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Marine Fish Passage—Underappreciated Threats to Connectivity Within the Marine Environment

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ABSTRACT

Habitat fragmentation is a major threat to aquatic biodiversity loss. However, much of the focus is on the connectivity of freshwaters, with much less attention given to marine ecosystems. We contend that coastal infrastructure including bridges, causeways, tidal turbines, land infilling and harbours, wharfs, quays, piers and docks have resulted in underappreciated impacts on the connectivity of fish movements resulting in passage challenges at sea. For each type of marine infrastructure, we synthesised the present status of knowledge to characterise the problems and future challenges and also identify mitigation options and passage solutions to restore connectivity for fishes. Bridges can disrupt currents, generate light and noise/vibration, and emit electromagnetic signals, so more work is needed to modify in-water designs to minimise the negative impacts on fishes. Causeways involve infilling, resulting in full in-water barriers, requiring fishes to circumnavigate these structures and there is limited research on mitigation (e.g., fishways). Tidal turbines are placed in areas with high currents, which can hinder movements and result in entrainment; however, monitoring fish movements is challenging in these unique areas. Offshore energy has grown in recent years and can impact fish connectivity via altered sediment dynamics and water currents, as well as through the generation of noise pollution and electromagnetic fields. Land filling results not only in habitat loss but also in fragmentation, and it will be imperative to identify important habitats and corridors to minimise impacts there. Finally, infrastructure associated with boats (e.g., harbours, docks) negatively impacts nearshore habitat, which can alter movement trajectories. In the collective, we found evidence that diverse types of marine infrastructure can impact connectivity and, ultimately, fish movement and migrations. Interestingly, bespoke fish passage solutions in marine environments seem rare. As coastal development will increase in the future, it is imperative that we assess the potential connectivity issues resulting from marine infrastructure and that we generate solutions to mitigate these issues for marine organisms.

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1 | Introduction

Habitat is a key element of ecology, viewed as the template upon which species adapt and evolve, and where individuals gather and expend energy (Jonsson et al. 2011). Habitat is dynamic, because successional processes sculpt the physical, chemical and biological aspects of the landscape across time, and in response to periodic disturbances (Roxburgh, Shea, and Wilson 2004). Fragmentation of habitat has become a major feature of an increasingly human-dominated world, an effect where habitat is fractured into smaller pieces and connectivity is lost or degraded to the detriment of biodiversity (Wilcove 1986; Fahrig 2003). Highly visible examples of habitat fragmentation have emerged from terrestrial landscapes where connectivity is severed by linear features such as roads, railways or pipelines (Wilson et al. 2016). Fragmentation is of particular concern to migratory animals if essential migratory corridors that connect habitats needed for different life stages or activities are impeded (Cooke et al. 2024). Some of the classic examples of such impacts arise in rivers where dams can block fish movement leading to collapse of populations or even extirpation of some species (Deinet et al. 2020).

Fish passage science has emerged at the nexus of biology and engineering to better understand where vulnerabilities exist for fish encountering barriers to connectivity in freshwater (Silva et al. 2018). Despite being an imperfect science, fish passage research has been an important field with actionable gains yielded from cooperation among industry, management and science/engineering (e.g., Stuart et al. 2024). Although fish passage is considered largely a freshwater conservation and sustainability challenge (Wohl 2017; Table 2), there are important examples in the marine environment that merit further consideration. Barriers to fish passage in the sea may be a surprising concept, because connectivity should be a ubiquitous feature of the marine environment. Yet, coastal ecosystems (and offshore areas) are increasingly wrought with structures that materially change the environment and can alter free passage of animals at a seascape scale because of behavioural, physiological or environmental responses that affect the animals. The scope of the problem is not well understood; the closest facsimiles of fish passage literature from the marine environment may be habitat fragmentation indices; yet, Yeager et al. (2020) noted that marine ecosystems had largely been overlooked when considering fragmentation, citing the review by Fahrig (2003) having <10% of examples coming from marine environments.

Unencumbered passage of animals in the marine realm is underappreciated and underdeveloped as a distinct research theme of marine ecology. Marine ecosystems are vast such that it is presumed fishes, mammals, turtles and other creatures can simply avoid any barriers by swimming around them. Yet, many marine species are necessarily limited to shallow, nearshore areas, and when those movement corridors are interrupted, there can be major negative consequences for fish populations (e.g., pushing fishes into suboptimal habitats, altering access to food and increasing predation risk). Not surprisingly, the preponderance (and growing abundance) of marine infrastructure is creating challenges to connectivity for marine animals that have not yet been thoroughly addressed by science or engineering, particularly from the perspective of fish passage. Marine biodiversity is

highest in the nearshore zones where the impacts of human development are most pronounced (Costello and Chaudhary 2017); therefore, we submit that connectivity and fish passage challenges in the marine realm predominantly related to coastal infrastructure around estuaries, fjords, sounds, bays and harbours must have effective fish passage consideration to maintain connectivity. In this paper, we synthesise literature on marine structures and evidence for how these structures can affect fish passage, and, to wit, connectivity between marine realms. This paper is a narrative and not a systematic review, given the sparsity of published or grey literature we could locate. Moreover, in some instances, the evidence base was so small that we had to rely largely on the experience of the authors to contemplate potential impacts. Collectively, this paper should provide information on the scale of the problem and reveal potential solutions that can improve conditions encountered by fishes and other marine animals encountering barriers.

2 | Marine Connectivity

Humans have been adding infrastructure to seascapes for hundreds of years (Coles et al. 2005; and possibly for much longer), oftentimes, with little thought on the negative impacts on aquatic animal movement. Six main types of marine infrastructure were identified that can alter connectivity of the marine environment, which are conceptually similar to fragmentation in terrestrial and freshwater ecosystems, where animal passage is more thoroughly studied. The selected impacts on the marine environment include bridges, causeways, tidal turbines, offshore energy, land filling and infrastructure associated with boats (e.g., harbours, wharfs, quays, piers and docks). For each type of marine infrastructure, we synthesise the present status to characterise the problem and identify future challenges to generate mitigation options, passage solutions to restore connectivity (summarised in Table 1), as well as impacts on these infrastructure types on connectivity.

