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A review of molecular, physiological, behavioral, and ecological studies in a Special Issue devoted to the movement ecology of fishes

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Abstract Much new information on the movement ecology of fishes is present in this Special Issue of *Environmental Biology of Fishes*. Authors submitted manuscripts in response to now-deceased Editor-in-Chief David Noakes' call for papers under the theme of "fish movement: molecules, models, and migration." In a little over a year and a half, 30 papers were submitted on the molecular biology, behavior, physiology, and ecology of bony and cartilaginous fishes (and even a jawless fish) that inhabit both fresh water and salt water. Briefly summarized in this introductory article are the findings of the authors published in this Special Issue, organized under six main themes—movement patterns, innovative techniques, anthropogenic disturbances, behavior and environmental relationships, predictive models, and management and conservation biology, and suggestions are offered for future research. We are pleased to see David's goal of integrating information at every scale of research, from genomics to theoretical models and landscape ecology, realized in this multi-disciplinary compilation. We dedicate this Special Issue to our fond remembrance of his friendship and his long-term leadership in ichthyological science.

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Introduction

Much new information on the movement ecology of fishes is present in this Special Issue of *Environmental Biology of Fishes*. Authors submitted manuscripts in response to now-deceased Editor-in-Chief David Noakes' call for papers under the theme of "fish movement: molecules, models, and migration." His objective was to integrate information at every scale of research, from genomics to theoretical models and landscape ecology. Our understanding of fish movement has important practical as well as theoretical aspects in disciplines as diverse as fisheries management, conservation, behavioral ecology, and evolutionary biology. In a little over a year and a half, 30 papers were submitted on the molecular biology, behavior, physiology, and ecology of bony and cartilaginous fishes (and even a jawless fish) that inhabit both fresh water and salt water. Briefly summarized in this introductory article are the findings of the studies published in this Special Issue, organized under six main themes—movement patterns, innovative techniques, anthropogenic disturbances, behavior and environmental relationships, predictive models, and management and conservation biology. As is generally the case in science, each published study reveals more unanswered questions, and some suggestions are therefore offered for future research. As is evident in the compilation presented here, David's goals for this multi-disciplinary Special Issue have been achieved. We dedicate this Special Issue to our fond remembrance of his friendship and his long-term leadership in ichthyological science.

Movement patterns

Fishes exhibit a diversity of movement patterns. Much of the descriptive biology of their movement ecology was historically performed on sharks and other large fishes because their size enabled them to be outfitted with relatively bulky electronic tags. Fishes carrying ultrasonic tags could be tracked by vessel, obtaining their geographical coordinates from the GPS-determined location of the tracking boat positioned above them. The longer distance movements of fishes can now be described using tags that either are tracked by the ARGOS satellite in real time, pop off at a preset time when they upload a record of positions to the satellite, or remain on the fish and are removed upon capture, although the pop-up and retrievable archival tags provide less accurate positions based on geolocational algorithms. Furthermore, small individually coded beacons can now be placed on smaller cartilaginous and bony fishes that are detected by autonomous receivers placed at sites along the migratory pathway of these species. Linear arrays of these receivers have provided an idea of the migratory movements of fishes within rivers, the degree of residency at islands, and, albeit less effectively, the movement of fishes between widely separated islands or archipelagos. We will not review the voluminous literature behind these technologies here because they are described, often in detail, within the papers of this Special Issue. We will give a few examples, with which we are familiar, to give an idea of the diversity of movement patterns in order to place the papers in their proper context before describing their contents.

Fishes may be relatively sedentary, staying within a small area around a thermal outflow, such as the Haller's round ray *Urolophus helleri* (Vaudo and Lowe 2006). Other species make diel migrations away from this central refuging area to feed, such as the blacktail reef shark *Carcharhinus amblyrhynchos* (Johnson 1978) and scalloped hammerhead shark *Sphyrna lewini* (Klimley and Nelson 1984). They may make seasonal migrations such as the white shark *Carcharodon carcharias* from a seal colony near shore, where they prey upon pinnipeds, out into the vast expanse of the eastern Pacific Ocean (Weng et al. 2007). They also may make annual migrations like the steelhead *Oncorhynchus mykiss* that swim as miniature smolts from their spawning ground within the Sacramento River to the sea (Sandstrom et al. 2020), migrate northward along the coastal shelf along the western coastline of North America, and return as adults a year later to their spawning site within the river (Teo et al. 2013). Species such as the salmon shark *Lamna ditropis* and mako shark *Isurus oxyrhynchus* migrate from warm summer waters in the Pacific Ocean off the northwestern coast of North America southward along the coast to warmer waters off Central California in the winter (Block et al. 2011). Conversely, basking sharks *Cetorhinus maximus* spend the summer in the warm waters off Cape Cod and move across the equator during the fall to spend the winter in the warm waters off Brazil (Skomal et al. 2009). Finally, itinerant adult female whale sharks *Rhincodon typus* move eastward out into the Equatorial Eastern Pacific, stop briefly at the "bus stop" reef off Darwin in the Galapagos Archipelago, before moving westward into the Humboldt Current off the coast of Peru and again returning to the "bus stop" (Hearn et al. 2016). It is obvious from these examples that fishes exhibit a broad range of movement strategies during their life cycles. Thirteen papers within this Special Issue, using varied and complementary technologies to understand the movement ecology of a variety of marine, anadromous, and freshwater fishes, help build upon this database of knowledge.

