for animal occurrence data (e.g. Global Biodiversity Information Facility and Darwin Core archives). The internationally certified OTN database houses over 300 million animal detections from over 75 000 aquatic animals tracked around the world. www.oceantrackingnetwork.org

European Tracking Network (ETN)

The European Tracking Network is a coordinated research effort to integrate all aquatic animal tracking (meta) data in Europe to scientific excellence and provide advice for EU species management and conservation. The network focuses on: 1) creating key arrays at straits that are ingress and egress points to Europe's major seas including Gibraltar, Kattegat, and Bosphorous and 2) advancing intercompatibility of currently available technology. The ETN mission is to improve coordination of European telemetry efforts by developing common e-infrastructure and standards for compatibility to track key species and their movements around Europe. www.europeantrackingnetwork.org

Great Lakes Acoustic Telemetry Observation System (GLATOS)

The Great Lakes Acoustic Telemetry Observation System network consists of fishery researchers across the Laurentian Great Lakes bordering Canada and the USA (Krueger et al. 2018). Initially this research initiative started with four projects designed to demonstrate how acoustic telemetry could benefit fishery management decision making in the basin; in 2020 there were 89 active projects, with approximately 1600 active receiver deployments. Since inception, 356 researchers representing 101 academic, state, provincial, federal, non-governmental, and tribal organizations have participated in telemetry studies through the GLATOS network. Studies designed to provide decision makers with information regarding the population dynamics, ecology, biology, and movement behaviour via large- and fine-scale projects of native and non-native species have been conducted to date.

Acoustic Tracking Array Platform (ATAP)

The Acoustic Tracking Array Platform (ATAP) comprises more than 300 moored acoustic receivers spanning approximately 2200 km of the South African coastline, from False Bay in the Western Cape Province to Ponta do Ouro at the South Africa/Mozambique border (Cowley et al. 2017, Murray et al. 2022). In its current format, this large-scale array design allows researchers to address a number of key questions pertaining to animal movement – information that is essential for the development of effective management measures, including movements in relation to MPA boundaries, transboundary movements, and a host of ecological aspects such as spawning aggregation dynamics, multiple habitat connectivity, and predator–prey interactions. The ATAP currently provides support to researchers from 28 different organizations.

Integrated Marine Observing System (IMOS)

The Integrated Marine Observing System comprises a continental-scale hydrophone array and coordinated data repository (Hoenner et al. 2018) that enables the monitoring of movements of tagged marine animals across scales ranging from 100s of meters to 1000s of kilometres. The IMOS Animal Tracking Facility network comprises more than 1000 receivers across a number of installations with IMOS-dedicated arrays complemented by installations of individual research projects undertaken by the Australian scientific community enabling large-scale studies and to reveal intra-specific differences in movement profiles and site residency of a wide range of species (Brodie et al. 2018). www.imos.org.au

Integrated Tracking of Aquatic Animals in the Gulf of Mexico (iTag) Network

iTAG is a science collaborative, with more than 200 members, focused on increasing knowledge of aquatic animal movements and their importance to management (Lowerre-Barbieri et al. 2019). The collaborative includes industry, stock assessment scientists, and researchers. iTAG facilitates movement ecology research at both small (e.g. estuarine, river systems) and large geographic (e.g. Atlantic, Gulf of Mexico and Caribbean Sea) scales through data exchange, strategic deployment of long-term monitoring arrays, workshops, and leading or contributing to regional scale and/or multi-species syntheses (Friess et al. 2021). myfwc.com/research/saltwater/telemetry/itag/network

MigraMar

MigraMar is a collaborative network of scientists dedicated to better understanding and safeguarding populations of marine migratory species in the Eastern Pacific Ocean (EPO). Over the last fifteen years, MigraMar's research has identified critical areas for migratory species, including feeding and breeding grounds and routes of seasonal migrations. These findings have informed governments and stakeholders on the functioning and connectivity of marine protected areas (MPAs) in order to improve the management and conservation of our oceans.

ACT and FACT

The ACT (Atlantic Cooperative Telemetry) Network developed as researchers along the Atlantic seaboard started to use telemetry more widely, necessitating approaches to support data management and sharing of detections. Over 100 species from Maine to Florida have been tagged as part of ACT, with acoustic arrays all along the coast. As of 2020, ACT is operated through the Smithsonian Environmental Research Network. Since 2007, the FACT Network along the southern US Atlantic coast has aimed to connect researchers working on tracking animals with acoustic telemetry. Starting in Florida, FACT now includes data from throughout the southern states along the Atlantic as well as Caribbean islands. FACT is independent from ACT but together these networks cover much of the western Atlantic coastline to connect researchers and allow fish to move within a connected network where data can easily be shared among members.