2.1 | Bridges

2.1.1 | Present Status

Bridges are major conduits for terrestrial connectivity, linking islands or spanning bays or fjords to shortcut across marine areas (Figure 1A). All readers will be familiar with bridges, but there are many different shapes, sizes and forms for bridges across marine areas, which generate different footprints in the marine environment. Bridges across bays, fjords and sounds allow water to pass beneath but pilings will affect water currents and mixing of salt around the piles. Stigebrandt (1992), however, estimated the effects of a new bridge construction on the mixing of water masses in the Baltic Sea, suggesting small alterations and minimal need for compensatory engineering. Pilings that disrupt flow and exchange of water mass along with pollution from noise, light and chemicals from roads can present a migration barrier that restricts the movement of migrating fishes in some cases and merits further discussion.

Mechanisms by which bridges may reduce marine connectivity include disruption of tidal currents and generation of light,

TABLE 1 | Summary of the present status and future challenges of marine infrastructures on connectivity of fishes, with potential passage solutions.

Marine infrastructure	Present status	Future challenges	Passage solutions
Bridges	<ul style="list-style-type: none"> Alter tidal currents, light, noise or electromagnetic signals Increased mortality Potential ecological traps 	<ul style="list-style-type: none"> Assess environmental impact (e.g., eddies and noise) in-water of pilings Address shortcomings of current designs 	<ul style="list-style-type: none"> Modify designs to minimise connectivity disruptions Modify lighting (e.g., narrow spectrum) or seasonal operation
Causeways	<ul style="list-style-type: none"> Infilling of marine environment creates in-water barrier Circumnavigation to get around causeways 	<ul style="list-style-type: none"> More research needed on the impact of causeways on hydrology, tidal patterns and larval patterns 	<ul style="list-style-type: none"> Removal or retrofitting of causeways Mitigation of environmental impacts to removal
Tidal turbines	<ul style="list-style-type: none"> Occur in restricted areas where currents are forced through narrow channels Fish collisions resulting in injuries and mortality <ul style="list-style-type: none"> Displacement or disruption of migratory routes 	<ul style="list-style-type: none"> Optimise monitoring of impacts with methods such as high-resolution acoustic imaging or acoustic telemetry <ul style="list-style-type: none"> Identify sites where operation results in minimal impacts 	<ul style="list-style-type: none"> Behavioural guidance to attract or repel animals using sensory cues <ul style="list-style-type: none"> Periodic shutdowns during migrations could mitigate impacts
Offshore energy	<ul style="list-style-type: none"> Bottom-anchored farms are restricted to shallow areas and alter the seabed <ul style="list-style-type: none"> Floating farms are installed in deeper waters <ul style="list-style-type: none"> Both can impact and generate noise pollution and electromagnetic fields, as well as alter sediment and water currents 	<ul style="list-style-type: none"> Unknown impacts of floating wind farms on migration corridors <ul style="list-style-type: none"> Need for baseline data on migration and migratory cues Assesses avoidance of offshore energy platforms for potentially impacted species 	<ul style="list-style-type: none"> Installation of physical barriers or non-physical deterrents to limit access to organisms Construction of passage corridors through farms to increase connectivity
Infilling	<ul style="list-style-type: none"> Direct loss of habitat Direct barriers as well as hydrological regime change <ul style="list-style-type: none"> Alteration of sedimentation processes 	<ul style="list-style-type: none"> Increasing demand for infilling for urbanization and agriculture 	<ul style="list-style-type: none"> Habitat compensation to offset losses Fish passage structures
Harbours, wharfs, quays, piers and docks	<ul style="list-style-type: none"> Modification of nearshore habitats Decreased habitat quantity and quality 	<ul style="list-style-type: none"> Fortification of infrastructure to climate change 	<ul style="list-style-type: none"> Knowledge of habitat requirements to inform design <ul style="list-style-type: none"> How to minimize footprint of design



FIGURE 1 | Types of infrastructure that impact marine connectivity of fishes, including (A) bridges: structures that allow for the passage of vehicles or pedestrians over a body of water, (B) causeways: embankments built across a body of water to create a land connection, (C) tidal turbines: devices that harness the energy of tidal currents to generate electricity, (D) offshore energy: collection of wind turbines that are located in the ocean, (E) infilling: the creation of new land by depositing material into a body of water and (F) harbours, wharfs, quays, piers and docks: structures built along the coast to provide access for boats and ships.

noise and electromagnetic signals. Few evaluations of bridges on the movement of animals have been published. However, bridges floating on pontoons seem to be hotspots for the mortality of migrating salmon smolts moving from their home rivers out of coastal areas towards the open ocean (USA: Moore and Berejikian 2022; Norway: Vollset et al. 2024). Extensive experiments conducted in the State of Washington have identified high mortality of juvenile salmonids around a floating pontoon bridge and implicated several potential factors including the noise and vibrations around the structure (Zang et al. 2023). In California, bridges produced areas of high magnetic anomaly, although Chinook salmon (*Oncorhynchus tshawytscha*) smolts were apparently unaffected in their migration past the structure's magnetic fields (Klimley, Wyman, and Kavet 2017). Other migratory species such as eel, lamprey, sturgeon, mackerel, herrings and codfishes might succumb to high predation around bridges if they form ecological traps where predators conceal themselves. In Florida, bridges are apparently hotspots for predation of migrating tarpon (*Megalops atlanticus*) by sharks like hammerheads (*Sphyrnidae* spp.) that use the cuts around bridges as refuge or ambush sites (Casselberry et al. 2024). Although recreational fishers report frequent incidents of predation by sharks while fishing for tarpon around bridges, it is not well established what role the bridge itself plays or if the phenomenon

is more related to the oceanography independent of the structure. One contributing factor to bridges facilitating predation is the creation of extensive shaded areas where predators can hide; Helfman (1981) showed a visual advantage to predators sitting in shade and observing targets swimming in the light. Artificial light at night produced on the bridge may be a factor aggregating predators or confusing migrating fishes, which tend to be active during nighttime, but we have not identified any studies that clearly test this for bridges in marine ecosystems. Nevertheless, alterations to flow around bridges could provide refuge to predatory fishes that can hide and use the tidal streams to feed on baitfish or juveniles.