Diel movements

Two articles in this Special Issue describe the diel migrations of fishes—the diurnal activity cycles of a large cyprinid in Estonia and the diel changes in the behavior of bonnethead *Sphyrna tiburo* and bull sharks *Carcharhinus leucas* in a Florida estuary.

Compared to many other migratory fishes, the exact movement parameters of migratory cyprinids are poorly known, and population-specific information is especially lacking. To fill this knowledge gap for a northern population of asp *Leuciscus aspius*, a potamodromous piscivore which has disappeared in several fragmented river systems in Europe, Kärgenberg et al. (2022, this issue) tracked adult fish tagged with acoustic transmitters for 32 months in the River Emajõgi in Estonia. Activity levels (i.e., swimming speed, swimming distance, and movement range) were generally higher at dawn and dusk, which may make asp more vulnerable at these times to fishing and removal of water for agriculture. This study also found that annual movement ranges (40–110 km, average ~ 80 km) in this near-natural system were higher than has been reported for this species in the much larger River Elbe (generally < 40 km; Fredrich 2003), highlighting the need for extensive continuous river systems for this cyprinid and the importance of region-specific research on the ecology and behavior of fish populations.

Similarly, Dawdy et al. (2022, this issue) illustrate the importance of assessing site-specific behavior of two mobile shark species in large estuaries, highly productive areas of ecological and economic importance that are susceptible to negative anthropogenic effects. Six bonnetheads and four bull sharks, carrying ultrasonic tags. were tracked by boat in Apalachicola Bay on the northwest coast of Florida, with the longest track being 52 h. Tidal and diel periods were found to have a significant effect on the swimming speed of both species, with increased rates of movement at dusk and dawn. Moreover, mature bonnetheads were found to leave and return to the bay multiple times per day, which may explain their high bycatch rates in the Gulf of Mexico shrimp trawl fishery. This should be considered when making conservation and management decisions for this species.

Seasonal movements

Two papers focus on the seasonal movements of anadromous fishes, striped bass *Morone saxatilis* and green sturgeon *Acipenser medirostris*, in the San Francisco Estuary Watershed, and one paper identified seasonal and vertical movement patterns in a marine species, the bull shark.

Striped bass were introduced into the San Francisco Estuary Watershed in 1879. They are currently the target of a recreational fishery, although the population has been in decline since the 1970s. Le Doux-Bloom et al. (2022, this issue) tagged 99 sub-adult striped bass with coded acoustic transmitters to investigate seasonal movement patterns and habitat use across three regions within the watershed (the bay, delta, and river) over a 2-year period. They demonstrated that some areas were high-density hotspots year-round, while other areas were used seasonally, and that water temperature and salinity affected habitat use. Habitat use also varied with age, with younger sub-adults spending more time in warm limnetic habitats, while older fish were observed in higher salinity habitats. Understanding the seasonal movement patterns and habitat hotspots of striped bass will help inform management decisions.

Thomas et al. (2022, this issue) used acoustic telemetry to investigate movement patterns of juvenile green sturgeon in the San Francisco Bay Estuary after release into an upstream delta habitat. They found support for several movement patterns of individuals monitored over a 9-month period, ranging from juveniles remaining in the upstream delta, moving downstream into several bay habitats, moving downstream and then back upstream, or entering the estuary and likely leaving the system entirely. Such variation in behavioral movement patterns was partly attributed to annual variations in water regimes, which is likely to affect the quality and quantity of suitable habitat for juveniles. Importantly, understanding the diversity of movement patterns of this threatened species can help with conservation efforts to ensure such diversity is maintained in the future.

Lara-Lizardi et al. (2022, this issue) studied the degree of residency of a large population of bull sharks within Cabo Pulmo National Park, a marine protected area located in the southwestern Gulf of California. Monitoring the movement of 32 bull sharks carrying individually coded beacons with an array of stationary autonomous receivers, they found the mean residency index (i.e., the proportion of time spent within the monitored area) to be 0.365. Sharks were present from December to May and absent from August to October. The bull sharks mostly preferred water temperatures below 28 °C and swam in water as shallow as 14 m, although they also moved into deeper waters (70–160 m). In addition to seasonal movement, sexual segregation was observed, probably due to females seeking more productive habitats with more energy-rich prey to sustain the greater cost of bearing young.