(*Arctocephalus pusillus doriferus*; Kirkwood and Dickie 2005). Continued monitoring of sharks at this site will compile additional information about the movement of white sharks around waters off Nova Scotia.

Migration routes

An unexpected marine migration route for European eel

The European eel *Anguilla anguilla*, a panmictic, facultatively catadromous fish species with a complex life cycle, inhabits coastal areas from northern Africa to Scandinavia, where it faces multiple anthropogenic pressures (e.g. climate change, habitat loss and fragmentation, introduction of non-native species, overexploitation, and pollution; Drouineau et al. 2018). A better understanding of their movement is crucial to restore the eel population, which has declined by 90–99% over the past 4–5 decades (Dekker and Casselman 2014). Despite the importance of migration barriers such as hydropower stations, shipping locks, and commercial fishing having been addressed (Winter et al. 2006, Aarestrup et al. 2010, Verhelst et al. 2018), eel migration routes and behaviour in the marine environment are still poorly understood. Shortly after the establishment of the Permanent Belgian Acoustic Receiver Network (PBARN; Reubens et al. 2019) in 2014, not only four eels from Belgian freshwater systems, but also six eels from the north of the Netherlands and west Germany (Huisman et al. 2016) were detected passing through Belgian coastal territory (Fig. 3a). These were the first observations that eels followed a southern route, as opposed to a northern route (Westerberg et al. 2014) towards the English Channel to reach the Atlantic Ocean before their route was mapped in more detail using archival tags (Verhelst et al. 2022).

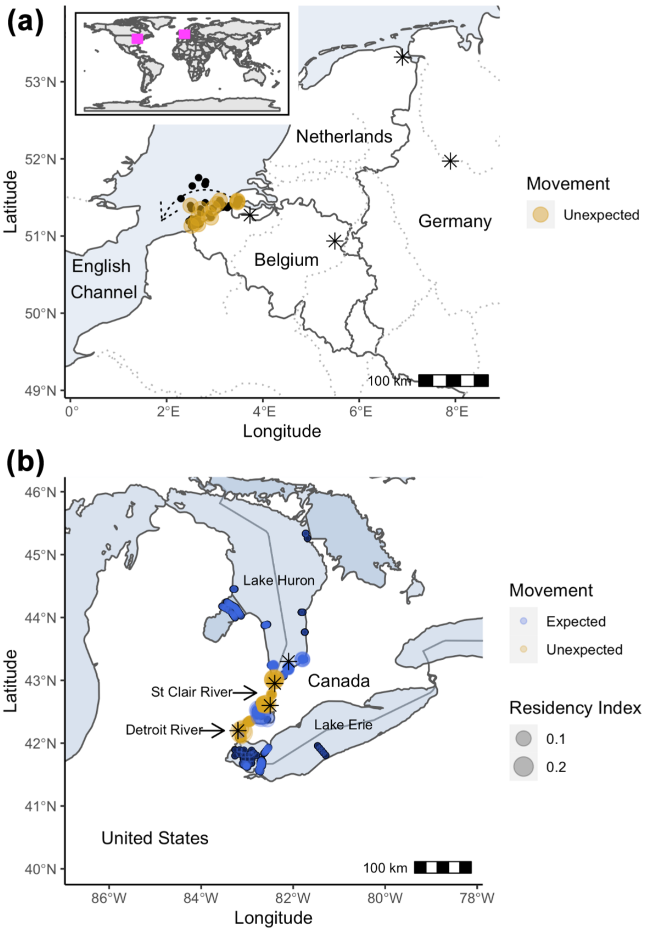

Figure 3. Movement data showing unexpected migrations by European eels (a) and lake sturgeon (b). Inset panel depicts global location of each illustration.

Unexpected diversity of migration patterns of lake sturgeon

Lake sturgeon *Acipenser fulvescens* are a long-lived species, and the largest freshwater fish indigenous to the Great Lakes Basin (Auer 1999). Until tracking research began, the understanding of lake sturgeon breeding ecology was that they reside in lakes and only migrate into rivers when they spawn (every 4–7 years for females, and every 2–4 years for males) in the spring and summer (Rusak and Mosindy 1997, Auer 1999). Closer investigation of the sturgeon by tracking within the GLATOS array, however, revealed five distinct migration behaviours based on phenology and duration of river and lake use (Fig. 3b). Within these five behavioural groups there were 14 subgroups based on regional and temporal use of the lakes and rivers. Specific behaviours included 1) year-round river residents; 2) seasonal river (summer) and lake (winter) use migrants; 3) lake-dominant, making short duration river trips, migrants; 4) seasonal lake (summer) and river (winter) use migrants; and 5) 'lake skipper', using rivers to transition between lakes. Remarkably, individuals did not switch between movement groups or contingent subgroups during the six-year study period, suggesting that these behaviours are persistent in lake sturgeon (Kessel et al. 2018).