2.1.2 | Future Challenges

Many of the most important and tractable locations for bridges have already been developed, so the rate of new major bridge projects is not particularly fast (Petroski 1998). Bridges tend to be built at the narrowest points or where it is sufficiently shallow so that pilings can easily be installed, so bridges may be associated with some oceanographic features that may increase the likelihood that the structure interacts with some unique or challenging habitat, as speculated above for the case of tarpon

TABLE 2 | Passage solutions for marine infrastructure drawing from freshwater examples.

Type of marine infrastructure	Example of freshwater passage solution	Considerations for marine applications	Example of successful application in freshwater	References
Bridges	Bridge design	<ul style="list-style-type: none"> Incorporate permeable decking, open-bottom designs or wider setbacks to minimize disruptions to connectivity 	Grid mesh was used for both fishways and culvert crossing in southeastern Australia to allow for light penetration through the infrastructure	Cotterell (1998); Jones and Hale (2020)
Causeways	Rock fishways	<ul style="list-style-type: none"> Fishways could be constructed at areas with natural hydrological flow to allow movement of organisms Include design aspects to be nature like to mimic environmental including gradual slope, variable flow velocities and natural substrates 	The Sandy Creek rock fishway was installed in Queensland, Australia, to permitting successful passage of multiple fish species over a causeway	Stuart et al. (2024)
Tidal turbines	Non-physical barriers	<ul style="list-style-type: none"> Non-physical barriers include those based on sensory capabilities Examples include bubble curtains, strobe lights, electric and carbon dioxide 	Bubble barriers were installed at Ume River to guide Atlantic salmon away from a hydropower plant and turbines, with a high degree of effectiveness (90%)	Leander et al. (2021)
Offshore wind	Floating Infrastructure	<ul style="list-style-type: none"> No freshwater examples for wind turbines; however, floating turbines moored to the seafloor could minimize barriers to connectivity Burying of inter-array cables could minimize barriers within the water column 	N/A	Maxwell et al. (2022)
Infilling	Bypass Channel	<ul style="list-style-type: none"> Installation of channels between water bodies to permit hydrologic flow and connectivity of organisms 	Bypasses were constructed to guide Atlantic salmon around the Herting dam in Sweden with passage efficiencies of 70%–95%	Nyqvist et al. (2018)
Harbours, wharfs, quays, piers and docks	Floating Infrastructure	<ul style="list-style-type: none"> Avoiding traditional fixed infrastructure can minimize physical barriers and reduction of habitat loss 	Slips within Toronto Harbour, Canada, were made to overhang from land rather than be fixed. There were also habitat enhancement efforts for fish	Veilleux et al. (2018)

predation in Casselberry et al. (2024). Engineering challenges will include considering how bridge supports, whether pilings or pontoons affect currents and eddies and whether noise or light pollution from the bridge exceeds thresholds that might affect animals swimming beneath (Davies et al. 2014; e.g. in freshwater Vega et al. 2024; Table 2). New materials and lighting systems and an explicit focus on the form and function of bridges when it comes to effective fish passage will be important to ensuring that bridges do not negatively impact connectivity between marine habitats.

2.1.3 | Passage Solutions

We do not know what kinds of bridges are easy or difficult for fishes to pass under. More interdisciplinary work is needed between biologists and engineers to identify the mechanisms of when, where, why and especially how bridges yield disconnection in the marine environment. There are questions as to whether the waters where bridges are likely to be built, often narrow areas, may already be challenging areas for migratory species or whether the anthropogenic factors that could be subject to mitigation, such as the introduction of physical structure and altered acoustics and lightscapes, are creating novel conditions that exacerbate mortality. Floating pontoon bridges have been evaluated in the Pacific Northwest (Moore and Berejikian 2022) and in Norway (Vollset et al. 2024) and flagged as likely impediments to marine migration. Bridge lighting could consider using narrower spectrum lighting to reduce impacts on animals, such as amber filters, that reduce blue light from white LEDs (e.g., Gaston and Sánchez de Miguel 2022). Seasonal modifications in illumination regimes might be considered to deluminate the water during some important migrations. Most bridges will not have any retrofitting possibilities to facilitate passage and the issue may have to be taken on a case-by-case basis depending on the specific species and connectivity questions involved.

2.2 | Causeways

2.2.1 | Present Status

Unlike bridges, causeways involve infilling of the environment to create a platform for a road between landmasses (Figure 1B; Gerwing et al. 2019) and are constructed to enhance transportation through coastal areas such as estuaries. Highly damaging to connectivity, causeways seem to be relatively uncommon in the marine environment, with a few highly visible examples. Alterations to the ecological community along a 500–700-year-old rock causeway connecting to an island at Nan Madol, Federated States of Micronesia, were recorded by Coles et al. (2005). More modern causeways connecting islands in Florida, USA (Florida Keys), Singapore to Malaysia (Johor–Singapore Causeway), Saudi Arabia to Bahrain (King Fahd Causeway) and mainland Nova Scotia to Cape Breton Island (Canso Causeway; see Box 1; Lott 2022) are notable examples. Although many modern causeways contain sections of bridges, there has been a significant amount of land reclamation and infilling in each instance. In addition to directly blocking the movement of organisms, these structures also impact the

dynamics of water, nutrients, sediments and plant propagules (Hood 2004; Reimer et al. 2015; Van Proosdij et al. 2009; Vilks, Schafer, and Walker 1975). Just like for bridges, it is also possible for light, noise and vibrations associated with causeways to interfere with fish movement. Such impacts could be indirect (e.g., those changes in ecosystem pressures alter the distribution of prey items, thus altering fish behaviour) or direct (i.e., light may deter fishes). Finally, it is likely that causeways increase human access to previously inaccessible coastal areas, and as a result, opportunities for recreational angling will increase (see Harris 1988) along with pollution and the settlement of invasive species.