General movement patterns

Eight papers investigated the general movement patterns of marine and anadromous fishes (white seabass *Atractoscion nobilis*, white seabream *Diplodus sargus*, three salmonid species, and one lamprey), as well as one freshwater catfish species.

Aalbers et al. (2022, this issue) placed electronic data storage tags, which also recorded swimming depth and water temperature, on 89 white seabass (family Sciaenidae, drums and croakers) along the northern coast of the Baja California Peninsula. Of the tagged fish, 24 were captured after an average of 608 days at liberty, during which time they moved a mean distance of 125 km. Half of the individuals were recovered within 50 km of the tagging location, suggesting seasonal site fidelity to specific geographic areas, while the others moved widely, including one individual that was detected 720 km from its point of release. White seabass spent almost all their time at depths < 60 m (maximum depth 158 m), and they spent the winter months in deeper water than the summer months. Some individuals were shown to move from Mexican waters into the waters off the state of California, indicating the necessity of managing this commercially important species through international agreements (see also "Management and conservation biology" below).

MacNamara et al. (2022, this issue) used a technique to study the long-term movement patterns of hatchery-reared white seabass that complemented the electronic tagging approach of Aalbers et al. (2022, this issue) described above. Fish were implanted with coded wire tags and released as juveniles (91–466 mm total length, TL) either from Santa Catalina Island, a large island off the coast of southern California, or from coastal areas along the Southern California Bight. The majority of fish (88%) released off Santa Catalina Island were recaptured within 22 km of the island up to 7 years after release, while fish released from coastal areas were recaptured for up to 20 years in nearly all areas after moving significantly farther. Those released from southern and northern coastal areas were recaptured an average of 145 and 83 km, respectively, from the point of release, and 27 individuals were recaptured > 200 km away. This study shows that it is important to consider area-specific movement and dispersal dynamics in the management of this marine fish species.

The white seabream (family Sparidae), a littoral species distributed in the eastern Atlantic Ocean and the Mediterranean Sea, is also commercially valuable, particularly in the artisanal and recreational fisheries. Giacalone et al. (2022, this issue) reviewed the current knowledge about the movement ecology of this species, summarizing information from a variety of studies using acoustic telemetry, underwater visual observation, traditional tagging, genetic analysis, and otolith microchemistry. Most studies investigated juvenile and adult habitat use and movement patterns (e.g., dispersal, diel activity, residency, home range), although some studied dispersal during the planktonic larval stage. Their review also identified important information gaps, most notably the need to better understand the effects of environmental variables on movement and better technologies to investigate the movement patterns of juveniles.

Salmon are widely known to exhibit variable and sometimes extensive migrations both as juveniles heading to sea and returning adults homing to their natal stream (McCormick et al. 1998). These migrations have typically been thought to occur over annual or seasonal timescales, although more recent studies have indicated that frequent short-term movement between marine and freshwater habitats can also occur (e.g., Morita et al. 2013). Morita (2022, this issue), using archival tags that recorded temperature and salinity on adult pink salmon *Oncorhynchus gorbuscha* captured as they ascended one of four rivers in northern Japan, likewise demonstrated that many upstream migrants make short-term returns to brackish or salt water. In 14 recaptured fish, the tag records of seven (six of which were male) showed abrupt changes in salinity—two of these seven were recaptured in the same river in which they were tagged and released; four were recaptured in coastal nets; and one was recaptured in another river. Because the tags showed that river temperatures were significantly cooler than those of the coastal waters, the author suggested that these initial—if temporary—freshwater incursions were the result the salmon seeking thermal refugia in cooler riverine habitats.

Alternative life histories are common among fishes, especially when considering migrant and non-migrant life histories of individuals within populations (Jonsson and Jonsson 1993). Many salmonid populations are composed of both migrants and residents, yet research is often conducted on only one of the life histories. In contrast, Futamura et al. (2022, this issue) investigated size-dependent mortality of both migrants and residents of masu salmon *Oncorhynchus masou* during their outmigration using passive integrated transponder (PIT) tags and antennas set up across the Horonai River in northern Japan. Size-dependent survival was observed only for the migrant, where larger individuals were more likely to survive the seaward migration. This was attributed to the presence of large piscivorous fishes, especially non-native brown trout *Salmo trutta*, in the migration corridor, while these predatory fishes do not occur in the upstream stretches occupied by the resident form.