Connectivity

Unexpected connectivity of a bull shark between the African mainland and Madagascar

Juvenile bull sharks *Carcharhinus leucas* display philopatric behaviour to their nursery habitats (Heupel et al. 2010, Tillett et al. 2012), whereas sub-adults and adults generally display residency in coastal areas interspersed with seasonal migrations (Brunnschweiler et al. 2010, Carlson et al. 2010, Daly et al. 2014, Lea et al. 2015a, b, Rider et al. 2021). A remote site with minimal human disturbances within the Ponta do Ouro Partial Marine Reserve (PPMR) in southern Mozambique is an important aggregation site for bull sharks (Daly et al. 2014). Movements of bull sharks tagged in the PPMR were monitored by receivers deployed at the study site, along with those of the Acoustic Tracking Array Platform in South Africa. In addition, three receivers were deployed off the western coast of Madagascar. Many of the bull sharks undertook extensive migrations along the continental coastline, up to 3760 km (Daly et al. 2014), but one female bull shark (2.54 m total length, TL) undertook a particularly unexpected movement. This individual displayed periods of long-term residency interspersed with short trans-boundary trips into South Africa and periods of prolonged absence during the winter. However, almost five years post-tagging, this shark crossed the Mozambique Channel and was recorded on a receiver positioned at Nosy Be, Madagascar (Fig. 4a), a cross-ocean distance of at least 2200 km in 127 days (17.3 km day^{-1}). The shark then made a return movement of at least 2300 km in 42 days (54.8 km day^{-1}), and was again detected at the remote Mozambican site. Although bull sharks have been recorded making large-scale movements elsewhere in the world (Carlson et al. 2010, Heupel et al. 2015, Lea et al. 2015a, b), this is the first record of an ocean crossing from southern Africa.

Unexpected downstream connectivity of Great Lakes lake trout

In Lake Erie, lake trout are the focus of an extensive rehabilitation program following extirpation from overfishing, parasitism, and competition from invasive species, and habitat degradation (Cornelius et al. 1995). In an effort to better understand the mechanisms behind the lack of successful natural reproduction in Lake Erie, a team of Lake Erie researchers began implanting acoustic tags into adult lake trout in 2016. Following fall turnover in mid-October, one exceptional lake trout moved east along the southern shore of Lake Erie and then into the head of the Niagara River, 98 km from where it was originally tagged. Lake trout are occasionally encountered in the upper Niagara River, but this fish was next detected in Lake Ontario, indicating that the fish continued downstream in the Niagara River and plunged over the 51 m high Niagara Falls on its way to Lake Ontario, and was confirmed alive via detections on other receivers (Fig. 4b).

Unexpected inter-island movement of giant trevally in Hawai'i

The giant trevally *Caranx ignobilis* is an important predator on the coral reefs of the Hawaiian Archipelago. Although giant trevally are considered mobile predators (Sudekum et al. 1991), little was known about their capacity to move among the Main Hawaiian Islands, leaving questions about the metapopulation dynamics of the archipelago's spawning stock. The Main Hawaiian Islands consist of a series of islands and interconnected channels, which could serve as a series of interconnected habitats for this species if they travel across the channels. Data sharing between the Main Hawaiian Islands array and the acoustic array operated by the Shark Lab at the Hawai'i Institute of Marine Biology (Meyer et al. 2018) revealed simultaneous detections of tagged giant trevally between two islands – south Kihei and Laparus, Maui (Fig. 4c). This provided strong evidence that the spawning stock of this species is mobile across the island chain, and highlighted the importance of Kaho'olawe and Molokini (two protected areas) to the fisheries of Maui (Filous et al. 2017), especially given their importance as both a recreational and subsistence fisheries species (Friedlander and DeMartini 2002, Mccoy et al. 2018).