2.2.2 | Future Challenges

The infilling associated with causeways causes oceanographic disruptions that alter the region in extensive and complicated ways, and the impacts on larval transport and tidal patterns cannot be reverted with canals alone. Infilling will be discussed below in more detail, but the rock infilling used to establish a causeway creates a local ‘artificial reef’ effect that may increase biodiversity in tracts of the seascape that would normally be inhabited by a few benthic or pelagic specialists. Removal of causeways can destroy established sessile communities that settle following establishment of the structure, which may be a complicating factor for seeking approvals. There has not been much research into causeways because they are relatively uncommon compared to bridges, which is a limitation that may need to be addressed in order to stimulate the necessary action towards addressing fish passage issues.

2.2.3 | Passage Solutions

One of the major future challenges to marine causeways is the need for removal (e.g., Gerwing et al. 2017) or retrofitting for fish passage (Marsden and Stuart 2019). Because causeways physically alter the marine environment so dramatically, they can severely alter the oceanographic and biological movements between marine areas. The removal of these barriers will hugely impact local conditions and can cause new changes to fish populations, in ways we do not yet fully understand. Some evidence has shown that the removal of causeways can improve water quality and the fish community (Gerwing et al. 2019). Although the addition of bridge sections or culverts within a causeway is a partial solution to fish movements, we have discussed above the ways in which bridges also impair marine connectivity. Additionally, as evidenced by the Canso Causeway case study (Box 1), integrated canals are not enough to mitigate the impacts on marine animals.

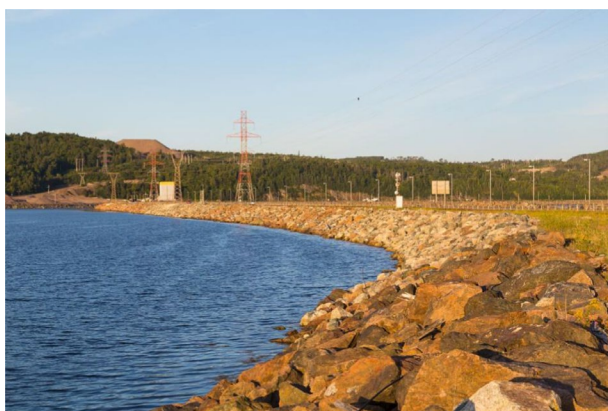
2.3 | Tidal Turbines

2.3.1 | Present Status

In-stream tidal power devices generate power via a turbine being turned by currents in tidal currents (Figure 1C). A variety of designs exist, including surface or bottom-mounted and horizontal or vertical-axis turbines. Interactions with tidal stream

BOX 1 | The Canso Causeway connects mainland Nova Scotia and Cape Breton, formerly an island. The causeway completely filled in the Strait of Canso, altering oceanographic regimes and severing biological connectivity between the Gulf of St. Lawrence and Atlantic Ocean.

In Cape Breton, Canada, the Canso Causeway was completed in 1955, connecting the island of Cape Breton to mainland Nova Scotia. Although only 1.4 km across, a rockfill causeway was selected in response to the strong currents and high seasonal ice cover in the Strait of Canso. Although favourable operationally to the overwhelmed ferries in the region, this causeway has severed marine connectivity in the Canso Strait except for a small canal for vessel passage. In the years following the completion of the Canso Causeway, the eastern end of the Strait of Canso remained ice-free as a result of hugely changed tidal regimes. This change impacts fishing pressure on ice-free areas and has increased industrialization (O'Halloran 2018). Migrating fishes like striped bass (pictured below), unless able to navigate the canal (which only opens briefly a few times a day for vessel passage), are now required to circumnavigate the entirety of Cape Breton island to enter and exit the Gulf of St. Lawrence. The changes to the tidal regimes disrupted larval transport of commercially important American lobster, causing shifts in species distributions and a reduction in recruitment (Dadswell 1979), and often traps schools of fishes such as Atlantic saury (*Scomberesox saurus*), allowing for high predation levels each fall (Penney et al., *in prep*). Herring fisheries in the region collapsed, and fishers blamed the Causeway for this disruption (Messieh and Moore 1979; O'Halloran 2018). Other fish migrations that are likely impacted by the Canso Causeway include the Atlantic salmon (*Salmo salar*) and American eel (*Anguilla rostrata*). Using the Canso causeway as a case study, it is clear that causeways are wholly disruptive marine barriers with far-reaching impacts. The addition of a canal for vessel passage did little to mitigate the impacts on the connectivity of the Strait of Canso and impacted taxa span beyond bony fishes.



energy are similar in concept to interactions with hydropower in rivers, with the key differences being that tidal power devices are generally deployed singly or in arrays of individual devices. As such, in-stream devices do not physically block passage the same way that dams or tidal barrage devices do. However, tidal stream energy development typically occurs in spatially restricted areas such as the Minas Passage in the Bay of Fundy (Karsten et al. 2008) or the flows between the Orkney Islands in Scotland (Murray and Gallejo 2017) where tidal currents are forced through narrow channels. In areas such as the Minas Passage, these channels may represent the only migratory pathway between the ocean and essential reproductive or foraging habitats for a variety of marine and diadromous fish species (Dadswell and Rulifson 2021). Depending on design, collision with turbines resulting in injury or even mortality is considered to be the greatest risk to fish populations around tidal turbines (see Dadswell et al. 2018), although displacement of distribution or migratory routes and interactions with electromagnetic fields are also possible (Copping et al. 2021). Indeed, electromagnetic fields emanating from the subsea cables transferring power from the generating site to stations onshore are believed to present a challenge to the many animals that use magnetic cues for navigation (Klimley et al. 2021). The probability of a fish collision can be thought of as a hierarchical continuum

from the fishes co-occurring with a device in space and time to a lethal direct collision with a turbine blade, and is influenced by fish behaviour, environmental conditions and device characteristics (Copping et al. 2023). Encounter and collision rates have traditionally been calculated using models adapted from predator-prey encounter risk analyses (Wilson et al. 2007), although these models require data on fish behaviour and population levels that may not be available or possible to collect at a local level. A variety of methods can be used for monitoring fish presence and behaviour around tidal power devices including acoustic telemetry, optical cameras and high-resolution sonar, but the effectiveness of each method will be strongly affected by local environmental and hydrodynamic conditions (Sparling et al. 2020).