Kuroda and Miyashita (2022, this issue) identified alternative migratory patterns in anadromous white-spotted char *Salvelinus leucomaenis* in southwestern Hokkaido, Japan. They did this by tracking continuous fish movement, making field observations, and conducting recreational angler questionnaires that collectively provided estimates of abundance in coastal and riverine areas throughout the year. As was the case with the Vecchio and Peebles (2022, this issue) study described below (see "Innovative techniques"), the integration of complementary methods provided a more complete understanding of the migratory patterns of this population than any of the methods alone. Of the 28 fish tagged with bio-loggers, only two were recaptured, but they suggested twice-yearly migration between fresh and salt water; these two fish ascended into the river in February, descended to the sea in April, ascended again in June, and descended in October to overwinter at sea. However, the field surveys and angler questionnaires showed that some char were found in both the sea and river during all winter months. Collectively, these observations suggest that, although some individuals migrate twice-yearly, some do not descend to the sea in the fall (thus overwintering in river), and some do not ascend upstream in February.

Lampreys also show life history variations, with some species that are exclusively or almost exclusively anadromous, some that are exclusively freshwater resident, and some—like the European river lamprey *Lampetra fluviatilis*—that are largely anadromous but with established freshwater populations (Docker and Potter 2019). Kucheryavyy et al. (2022, this issue) described a cohort of juvenile European river lamprey outmigrating to the Gulf of Finland from a small lake in Russia that they suggested may be anadromous offspring of a freshwater-resident population. This so-called *lacus* form was larger (148–165 mm) than the usual *flumen* emigrants from the lake (109–137 mm), suggesting longer residency in fresh water before outmigration. Outmigration of the *lacus* form does not occur annually, but it was apparently triggered by extreme flooding in the spring. However, outmigration occurred only at night, indicating that individuals were not merely removed from the substrate involuntarily by the current; rather, it indicates volitional movement into the water column during these periods of high flow, perhaps in response to degradation of environmental conditions in fresh water.

Stream fish communities are often dominated by non-migratory species. However, these species nonetheless still exhibit important movements related to dispersal, recolonization, and recovery of local populations. De Fries et al. (2022, this issue) performed a capture-recapture study to investigate individual movement patterns of the armored catfish *Rineloricaria aequalicuspis* in Brazil. They sampled fish monthly over a 5-month period along a 430-m reach of stream. The catfish exhibited heterogenous movement patterns, which fell into two groups: stationary and mobile. The average distance that fish moved was nearly 100 m, with a maximum observed movement of 248 m downstream and 208 m upstream. The authors concluded that density was the main factor driving their movement patterns. This study highlights the importance of considering movement and variation of movement patterns within populations, even for species often considered non-migratory or of low mobility.

Innovative techniques

Our knowledge of fish movement is often limited by the available technologies, given that it is difficult to see fish underwater and to track them in three-dimensional space. It is also particularly difficult to track small-bodied species and stages. However, the advent of novel methodologies is helping to fill gaps in our understanding of the movement ecology of various species, as shown in three articles in this Special Issue.

Vecchio and Peebles (2022, this issue) demonstrated the usefulness of a novel type of isotopic analysis to study ontogenetic shifts in the habitat and diet of marine fishes, particularly when used together with traditional fisheries records. Large fisheries datasets that contain length frequency estimates, capture depths, and stomach content analyses provide a series of instantaneous "snapshots" of habitat and diet of individual fish from a single ontogenetic stage. However, chemical archives—such as otolith chemistry and stable isotope analyses of fin spines, vertebrae, and eye lens—preserve information from a single individual across all preceding stages. Using $\delta^{13}C$ and $\delta^{15}N$ bulk values for sequential laminae in eye lenses of red grouper *Epinephalus morio* (family Serranidae) captured in the eastern Gulf of Mexico, Vecchio and Peebles (2022, this issue) found that spawning occurred on the mid-to-outer continental shelf each year. The $\delta^{15}N$ values indicated that trophic position increased with size, and this was consistent with the analysis of stomach contents that showed an increase in the proportion of fish in the diet of larger individuals. Collectively, the data suggested that the larvae of most red groupers are transported into nearshore waters where they settle, spend several months in shallow water feeding on benthic prey, and then gradually move offshore toward deeper water where they mature. This study exemplifies how isotopic analysis can help recreate the movement history of fish without having to tag and track them.

Ghosh et al. (2022, this issue) used an isotopic analysis of the otoliths of the hilsa shad *Tenualosa ilisha* (family Clupeidae) to examine the migratory behavior of this anadromous species in the Hooghly River in India, a tidally influenced ecosystem providing nutrient-rich seasonal water for growth and development. Hilsa shad were captured in the upper and lower regions of the river, and otolith $\delta^{13}C$ and $\delta^{18}O$ were determined using an Isotope Ratio Mass Spectrometer. Otolith $\delta^{18}O$ showed significant relationships with fish length and weight, and with distance from the river mouth. This led the authors to infer that smaller individuals inhabit upstream areas near their place or birth; as they grow, they move into the downstream reaches of nearshore coastal waters where adults (4–5 years old) subsequently spend most of their lives in the Bay of Bengal or at the mouth of the estuary. Although most (81%) of individuals could be assigned to either upstream or downstream reaches, some (mostly 1–2 years old) appear to be highly mobile.