Unexpected evidence of trans-Pacific connectivity among green turtles

Sea turtles are highly migratory and vulnerable species that use oceanic islands as essential habitats for resting and feeding during their large-scale migrations. Cocos Island, in the eastern Pacific, has been identified as an important feeding area for juvenile and subadult green turtles (*Chelonia mydas*; Heidemeyer 2015), although information on the migratory movements of these sexually immature life stages is largely unknown. From 2012 to 2015, 38 green turtles were tagged at Cocos Island with acoustic transmitters to study their residency and movement patterns (Heidemeyer, unpubl.). One individual was detected almost 1000 km away, near Gorgona Island, Colombia, 104 days after its last detection at Cocos Island. The other individual stayed at Cocos Island for almost 249 days, then traveled 530 km to Golfo Dulce, southern Costa Rica, in 21 days (Fig. 4d). This evidence suggests that the movements of highly migratory species between islands and other oceanic habitats of the eastern Pacific are not random; instead, sea turtles and similar species migrate along these ecologically important swimways throughout the ocean (Peñaherrera-Palma et al. 2018).

Unexpectedly long northward migrations by Atlantic tarpon

Atlantic tarpon *Megalops atlanticus* is a highly sought-after mesopredator targeted by recreational anglers along the southeastern USA, Gulf of Mexico, and across the Caribbean. New movement data suggest a small proportion of individuals migrate between the Florida Keys northward as far as Virginia Beach, USA, distances far beyond those expected. One relatively small male (119 cm fork length) tagged in the Florida Keys in May 2017 was later detected in the near-shore waters off Ocean City, Maryland, USA in July 2018, over 2000 km from where it was caught (Griffin et al. 2022, Fig. 4e). Acting upon this new information, the Maryland Biodiversity Project (marylandbiodiverisy.com) have now included Atlantic tarpon into their species registry. Chesapeake Bay and Delaware Bay are extremely productive estuarine systems that may