2.3.2 | Future Challenges

Hydrokinetic turbines in coastal and estuarine environments are becoming increasingly common to harness tidal energy as a 'green' alternative to fossil fuels, and with that, numerous challenges for marine life and environmental decision makers are emerging. There are opportunities to install non-physical barriers, based on sensory capabilities (e.g., bubble curtains, electricity,

strobe lights, or carbon dioxide), at turbine sites (see Leander et al. 2021 for usage at hydropower turbines). This solution would not only minimize the risk of injury or mortality but also guide organisms around the infrastructure, thereby mitigating barriers to connectivity caused by the turbines (Table 2). Traditionally, monitoring for interactions between animals and tidal power devices has occurred at the device location using static methods of biodiversity observation. Optical cameras and high-resolution sonar can provide visual data on fish presence in the vicinity of a device (Sparling et al. 2020). However, cameras are limited by visibility in the surrounding water, so their effectiveness declines rapidly in low-light or turbid conditions (Joslin, Polagye, and Parker-Stetter 2014). High-resolution acoustic imaging is not limited by light levels, but the current resolutions available are insufficient to identify smaller, less-distinctively shaped fishes to the species level and acoustic noise created by turbulent water can further limit monitoring efficiency (Cotter and Staines 2023). Both methods are also demanding on data analysis resources from both personnel and computing perspectives, and can also be taxing on data storage resources (Viehman and Zydlewski 2015). Identifying the costs, in addition to the benefits, of specific sites for turbines to be located and operating schedules that minimise potential interaction with animals may be keys to reducing impacts of marine turbines on the connectivity.

2.3.3 | Passage Solutions

Tidal streams can offer a free ride to animals that wish to move while conserving energy, and species like eels may use tidal stream transport as part of their mobility strategy (Deveau 2022). For other hydrokinetic turbines like those in rivers, fishways or ladders are used to circumvent the structure for upstream and downstream passages around the turbine. However, facsimiles in the ocean are not feasible because of the open landscape on the bottom of the sea. Behavioural guidance has been used for a variety of species to attract or repel species towards safety (Noatch and Suski 2012). Sturgeon, a benthic species considered to be at risk of entrainment in tidal turbines, is equally a species of concern at riverine hydrokinetic turbines, and there is a rich literature on the use of lights and other sensory cues for guiding sturgeon away from turbines in rivers (Cooke et al. 2020a; Cooke et al. 2020b). There may be opportunities to integrate behavioural guidance to facilitate passage of animals around hydrokinetic tidal turbines, but there is much work to do to understand how effective such approaches can be and how species-specific some interventions are. Additionally, in high flow areas where some animals use tidal stream transport, periodic shutdowns during migratory seasons may be necessary, but where animals can avoid the turbine areas, behavioural guidance tools may be tested to mitigate potential interactions.

2.4 | Offshore Energy

2.4.1 | Present Status

Over the past 20 years, the development of offshore energy has seen substantial growth, particularly in offshore wind, transforming it from a hopeful technology to a component

of the global renewable energy landscape (Breton and Moe 2009; Figure 1D). This expansion is driven by technological advancements, increased investments and supportive governmental policies aimed at reducing carbon emissions and climate change mitigation. Currently, offshore wind farms are operational in many parts of the world, with most facilities installed in Europe, Asia and North America (Díaz and Soares 2020). Offshore wind farms are categorised mainly into two types based on the foundation technology used: bottom-anchored and floating wind farms (Wu et al. 2019). The choice between the two depends on water depth, seabed conditions, environmental impact and economic considerations. Bottom-anchored wind farms are effective in shallow waters, whereas floating wind farms expand the geographical scope for offshore wind into deeper water where installation of pilings is challenging. This rapid increase in offshore wind farms raises connectivity concerns, particularly regarding their impact on marine ecosystems (Gill 2005). The construction and operation of these installations can directly affect fishes by noise pollution (Wahlberg and Westerberg 2005), generating electromagnetic fields (Gill, Bartlett, and Thomsen 2012), novel sediment transport patterns (Davis, VanBlaricom, and Dayton 1982) and altered water currents through the farm. Indirect effects include habitat fragmentation and changes in food availability that lead to altered predator-prey dynamics. The potential effects of offshore wind farms on marine life have been frequently addressed during the planning process through environmental impact assessments, as required in most countries. However, comprehensive empirical studies on the effects of large-scale offshore wind farms remain scarce (Lindeboom et al. 2011). The population- and community-level effects of massive installations of new infrastructure in the offshore zone are not well understood, because existing studies have focused on micro- or mesocosm experiments that do not necessarily scale to understand how large-scale installations will influence resident and migratory species at an ocean basin or seascape scale.

2.4.2 | Future Challenges

The wind industry is projected to grow in the coming decades, driven by the increasing global demand for renewable energy, technological advancements and supportive policy frameworks in nations transitioning away from fossil fuels (Esteban et al. 2011). The footprint of the industry on the ocean is therefore likely to rapidly expand (Wu et al. 2019), and this is concerning because how important it is for migrating animals to stay away from large-scale offshore wind is not yet known. In particular, the offshore floating wind turbines hold significant potential for expansion because they are not limited by the need to have a shallow seabed for anchoring the platforms. We still know very little about how dense, sprawling windfarms spanning tens of thousands of square kilometres will impact seascape water circulation and the cues used by animals to migrate. Migration corridors with thousands of turbines installed or thousands of square kilometres of permanent shadow cast by floating wind farms are still beyond our understanding. There is a need for better baseline data for understudied species, especially those that rely on magnetic cues for navigation such as turtles, salmonids, and eels, which will have to transit across

dense areas of electromagnetic fields generated by wind farms at an unprecedented scale. The establishment of novel animal communities living around farms in the open ocean will likely attract fishing and predators such as sharks and seals, which have been demonstrated to use offshore platforms as foraging hotspots (Russell et al. 2014). Cumulative impact assessments will probably become increasingly important as more than one wind farm project may occur within the home range of a population (Bailey, Brookes, and Thompson 2014). Fish avoidance of an offshore wind farm is perhaps a more likely scenario than direct mortality, but there is uncertainty due to a lack of research. Therefore, greater emphasis should be placed on assessing large-scale migratory behaviour of animals at the seascape scale and investigating the long-term behavioural responses, including changes in energetic costs, survival and fecundity, associated with delays or impacts of migrating through or around offshore wind installations.