Mitamura et al. (2022a, this issue) developed an acoustic zone monitoring technique to quantify fine-scale movements in a narrow water body using only a few acoustic receivers, and they tested its effectiveness by performing stationary and moving tests of transmitters in a river that was ~ 80–100 m wide. Although narrow water bodies require many more receivers than open water to form enough equilateral triangles for hyperbolic localization, this study used only eight acoustic receivers (deployed 100–270 m apart) to arrive at accurate estimates of the position of a transmitter towed by a boat. They further demonstrated the ability of this method to monitor the movement of two tagged channel catfish *Ictalurus punctatus*, which are invasive in Japan. Although the acoustic zone monitoring method assigns a fish to a pre-defined zone—and thus does not monitor movements within a single zone—it will be helpful in identifying, for example, the dominant habitats and general distribution of fishes (including newly invading species) in creeks, canals, and small rivers.

Anthropogenic disturbance

Environmental alterations as a result of anthropogenic disturbances can be ubiquitous across habitat types. The Everglades in Florida is no exception. This region has undergone numerous alterations by humans for over a century, consisting of the use of levees, dikes, and canals for drainage and flood control. Although many studies focus on large fish that are important to commercial and recreational fisheries, Hoch et al. (2022, this issue) explored the effects of canals and levees on the movement of seven small-bodied fish species throughout the year in a seasonally fluctuating marsh in the Everglades National Park. Between 2003 and 2016, the authors used directional traps to measure activity and direction of movement for these species at either canal or levee sites. Unlike levees, canals provide a deep-water refuge site for fish and a means to move to other sections of the Everglades, but they can also lead to aggregations of predators such as wading birds. Hoch et al. (2022, this issue) found that some species (eastern mosquitofish *Gambusia holbrooki*, sailfin molly *Poecilia latipinna*, bluefin killifish *Lucania goodei*, and the non-native African jewelfish *Hemichromis letourneauxi*) used canals during the dry season, possibly as a refuge from droughts, while others (flagfish *Jordanella floridae*, golden topminnow *Fundulus chrysotus*, and marsh killifish *F. confluentus*) did not appear to use canals as a refuge. Monitoring indicator species, such as those described in this paper, can provide valuable insight into possible ways fishes respond to habitat alterations.

Anthropogenic structures at sea can affect the movement of marine fishes as well. Offshore structures such as oil platforms, aquaculture cages, and manmade islands can form so-called artificial reefs that may be beneficial for some species by providing improved feeding and sheltering opportunities, landmarks for navigation, or meeting points for some pelagic and benthic fishes. However, such structures may also have negative effects on the migration of marine fishes, and little is known about their potential impact on migratory demersal flatfishes. Mitamura et al. (2022b, this issue) used biotelemetry to study the effect of an artificial reef created by Kansai International Airport in the shallow waters of Osaka Bay on marbled flounder *Pseudopleuronectes yokohamae*. Marbled flounder is an important commercial species that typically exhibits seasonal migration between shallow water for spawning in winter and deeper water in summer. However, this study showed that approximately one-third of the marbled flounder in Osaka Bay did not exhibit seasonal migration, staying instead in the shallow water around the artificial reef. The authors suggested that the abundant food supply associated with the artificial reef was attractive to these fish, even though the water temperature (26 °C) was high in summer.

Behavior and environmental relationships

Five papers in this Special Issue deal with the relationship between migratory behavior (particularly inter-specific behavior) and environmental factors that trigger movement in a range of taxa: sharks, salmonids, and a damselfish (family Pomacentridae).

Klimley et al. (2022a, this issue) conducted a pilot study using acoustic telemetry to examine the habitat use of a multi-species assemblage of sharks at Roca Partida, a small island (length 100 m) within the Revillagigedo Archipelago. Despite its small size, Roca Partida is highly productive, and it may represent an “oasis” in the open ocean for large marine predators. In this study, individuals of four species, dusky shark *Carcharhinus obscurus*, Galapagos shark *Carcharhinus galapagensis*, silvertip shark *Carcharhinus albimarginatus*, and whitetip reef shark *Traenodon obesus*, were detected at Roca Partida for varying periods over 2.5 years, exhibiting high levels of residency. The authors found evidence for vertical habitat partitioning between species (e.g., Galapagos sharks generally used shallower depths than whitetip reef or silvertip sharks), which may be due to feeding on different prey, as well as horizontal partitioning (i.e., with some sharks staying on only one side of the island). Temporal partitioning may also occur, with differences in the time during which they are most active. This preliminary study suggests that Roca Partida may be an ideal location to study niche partitioning among sharks due to limited habitat availability but high productivity over small spatial scales.