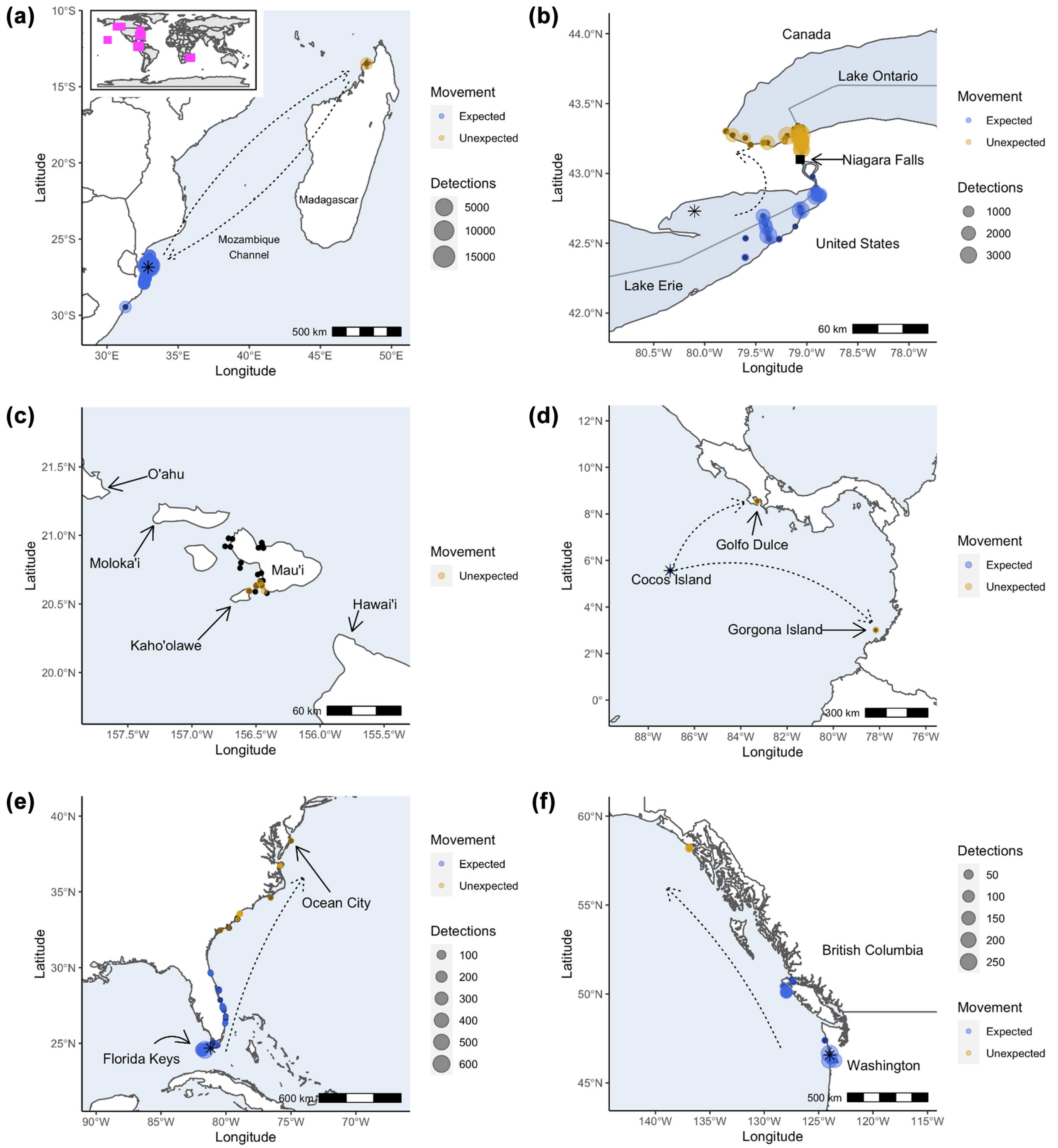

Figure 4. Movement data showing unexpected habitat connectivity for bull shark (a), lake trout (b), giant trevally (c), green turtles (d), Atlantic tarpon (e), and green sturgeon (f). Inset panel depicts global location of each illustration.

provide important habitats for tarpon growth and post-spawning recovery. Previously unknown, these data yield new insights into the extent that tarpon migrate north to feed on the large biomass of forage fish. Because tarpon must travel across multiple state lines to reach these potentially important foraging grounds, management should be extended to reflect their migratory range. Currently, tarpon harvest regulations differ on a state-by-state basis across their USA range, from catch-and-release only (Florida, North Carolina, Virginia), to limited harvest with varying restrictions (Texas, Alabama, Georgia, South Carolina), to no harvest limits or restrictions (Louisiana, Mississippi, Maryland).

Unexpected international movements of California green sturgeon

The North American green sturgeon *Acipenser medirostris* is an anadromous sturgeon that spawns in just a few rivers in northern California and southern Oregon, spends much of its life in the coastal ocean, and aggregates in large estuaries along the US west coast in summer months (Adams et al. 2007). In the late 1800s, green sturgeon were likely heavily overharvested in commercial fisheries targeting white sturgeon, and their freshwater habitats, especially in the Sacramento River, have been seriously restricted and degraded by dams and myriad other human impacts. Remarkably, thanks to the expansion of the Pacific Ocean Shelf Tracking (POST) array (now operated by OTN), green sturgeon were found to undertake extensive seasonal migrations, summering in non-natal estuaries or making spawning runs in natal rivers, and overwintering in marine waters off northern British Columbia, up to 1600 km away (Lindley et al. 2008, Fig. 4f). Much of the information about green sturgeon life history in the recovery plan is based on the acoustic telemetry studies carried out by this coast-wide collaboration that provided a major increase in our understanding of a previously understudied species of international concern.

Individual variability

Unexpected long distance dispersal of an anadromous Arctic charr

Arctic charr *Salvelinus alpinus* are a phenotypically diverse species of salmonid fish distributed throughout the Holarctic. In the anadromous life-history form, Arctic charr migrate regularly between freshwater and the marine environment for summer feeding. In June 2015 Arctic charr (n = 51) were acoustically tagged in Muddy Bay Brook, Labrador (53.62°N, 56.88°W) as part of a program investigating thermal habitat use and near-shore marine feeding of the species (Mulder et al. 2020). Post-tagging, most fish relocated several times within the vicinity of the Muddy Bay Brook coast, displaying the typical pattern of coastal residency (Rikardsen et al. 2007, Moore et al. 2016). A number of fish, however, yielded unexpected detections that were brought to light by OTN. One charr with a V9T tag was not located again until 26 August 2015 as it passed a receiver line (51.42°N, 56.64°W) maintained by OTN when passing through the Strait of Belle Isle, some 475 km from where it was first tagged. A second 42 cm fish was detected twice east of Cape Breton approximately 15 km from the coast and 820 km southwest of its tagging point. Assuming a coastal migration path, the fish would have moved approximately 1100 km (Fig. 5a). Four additional exceptional detections in August 2015 included three Arctic charr, ranging in size from 36 to 45 cm, detected in the inner Bay of Fundy in late August, and a single 39.5 cm fish detected in the eastern Gulf of Mexico offshore from Pensacola, Florida. These unexpected detections are believed to have resulted from the Arctic charr having been predated by large mobile predators such as porbeagle sharks *Lamna nasus* known to move long distances between colder Arctic and warmer southern Atlantic waters (Saunders et al. 2011, Biais et al. 2017) and opportunistically predate on teleost fishes (Joyce et al. 2002).