2.4.3 | Passage Solutions

Animals that have to pass through offshore energy platforms to reach feeding or breeding grounds may be delayed or confused, and may never make it out of an extensive wind farm if they enter the maze of gridded platforms. Confusing currents, electromagnetic fields or dense predator aggregations may make farm sites quite challenging for animals such as salmon smolt, herring, or mackerel to pass through. If it is perceived that offshore energy sites pose significant threats to the connectivity of the ocean for animals moving between critical habitats, physical barriers may have to be installed to limit entry into the farm by animals that could become entrained into the maze, or non-physical deterrents may have to be established to guide animals along the outskirts. Tapering the edge of the farms so that they can guide animals moving north–south may be an option to facilitate passage around and reduce entrainment in the concession area. Establishing dedicated corridors through the middle of farms or limiting the allowable area of farms so that there are safe passageways between sites could be considered, but given how little we still know about the drivers of offshore movements by migratory ocean animals, it is uncertain how this will work and it is logistically challenging to test it at scale.

2.5 | Infilling

2.5.1 | Present Status

Land infilling is the process of depositing soil, rocks or other materials into bodies of water with the goals of creating new land or expanding existing areas to benefit human use (Figure 1E). Despite directly modifying aquatic habitats, this practice is heralded as a solution to increasing societal demand for various necessities including city expansion (e.g., Hong Kong, China), industrial use (e.g., port expansion in Singapore), agriculture (e.g., saline agriculture in Bangladesh) and infrastructure associated with flood mitigation (e.g., levees in New Orleans, USA; Wang et al. 2014). In addition to the permanent removal of habitat (e.g., loss of spawning sites), land infilling negatively impacts marine ecosystems through

degradation, which can impair the health and fitness of organisms (Shen et al. 2016). Habitat loss caused by infilling can also result in indirect and adverse effects on connectivity by impeding movement of organisms between different habitat types. For example, in the Curonian lagoon (Lithuania/Russia), land reclamation and diking within the delta for agricultural purposes resulted in decreased connectivity of many intersecting rivers, ultimately impeding movements of multiple fishes through migration corridors to spawning habitats (Breber, Povilanskas, and Armaitienė 2008). Fragmentation from land infilling not only stems from direct barriers to fish movement but can also impede passage in ways other than physical barriers (e.g., causeways). Through land filling, hydrological regimes can be disrupted, whereby the volume of water transported in waterways (e.g., streams or channels) is reduced, indirectly decreasing marine connectivity and impeding access to fish movement (Wilson et al. 2017). Natural sediment transport can also be negatively impacted by land infilling in that sedimentation can increase to a point of blocking waterways. For example, land infilling in Bangladesh to create agricultural islands (i.e., polder systems) has resulted in complete blockage of waterways (Wilson et al. 2017). Hypoxia can be induced by infilling as currents and water mixing are altered, which can also indirectly increase fragmentation as fishes avoid hypoxic areas (Karim, Sekine, and Ukita 2003). Taken together, these decreases in connectivity are concerning because impacts include increases in isolation and crowding, reduced habitat (e.g., spawning sites) and the use of suboptimal environments that are stressful for animals and slow growth or maturation of animals living in these environments (Jeffrey et al. 2015). Marine fragmentation can therefore lead to impaired growth and altered metabolic rates that can have population-level implications.

2.5.2 | Future Challenges

Looking to the future, land infilling is likely to remain a threat to marine connectivity and fish movement. As human populations are projected to continue to increase, there will be more and more demands for housing, infrastructure and industrial activities, leading cities to look to infilling for additional land area (Sengupta et al. 2023). Dangerously, coastal areas that provide habitat for fishes will likely remain important areas for development due to their proximity to waterways. For example, infrastructure that may require more land could include airports, ports and industrial areas (Horner and Nadvi 2018). An additional source of pressure for land infilling due to growing populations will be the need to produce enough food through agriculture. For example, the shortage of grain in China prompted land infilling on tidal flats for the establishment of new agriculture (Wang et al. 2014). There will be increasing pressure to meet the societal needs for land, and unfortunately, land infilling can accommodate growing populations, economic opportunities and food security. Another factor that could contribute to an increased reliance on land infilling in the future is global climate change. Because many cities have been built on low lying coastal areas, the increase in sea levels and storm strength/frequency will likely require additional mitigation efforts. This has already started in Rotterdam, The Netherlands, where the ‘Massvlakte 2’ project has aimed to mitigate against

climate change by creating elevated areas to act as buffers against storms and flooding via land infilling (see <https://www.portofrotterdam.com/en/building-port/ongoing-projects/maasvlakte-2>).

2.5.3 | Passage Solutions

As land infilling will likely continue to impede fish movement in the marine environment, mitigation efforts will be required to minimise associated impacts. First, it will be important to identify the remaining and intact fish movement corridors to protect these areas from development including land infilling. In areas that have already suffered from habitat loss and/or fragmentation via infilling, habitat compensation will be required (i.e., the creation of new habitat), although this can be difficult to execute in practice (Quigley and Harper 2006). Wise land-use planning could also play an important role in mitigating against future land infilling projects by making smarter decisions about new developments by using pre-existing (and previously developed) land. Similar to other threats to marine connectivity, fish passage structures could also be implemented in cases where land infilling has blocked access to habitats (e.g., spawning sites; Stuart et al. 2024). Although fishways are more commonly associated with other anthropogenic activities (e.g., hydropower dams), a fishway has been constructed at a highway created through land infilling in the Netherlands (see <https://theafsluitdijk.com/projects/fishmigrationriver/why/>) after the highway directly blocked fish migrating from the ocean to riverine spawning sites and the Fish Migration River was designed to enable passage.