Many fish species form shoals, which are commonly thought to help reduce individual predation risk while increasing foraging efficiency. Although large-scale displacements and migrations often come to mind when considering fish movement, small-scale fish movements may be equally important for survival and fitness. Although shoaling is most often thought of as a single-species behavior, mixed-species shoals are frequently observed but less understood. Paijmans et al. (2022, this issue) used in situ stereo-video techniques to investigate shoal cohesion and individual alignment in mixed- and single-species shoals containing the Indo-Pacific sergeant major damselfish *Abudefduf vaigiensis*. This species is native to tropical north-eastern Australia, but vagrants—transported as juveniles to temperate south-eastern Australia, where they persist for the summer months but die off over winter—have been shown to form both single- and mixed-species shoals with native temperate fishes (Smith et al. 2018). Paijmans et al. (2022, this issue) showed that mixed-species shoals were less aligned than single-species shoals. Interestingly, single-species subgroups were observed within the larger mixed-species groups, demonstrating that multiple levels of social structure may exist within mixed-species shoals.

Fish movement can be triggered by a number of environmental factors (e.g., changes in water temperatures may cause fish to move to a more suitable habitat), and these changes in the external environment can also trigger physiological changes. This can be particularly pronounced in anadromous species migrating between fresh and salt water. Pavlov et al. (2022, this issue) investigated the influence of short- and long-term exposure (3 days and 3 months, respectively) to two water temperatures (13 and 18 °C) on the direction of movement of juvenile rainbow trout *Oncorhynchus mykiss* in flowing water and its concomitant effect on thyroid hormone concentrations. They found that short-term and long-term exposure to cold water led to fish having an equal probability of moving upstream or downstream. These fish also had lower concentrations of free triiodothyronine (T_3) and total T_3 and a higher thyroxine (T_4):T_3 ratio compared to fish in the two warm-water treatments. Conversely, short-term and long-term exposure to warm water was more likely to elicit movement upstream, and the experiments with short-term transfer from 13 to 18 °C and vice versa indicated that the changes were reversible. In summary, increased water temperature appears to stimulate juvenile rainbow trout to leave their location, and this behavior appears to be accompanied by changes in the synthesis of thyroid hormones long before juveniles are ready for downstream migration to the ocean. Because these processes are energetically costly, understanding the response of juvenile salmon to increasing water temperature—as is expected with climate change—is very important.

It has been proposed that the basking shark uses seasonal changes in water temperature as a cue for dispersal from coastal hotspots. However, if such latitudinal movements allow individuals to remain in an optimal thermal range or "thermal envelope" year-round, why do some individuals disperse from coastal areas and others remain? The variation in the timing, direction, and depth of dispersal observed in basking sharks in previous studies (e.g., Doherty et al. 2017) suggests a more nuanced explanation. Johnston et al. (2022, this issue) used data from pop-off archival transmitters attached to basking sharks in Irish waters to show that there was no apparent link between the timing of offshore dispersal and seasonal variation in water temperature. Furthermore, they did not occupy a sustained thermal envelope over time. Individuals appeared to respond to a range of temperatures within both coastal and offshore areas irrespective of latitude. Indeed, two basking sharks that moved offshore and into more southern latitudes off Africa experienced cooler minimum temperatures during the winter than sharks residing off the coasts of Great Britain and Ireland due to the latter's daily cycle of deep dives. Thus, horizontal movements to southerly latitudes alone do not explain the differences in temperature experienced by coastal and offshore basking sharks. This indicates that more extensive studies of the deepwater forays of this species in offshore areas are needed.

In addition to tracking abiotic conditions, marine vertebrates often match their movements to resource availability, particularly where there are ephemeral pulses of productivity. In the Arctic, seasonal ice breakup provides a brief, high-magnitude resource pulse that is exploited by marine consumers, including migratory species. Anadromous Arctic char *Salvelinus alpinus* migrate into marine waters presumably to take advantage of these short-lived feeding opportunities. However, it is unknown whether entry occurs prior to or at the start of marine ice breakup is unclear, although it has important consequences for char fitness. Thus, Hammer et al. (2022, this issue) tagged 34 Arctic char with acoustic telemetry transmitters within Tremblay Sound, Nunavut, Canada, between July and September in two successive years (2017 and 2018). All tagged fish entered the marine environment the following year before the coastal ice-off date, an average of 6 days before in 2018 and 11 days before in 2019. Further movement metrics (residency indices and mean latitudes of home ranges) revealed that char used much of Tremblay Sound before the ice-off date. This indicates that they were well positioned to feed in the system prior to the resource pulse. Such resource tracking will be important in the rapidly warming high Arctic.