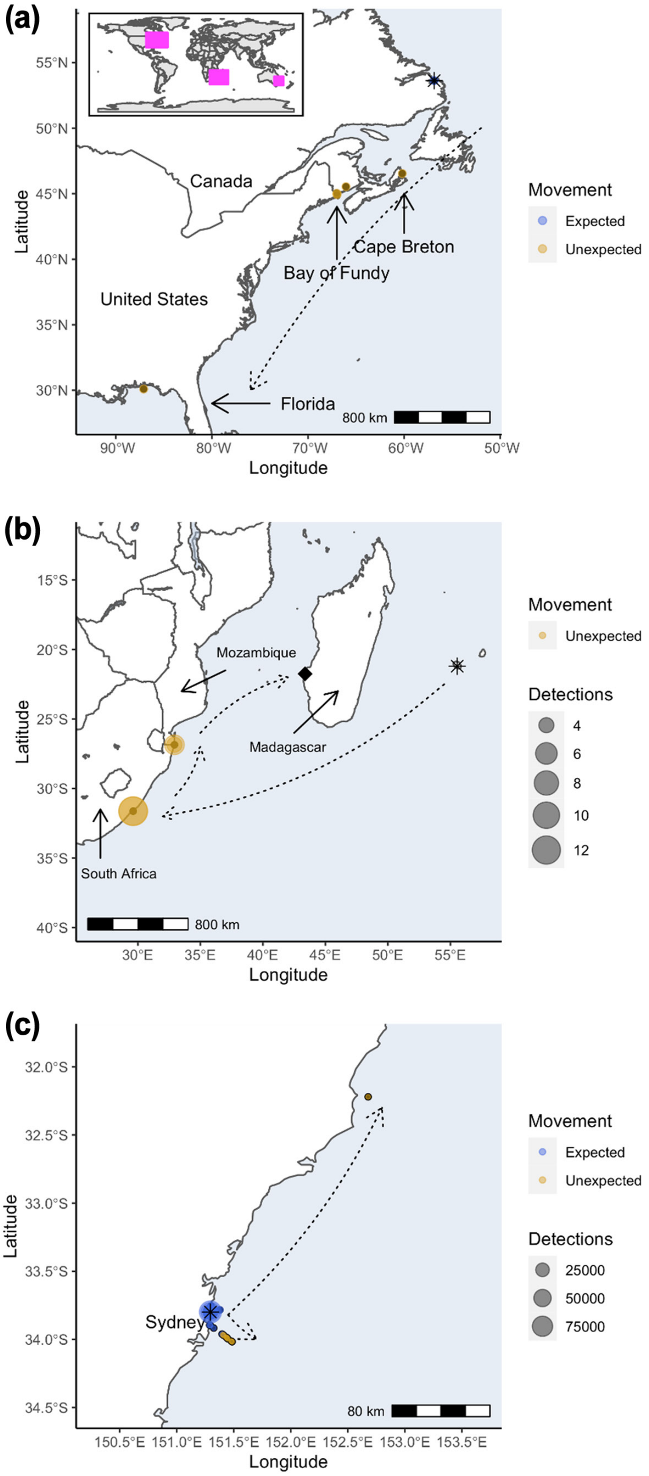

Figure 5. Movement data highlighting unexpected individual variability in Arctic charr (a), tiger sharks (b), and spotted wobbegong (c). Inset panel depicts global location of each illustration.

Unexpected connectivity of tiger sharks in the western Indian Ocean

Tiger sharks *Galeocerdo cuvier* are globally distributed nomadic apex predators, occupying warm–temperate, subtropical, and tropical seas. Tiger sharks play an important ecological role, shaping marine communities via non-consumptive risk effects and direct predation (Dicken et al. 2017). Locally abundant food resources encourage tiger sharks to remain within relatively small areas (Acuña-Marrero et al. 2017) or undertake pelagic migrations (Hammerschlag et al. 2012, Lea et al. 2015a,b). Fifty-five tiger sharks were tagged between October 2011 and July 2014 and monitored until 2014 at Reunion in the Indian Ocean. At least 43 sharks remained within the vicinity of Reunion and individuals were rarely detected on the coastal network of receivers. One female adult (~ 307 cm TL) was tagged on this plateau (21°00'54.0"S, 55°10'48.0"E) on 6 December 2012 but never recorded on receivers at Reunion. However, the shark was detected along the east coast of South Africa at Port St Johns 131 days after being tagged, before moving up the coastline into southern Mozambique 95 days later, equating to a minimum distance traveled of at least 3500 km (Fig. 5b), and a minimum travel speed of at least 15.5 km day^{-1}. This individual was never detected again, but was caught by an artisanal fisher on 28 August 2013 (39 days later) at Morombe, Madagascar, having moved another 1200 km, traveling approximately 31 km day^{-1}. Tiger sharks have been recorded crossing the Mozambique Channel to Madagascar (Wintner 2004, Daly et al. 2018), and the entire Indian Ocean (~ 6500 km between southern Mozambique and the Mid-Indian Basin; R. Daly, Oceanographic Research Institute, pers. comm.); however, this was the first record of an acoustically tagged shark undertaking a movement of this kind, and suggests a stronger need for multi-national protection of this species, especially considering the exceptional distances covered by the animal and it being (re)captured in an unsustainable shark fishery in Madagascar (Le Manach et al. 2012).