2.6 | Harbours, Wharfs, Quays, Piers and Docks

2.6.1 | Present Status

One of the primary forms of human development in estuaries and coastal environments is infrastructure associated with boats, including various forms of harbours, wharves, quays, piers and docks (Bulleri and Chapman 2010; Figure 1F). Harbours are constructed at scales ranging from small recreational facilities and fishing harbours to massive shipping terminals and naval bases. These docking facilities can take many forms and often include various quays for offloading or breakwaters to protect infrastructures from wave energy (e.g., groynes or revetments). Concrete is a common construction material for retaining walls although sometimes steel sheet pile is used to replace natural shoreline and fortify areas against wave energy (see Cooke et al. 2020a; Cooke et al. 2020b). In addition to concrete quays and wharves used for docking (historically, these were made of wood and rock), other dock structures may include those that float or are suspended above the water using concrete, wood or steel pilings. Piers are constructed in some coastal areas to provide access to deeper water, usually for recreation such as fishing or for ferry use. All of these aforementioned structures require modification of nearshore habitats, leading to changes in ecosystem structure and function. The footprint from infilled areas represents a loss of habitat, and given that estuarine and coastal environments serve as swimways for aquatic animal movement (Worthington et al. 2022), any modification to those habitats has the potential to impact connectivity by

altering movement trajectories either via direct interaction with the modified shoreline or by altering currents or wave hydraulics. Additionally, once in a harbour, it is possible for animals to become behaviourally entrained if they are unable to locate an exit. Gahagan, Fox, and Secor (2015) tracked striped bass in the vicinity of the Hudson River Estuary and documented that some fishes were functionally resident in the New York Harbour. The overhead structures installed in coastal areas such as floating docks and elevated piers will affect the free passage of animals. Barilotti, White, and Lowe (2020) revealed that some fishes were attracted to piers and were resident for long periods despite being migratory species. The reasons for that residency were unclear and could be a result of overhead cover or food availability (including provisioning from anglers). In a study in the lower Hudson River, New York, USA, Able, Manderson, and Studholme (1998) reported that the abundance and species richness of fishes were typically low under piers relative to pile field and open-water stations where abundance and species richness were comparatively high. The authors concluded that habitat quality under large piers (> 20,000 m²) is generally poor and largely unsuitable for early life stages of fishes. In a study in the Pacific Northwest (Munsch et al. 2014), fish species assemblages at modified sites with piers differed from those at reference sites. At sites with piers, the distribution of fishes and assemblage structure varied with proximity to the shade cast by piers, where fish abundance, including juvenile Pacific salmon, was lower under piers. The authors concluded that piers may interrupt movements of juvenile salmon given that they tend to avoid shade cast by piers (Munsch et al. 2014), but they may also generate a landscape of fear because predators tend to hide under these structures.

2.6.2 | Future Challenges

Human coastal development will undoubtedly continue, and in doing so, we anticipate further potential for infrastructure described here to have negative impacts on marine fishes. It is important to note that the evidence base on this topic is relatively small with almost all of the research on the topic conducted in North America. Coastal development is occurring around the globe such that there is a need to understand how such developments impact marine fishes in all regions. With climate change, there are efforts to reinforce the existing infrastructure to ensure it is able to withstand more intense storms and sea level rise (Toimil et al. 2020). In that regard, we anticipate more efforts to try to 'engineer' structures rather than to rely on more natural approaches (Becker et al. 2011; Nazarnia et al. 2020). Of course, backing off from coastal areas would be logical but is rarely considered given the need/desire for coastal infrastructure that allows humans to interact directly with coastal systems. Such efforts are laudable, and we anticipate the need for cost-benefit analysis, human dimension studies and other studies to inform future discussions about sustainable and responsible coastal development.

2.6.3 | Passage Solutions

Assuming human development related to harbours, wharves, quays, piers and docks will continue, there are a number of

opportunities for conservation gains related to fish connectivity and passage. First and foremost, knowledge of the habitat requirements and space use of fishes across life stages and locations (i.e., for migratory fishes) is essential for designing infrastructure that mitigates impacts on fishes. However, even in the absence of such knowledge (which is the norm), there are some general opportunities for improvement. First is the need to minimise footprint impacts such that there are no losses in habitat areas associated with such infrastructure. That may involve the use of piled (elevated) structures rather than conventional in-filled structures that are typically lined with concrete or steel. Similarly, there is opportunity to revisit the actual configuration of retaining wall structures to include more structural complexity (Chapman and Underwood 2011). For example, biologically inspired designs are being developed that emulate mangrove prop roots and create usable fish habitat that may facilitate more unencumbered passage (Kazemi et al. 2018). When infrastructure is installed, there should also be efforts to minimise lighting or use light types that are evaluated to be minimally disruptive to fishes. Similarly, efforts to limit noise and boat traffic during key periods of the year when fishes are engaged in important life-history activities would be beneficial. The physical configuration of infrastructure should be implemented in a way that does not create confusing hydraulic cues for fishes and creates various pathways for entry and egress. In some cases, coastal engineering can improve connectivity for fishes as was observed in a study of bonefish (*Albula vulpes*) movement in the Bahamas, where a canal was used by fishes as a ‘shortcut’ to key spawning sites (Murchie et al. 2015); in this case, there was a serendipitous outcome but with careful planning, such opportunities could be realised elsewhere. On the basis of the evidences that shading from piers can impact fish migration and that larger piers can create habitat deserts underneath, the use of smaller piers or those that allow more light to pass (i.e., grated) would seem to be desirable (Munsch et al. 2014). Any required dredging or other maintenance/construction of coastal infrastructure outlined here should be done according to best practices that minimise noise, vibration, silt and general fish disturbance (e.g., use of construction timing windows; Wenger et al. 2018). Finally, as efforts are underway to future-proof coastal infrastructure and ensure it is able to withstand climate change-related pressures, there is a need to consider the role of green infrastructure and nature-based solutions to complement the ‘grey’ (aka-engineered) infrastructure that has become the norm (Kuwaie and Crooks 2021). Doing so has a great potential to improve habitat and the fishes that depend upon it.