Predictive models

Models have great value in predicting outcomes, especially when they are based on assumptions with strong empirical support. Three papers within this volume illustrate the value of this approach to providing valuable guidance in resource management.

The use of electronic tags in combination with fixed-station receiver arrays is useful for mark-recapture studies of fish populations because they can determine a recapture rate of tagged fish without having to physically capture the fish. A range of statistical techniques have been developed to analyze these detection records to address a number of scientific questions (Whoriskey et al. 2019). Among them, spatial Cormack-Jolly-Seber models are used to calculate the rates of survival of tagged fish, given the detection probabilities at receivers (e.g., Michel et al. 2013; Sandstrom et al. 2020). However, these models assume characteristics of movement and detection, assumptions that are not always met by electronic tagging studies, especially those involving acoustic telemetry technology. Fischer et al. (2022, this issue) tested underlying assumptions by simulating detection histories in a riverine environment using two types of movements, one based on movement around activity centers and another using stepwise movement with detections based on proximity to a receiver. They incorporated different life histories and movement patterns into their model as well as four receiver spacings. The purpose of doing this was to determine how study design influenced model performance. When the movements were stepwise, convergence was low for all parameters and variability between activity centers was biased positively. If individuals were undetected for several time steps, the estimates of activity centers drifted to the separated areas in receiver arrays. Minimizing receiver spacing likely improves reliability of activity center estimates when stepwise movement behavior is expected.

Another model, a correlated random walk, was used by Lilly et al. (2022, this issue) to provide insight into how Atlantic salmon *Salmo salar* migrate through Loch Lomond, the largest lake in Scotland. They applied a random walk model to detections of tagged smolts released into the River Endrick, which drains into Loch Lomond, with a stationary array of receivers located within the lake. Consistent with other studies (e.g., Jepsen et al. 1998; Aarestrup et al. 1999), they found a high rate of smolt mortality in the lake, at least partially attributable to predation by birds and northern pike *Esox lucius*. The smolts migrated slowly through the lake, and there was no particular behavioral trait or migratory pathway that distinguished successful from unsuccessful smolts, leading the authors to conclude that movement through Loch Lomond is random. However, there was a distinctive difference in the behavior of successful smolts once they came within ~ 2 km of the exit from the lake; they stayed momentarily in this region before entering the River Leven, the outlet to Loch Lomond, suggesting that they perceive the outflowing current to aid in migration to sea. Future studies comparing the movements of fish to random walk models, and identifying which environmental variables underly the movement patterns exhibited by smolts in lakes, would be valuable. Such studies would be even more definitive if the smolt movements were monitored continuously by a fixed array of VPS monitors (e.g., Steel et al. 2013), rather than intermittently by spaced monitors.

Dodrill et al. (2022, this issue) applied continuous time multistate Markov models to examine the influence of (1) tidal and riverine hydraulics; (2) behavioral factors; and (3) management actions on the route choice of Chinook salmon *Oncorhynchus tshawytscha* smolts through a network of branching channels in the Sacramento–San Joaquin River Delta to the sea. Several key junctions enable smolts to swim along more direct paths to the ocean, while others route them towards the interior Delta, a region previously associated with decreased survival (e.g., Perry et al. 2013). Using a model that incorporates more information from acoustic telemetry compared with previous approaches, these authors showed that increasing net flows generally increased movement rates, while flood tides decreased movement rates, and ebb tides enhanced downstream movement. They also demonstrated that a barrier installed to decrease entrainment into the interior Delta was indeed effective. Understanding factors that help route smolts to a more direct route to the ocean (e.g., away from pumping structures and other infrastructure) has important management applications.

Simulation testing is a powerful tool to assess the outcomes of various plausible behavioral scenarios. Poulet et al. (2022, this issue) developed the HoOS (Hasty or Omniscient Shad) simulator to assess how upstream migration and spawn timings in relation to temperature influence the survival of early-life stages of allis shad *Alosa alosa*. In their simulator, two reproductive strategies were evaluated: “omniscient” fish synchronize their spawning with optimal temperatures for offspring survival, while "hasty" fish spawn immediately upon arrival to the spawning grounds. The early-stage survival rate (up to 14 days post-hatch) was calculated for each of the two reproductive periods using a range of adult migratory speeds upstream and physiological constraints to spawning by adults. The authors showed a dome-shaped relationship between temperature-dependent survival of early-life stages and adult migration timing, and that a good match of spawning activity with optimal thermal conditions was particularly important for early-arriving adults.