Unexpected dispersal capacity underlying stock connectivity of spotted wobbegong

The spotted wobbegong *Orectolobus maculatus* is an endemic Australian shark that grows up to 300 cm in total length and is usually found in coastal shallow water (0–218 m; Last and Stevens 2009). Its diet consists primarily of bony fish, complemented by cephalopods and chondrichthyans (Huveneers et al. 2007a). For many years, they were targeted by commercial fisheries as a staple of the fish and chip market (Huveneers et al. 2007b). They are considered slow-growing (Huveneers et al. 2013) with low fecundity resulting from a triennial reproductive cycle. All evidence to date suggested limited movements and dispersal of spotted wobbegongs. Early acoustic telemetry studies of spotted wobbegong demonstrated multi-annual site fidelity with individuals detected seasonally within a small 0.2 km^2 marine reserve for up to five years (Lee et al. 2015). However, through the IMOS Animal Tracking Facility (Box 1), one spotted wobbegong was detected ~ 230 km away from its tagging location, while other individuals were detected ~ 17 km offshore, both large movements that were unexpected based on the earlier studies that suggested primarily coastal distribution and strong site attachment (Fig. 5c). These detections suggest that wobbegongs are irruptor-type movers, with occasional long-distance movements (Brodie et al. 2018) and show that spotted wobbegong might disperse more widely and into habitats beyond those assumed by current fisheries management, with implications for management due to potential catches across different fisheries.

Discussion

Unexpected movements are, like other rare events in ecology (Weatherhead 1986), inherently challenging to seek and to find. Although outliers may be considered distracting from experiments or analyses aimed at describing typical patterns from large samples, they may provide important insights and even *Eureka!* moments that break from expectations and shift paradigms about species' biology (Benhadi-Marin 2018). Because tracking studies embrace larger sample sizes and consider more species, intra- and inter-specific variations in movement patterns will be increasingly observed, while the potential for unexpected movements to be observed will presumably grow. There is a great deal to learn about animal ecology from unexpected movements, because they can fundamentally revise our concepts for a population or species, and effective management depends on thorough knowledge of spatiotemporal habitat use of animals. Although management models will not focus on outliers, there is meaningful information in these unexpected movements about stock connectivity (e.g. exchange of genetic material), potential range shifts, resource selection, climate resilience, and other details that may inform present management as well as prepare for future management challenges in a rapidly changing aquatic realm (Harrison et al. 2018, Barkley et al. 2019).

The world seems much smaller when seemingly distant habitats are connected by the long-distance movements of a single animal, as we see from the northward migrations of Atlantic tarpon from the Florida Keys to Virginia Beach or green sturgeon from California nearly to Alaska. Movement across large scales and through different jurisdictional zones calls for cross-border action by managers, especially for species at risk such as the Critically Endangered European eel that move southwards through the English Channel from rivers in Germany and the Netherlands towards the Sargasso Sea to spawn, or green turtles moving westwards from the Costa Rican waters of Cocos Island to Gorgona Island, Colombia. Unexpected movements can provide insights in species' ecology, such as sources of mortality as was noted for Arctic charr. But unexpected movements need not be extensive to be important: movements just offshore by red drum, bluespotted flathead, and spotted wobbegong provided evidence of these animals in entirely new habitats, expanding knowledge about habitat use and requirements with direct implications for their conservation. Moreover, the long-distance movement of spotted wobbegong suggests that putative discrete stocks may in fact be mixed stocks connected by individuals making unforeseen long-distance movements. Fisheries management and marine spatial planning both benefit from data on the movements of aquatic animals to make evidence-based cases for spatial or temporal protections from activities such as shipping, fishing, and industrial uses (e.g. mining, pile driving for wind turbines, seismic surveys). Revealing unexpected movements is therefore essential to expose data gaps that may hinder effective management protocols in the aquatic environment.