3 | Discussion

We set out to better understand how fish passage has been considered in the marine environment, and to contrast the knowledge base with what has emerged from freshwater systems where fish passage is a ubiquitous topic. Several seminal reviews of fish passage and connectivity in the freshwater realm have been provided (e.g., Silva et al. 2018; Hershey 2021). However, contemplation of fish passage in the marine environment has heretofore not been fully elaborated upon. We found evidence that a variety of different activities in the marine environment can affect fish passage and that such installations should fall under the purview of municipal planners, federal fishery management

agencies and port authorities to consider the role of approved marine structures in fish passage as animals depend on the ability to move freely as part of both daily activities and specialised movements like migration. Indeed, legislation around the world that protects the free passage of fishes in freshwater can and should be applied to protect marine connectivity against deterioration due to human installations, such as the European Union Water Framework Directive, the Fisheries Act in Canada and the Endangered Species Act in the USA.

This review focused predominantly on fish passage, which implies a focus on migratory species and their ability to effectively use their environment for the full suite of activities necessary to complete the life history (Secor 2015). Marine migrations include amphidromous species such as eels, salmonids, shad and many sharks that use estuaries as nurseries; there are also highly migratory oceanadromous species, such as tunas, large sharks, tarpon and trevallies, that move across ocean basins. Marine infrastructure that overlaps with areas used by marine species evidently can affect connectivity among habitats for these iconic species in ways that may necessitate consideration of fish passage in the ocean. Migration is an essential ecosystem service, as animals connect distant habitats with their movements across boundaries, shunting nutrients and energy between oligotrophic and eutrophic habitats with seasonal cycles of productivity (Cooke et al. 2024).

There are some emerging threats to connectivity in the marine environment that we did not explicitly consider in our review, but are notable and emphasise the scale at which connectivity in the ocean is declining as a result of human activities (Lott 2022). For example, we did not explicitly consider secondary impacts of human infrastructure on marine connectivity, but there is evidence that marine noise could alter settlement patterns of coral reef larvae. Connectivity between reef habitats can therefore be altered where noise affects the ability for larvae to settle (Simpson et al. 2004). Noise may also create a barrier for whales (Weilgart 2007) or for fishes that are displaced by noisy areas of high human use; for example, Filous et al. (2017) found that marine fishes were repelled from a marine reserve in Hawaii during hours of high human use. In coastal areas, hydropower structures in rivers can alter flows in estuaries and at sea, which alter the drift patterns of propagules such as the eggs of Atlantic cod, whose passage to developmental grounds at sea can be disturbed by altered flow created by human activity (Myksvoll et al. 2014). Construction of the Canso Causeway (Box 1) is also thought to have severed larval connectivity for American lobster between the Gulf of St. Lawrence and the Atlantic Ocean (Dadswell 1979). Although there is a strong understanding of the importance of connectivity, there are clearly many examples of how connectivity is being lost in the ocean that require more attention and new research.

Fish passage in freshwater is predominantly related to physical barriers that affect the capacity for animals to move from one area to the next (Hershey 2021). We found that barriers to fish passage in the marine environment included physical features, as well as other, more physiological and behavioural impacts on animals (e.g., avoidance of hypoxic areas). Activities such as landfilling and structures such as bridges that span across marine areas can eliminate marine areas that were historically navigated by animals, with a prominent example being the Canso Causeway in Nova Scotia, where a key migratory route

for Atlantic salmon, American eel, Atlantic bluefin tuna and many other species has been completely eliminated between the Gulf of St. Lawrence and the Atlantic Ocean (Box 1). Research on the Hood Canal Bridge in the State of Washington has also been seminal in identifying the connectivity challenges emanating from the installation of bridges (Moore, Berejikian, and Tezak 2013; Moore and Berejikian 2022). More research seems to be needed to understand how shading from structures, perhaps combined with artificial light pollution from the structures, alters passage success for fishes through marine areas as well as the impact of noise and vibration from structures on the physiology and behaviour of fishes moving through marine habitats.

An exacerbating factor for marine infrastructure on fish passage seems to be impacts related to predation around structures or baffles. Casselberry et al. (2024) described high recreational angling pressure around a bridge that coincided with extensive post-release predation on tarpon, the target species, by sharks. Many human infrastructures in the marine environment provide shelter to ambush predators, and bridges, docks, wharves or causeways may generate novel habitat for predators to increase their success targeting passing fishes. Research has shown how overhead structures like docks, which are completely unnatural in the marine environment, offer shelter that benefits ambush predators' ability to see passing animals (Helfman 1981). Moreover, noise from ships or vibrations of bridges may conceal predators from their prey, facilitating attack. Particularly for acoustic animals like Atlantic cod, artificial noise in coastal environments may be a key inhibitor of fish passage, and more research is needed to understand how noise could affect fish passage success through marine habitats.

Humans have an outsized impact on ecosystems, and although the marine environment is vast and the connectivity seems limitless, there are key considerations for engineers and biologists to investigate fish passage in the ocean. Given developments in tracking aquatic species at sea, there are opportunities to use those and other tools for assessing the impacts of marine infrastructure on fish passage, particularly in coastal and estuarine systems. However, there should be increasing focus on testing mitigations as well, similar to what has been done for dams and other barriers in rivers that affect freshwater fish passage. This review has identified several priority areas for research that could direct new questions relevant to the ecology of marine fishes and forge new partnerships between biology and engineering disciplines to enhance the sustainability of marine infrastructure and development and improve marine habitat.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

No data are used in this article.

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