Management and conservation biology

Virtually all of the articles within this Special Issue have provided insights that can help inform management decisions, but we highlight three below that have even more direct application to management.

The ability of fish to migrate up a river is often facilitated by the construction of fish-bypass channels, but it is essential to monitor how effective such fish passage structures are**.** Epple et al. (2022, this issue) evaluated the ability of four salmonid species (brown trout, rainbow trout, grayling *Thymallus thymallus*, and Danube salmon *Hucho hucho*) to migrate upriver through five fish-bypass channels in a sub-alpine stream in southern Germany. Using daily fish counts within pools from April 2017 to December 2019, they used general linear models to determine whether any of 14 abiotic environmental factors affected the success and speed of migration through the bypass channels. They found pronounced differences among species and between adults and juveniles of the same species. For example, although the rates of grayling and Danube salmon upstream migration were strongly correlated with water temperature and day length, the rate of ascent of rainbow trout was much less correlated with environmental factors. Therefore, even for closely related species, it is important to consider migration behavior in response to environmental conditions at the species and stage level rather than extrapolating among and within species.

Understanding fish movement in relation to seasonally flooded habitats is essential for the effective management of fish stocks in the Amazonian River basin. Many floodplain fishes, like giant arapaima (genus *Arapaima*), migrate in the rainy season laterally into seasonally flooded habitats to feed and reproduce. Gurdak et al. (2022, this issue) used ultrasonic telemetry to understand the home range, dispersal, and migration behavior of arapaima across two fishing communities. Arapaima were tagged in three discrete lakes during the dry season, and they were monitored over two annual flood cycles; the entire area is interconnected when inundated during flooding. No tagged arapaima were found outside their lake of origin during successive dry seasons, but they were detected moving between the three lakes during rising and high-water periods, and three arapaima were found outside their community management units during high water. Thus, home range expands and contracts with the flood season, and the authors suggested that site fidelity to lakes likely decreases the chance that arapaima will be stranded in shallower areas during the dry season. Community-based management efforts, with regulation of fishing activities within community zones, are helping to recover arapaima populations, but management could be improved by creating larger or collaborative management units that encompass the complete life histories of arapaima.

Klimley et al. (2022b, this issue) reviewed a compilation of published shark telemetry studies—and complemented by some new data—that have led to the expansion of marine protected areas (MPAs) in the Eastern Pacific Ocean. In addition, they presented evidence that fishing effort by commercial vessels carrying satellite-communicating radio beacons that monitor their locations decreased within the expanded MPA boundaries. The summarized research described the movement ecology of nine shark species at islands in the Tropical Eastern Pacific (e.g., the Galapagos Islands off Ecuador, Malpelo Island off Colombia, Cocos Island off Costa Rica, and Revillagigedo Islands), using two main telemetric techniques: 1) placing coded ultrasonic beacons on individuals and detecting their presence with stand-alone receivers deployed along the coasts of the islands; and 2) outfitting individuals with SPOT and PSAT satellite transmitters. It is exciting to see how the results from these studies have directly informed conservation and management decisions, allowing resource managers to match the size of their marine reserves to the spatial ecologies of the species within them. For example, such studies have led to the government of Mexico creating Revillagigedo National Park, the largest no-take area in the Northern Hemisphere; they have also prompted Colombia to increase the size of the Malpelo Fauna and Flora Sanctuary, and provided support for expanding the boundaries of Cocos Island National Park. Satellite tracking of sharks outside the current boundaries of the Galapagos Marine Reserve likewise supports the need to increase the size of the protected area at the archipelago.

Concluding comments

In this Special Issue, we have presented the results of a diversity of studies conducted on the movement ecology of fishes. The subjects of the articles have ranged from freshwater fishes such as the asp and arapaima; anadromous species such as the European river lamprey, green sturgeon, striped bass, shads, and various salmonids; and marine fishes such as the white seabass and reef, hammerhead, and basking sharks. Studies have focused not only on the behavior and ecology of adults, but also that of juveniles such as salmon smolts. The geographic localities of the studies have covered five continents North and South America, Europe, Asia, and Australia/Oceania. Many of the papers focus on conservation issues such as the effects on the movement of fishes through bypass channels in river streams, the ability of salmon smolts to move between rivers or reach the sea, the degree of fidelity to lakes where individuals are resident during the dry season but leave during the wet season, and the matching of marine reserve sizes to encompass the movements of the species within them.

We hope that this collection of articles will stimulate young investigators to further study the movement ecology of fishes, using new techniques as they become available to the scientific community. These techniques can vary from electronic tags, to new predictive models, to molecular identification of species and the use of isotopes in understanding feeding and trophic ecology. The field of movement ecology has blossomed in recent years, and we believe that it will provide many more important insights into the biology of fishes in the future.

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