Broad conclusions about how fisheries should be managed, and how jurisdictions need to cooperate to develop compatible policies, are predicated on knowledge facilitated by data. Oftentimes, the data are too limited to make conclusions, and this is often the case with telemetry (McGowan et al. 2017). The story of unexpected movements contains both positive lessons for how collaboration can be beneficial, but also emphasizes the challenges that we often face with limited observing capacity, even in the most optimistic scenarios. How many incredible and meaningful unexpected movements go undetected? We continue to scale up efforts to track animals with regional, national, and international networks for telemetry that are now online with digital infrastructure that archive and enable sharing terabytes of animal movement data (Hoenner et al. 2018). While we laud the revelations facilitated by this approach, we recognize that there is more to be done to fulfill the potential of telemetry networks, particularly through building capacity in research and monitoring aquatic resources in developing nations. Participating in networks and sharing data are crucial to ensure that users have access to the data they need to identify unexpected movements among tagged animals. Nguyen et al. (2017) identified some barriers to cooperation that must be addressed to maximize inclusion and representation in these networks. Software compatibility issues threaten the viability of networks to identify the unexpected movements that have such great potential to reveal unique insights into individual animal biology. To reveal more unexpected and large-scale movements it is essential that different acoustic telemetry system brands work towards compatible protocols on their tags and receivers (Reubens et al. 2021). Compatibility can come in different forms for different researchers at different scales depending on the receivers that are deployed and the software installed on those receivers. To maximize compatibility, options such as the Open Protocol have been developed, which is an open source PPM code set that is available from multiple manufacturers. Using Open Protocol tags can ensure that they are detectable across a large number of manufacturers' receivers, facilitating connectivity and collaboration to identify unexpected movements.

This paper reveals both limitations and opportunities for using acoustic telemetry as a tool to better understand the oceans, their habitats, and how key species use them. Acoustic technology is prone to occasional false detections when an ID is incorrectly registered at a receiver, creating the illusion of a movement. Common filtering tools include speed and distance filters to flag unrealistically rapid movements as false. The Pincock algorithm is also commonly used and is implemented in the R package 'glatos' (Holbrook et al. 2022); the algorithm makes the assumption that a true presence should be represented by multiple detections of an animal at a given station within a time interval (Holbrook et al. 2022). PPM-type transmitters are more prone to false detections than CDMA are. PPM protocols such as S256 are very prone to generating false detections, and filters should be adjusted accordingly, otherwise incorrect unexpected movements are much more likely to manifest in datasets. Additional misinterpretations can be caused by tags being moved by people (e.g. tags from harvested fish deposited around a receiver) or movements of predators; predation can be ascertained with various tags and tools for investigating fish fate in detail (Lennox et al. 2023). Acoustic telemetry is limited in scale by how many receivers are deployed and where they are active, because acoustic transmitters can only be detected where receivers are active. Ideally, receivers can be deployed everywhere to listen for tags everywhere at all times, but this is limited by the technology, the cost of receivers prohibits exhaustive coverage, and the labour required to maintain receivers is prohibitive. There are opportunities to expand coverage with acoustic telemetry using platforms of opportunity such as marine infrastructure or other monitoring tools such as oceanographic buoys that can extend coverage into new areas (Lennox et al. 2017). However, it is also essential to focus coverage on key areas and jurisdictional boundaries with lines of receivers forming gates. Key examples include the Cabot Strait, the largest ingress point into the Gulf of St Lawrence, the world's largest estuary, which has helped understand the biology of Atlantic bluefin tuna (Block et al. 2019). Abecasis et al. (2018) suggested receiver gates in Europe that would assist with determining movements across key jurisdictions, and there are more opportunities still to investigate lines that will facilitate the discovery of key movements by species across scales in the ocean, as well as in freshwater.

The case studies described in this paper are a small sample of the exciting potential that acoustic telemetry networks have to provide unique and surprising details about aquatic animal ecology. Support for the long-term installation of arrays deployed at key sites is important to ensure that we can monitor international movements across the globe. Investment in long-term fixed compatible infrastructure and development of methods for mobile tracking with aquatic vehicles will ensure that more unexpected movements of animals are detected, and that fisheries management and marine spatial planning efforts are buoyed with the necessary data to identify evidence-based solutions to manage aquatic environments. The insights obtained from these unexpected movements add to the new information (Ledee et al. 2021) that is markedly changing our understanding of how critical movements of individuals are to the fundamentals of population and stock structure in the marine environment.

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