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Aquatic connectivity: challenges and solutions in a changing climate

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Abstract

The challenge of managing aquatic connectivity in a changing climate is exacerbated in the presence of additional anthropogenic stressors, social factors, and economic drivers. Here we discuss these issues in the context of structural and functional connectivity for aquatic biodiversity, specifically fish, in both the freshwater and marine realms. We posit that adaptive management strategies that consider shifting baselines and the socio-ecological implications of climate change will be required to achieve management objectives. The role of renewable energy expansion, particularly hydropower, is critically examined for its impact on connectivity. We advocate for strategic spatial

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planning that incorporates nature-positive solutions, ensuring climate mitigation efforts are harmonized with biodiversity conservation. We underscore the urgency of integrating robust scientific modelling with stakeholder values to define clear, adaptive management objectives. Finally, we call for innovative monitoring and predictive decision-making tools to navigate the uncertainties inherent in a changing climate, with the goal of ensuring the resilience and sustainability of aquatic ecosystems.

KEYWORDS
biodiversity conservation, climate change, ecosystem resilience, fish passage, migration, spatial planning

1 | INTRODUCTION

Aquatic ecosystems comprise most of the global biosphere, but aquatic biodiversity is disproportionately in decline (Barbarossa et al., 2021; Hodapp et al., 2023). Both freshwater and marine ecosystems consist of an extensive series of interconnected biomes and environmental gradients. The resilience of aquatic populations to disturbance depends greatly on the extent to which aquatic ecosystems are interconnected (Thieme et al., 2023; Timpane-Padgham et al., 2017; Young et al., 2018). Maintaining connectivity between and within aquatic ecosystems is therefore essential to sustaining and restoring aquatic life globally.

Connectivity – the flow of energy, materials, and organisms across space and time – in aquatic ecosystems is multidimensional (Ward, 1989) and may be structural or functional (Tischendorf & Fahrig, 2000), but the importance of different dimensions (longitudinal, lateral, vertical, temporal) of structural and functional connectivity varies between freshwater and marine environments. Structural connectivity is the physical attributes of sea- or riverscapes that describe the contiguity or continuity of the physical environment (Auffret et al., 2015; Kindlmann & Burel, 2008; Tischendorf & Fahrig, 2000). Functional connectivity is organism-orientated and describes biological and behavioral responses (from genes to populations) to the physical environment (Kindlmann & Burel, 2008; LaPoint et al., 2015; Tischendorf & Fahrig, 2000). Depending on a species' natural history and capacity for adaptation, structural fragmentation may not impact functional connectivity (Bradbury et al., 2009). Human alterations to sea- and riverscapes disrupt structural connectivity and inevitably affect the ability of some species to carry out critical aspects of their life history, particularly in dendritic river networks (Fagan, 2002). For instance, the presence of hydropower infrastructure may significantly delay or hinder fish migration due to fish behavior (Piper et al., 2015). Even when a fishway is installed, fish may choose not to pass through it due to their instinct to follow the main flow (Coutant & Whitney, 2000).

Loss of structural and functional connectivity is a major contributor to observed declines in aquatic biodiversity, particularly for fully or partially migratory species (Dunn et al., 2019; Silva et al., 2018). Many of the world's rivers are highly fragmented by constructed barriers that impede or prevent the movement of aquatic organisms (Belletti et al., 2020; Franklin et al., 2022; Grill et al., 2019; Jones et al., 2019). Impassable barriers impose direct effects on the abundance and persistence of migratory fishes, as they are excluded from the critical habitats required to complete their life cycles (Thieme et al., 2023). For example, both Nislow et al. (2011) and Perkin and Gido (2012) demonstrated that fish communities upstream of barriers at road crossings were characterized by lower species richness and reduced total abundance. Similarly, Sor et al. (2023) reported that fish diversity was reduced by the presence of hydropower dams in the Lower Mekong Basin. Globally, instream barriers account for approximately half of the decline observed in freshwater migratory fishes between 1976 and 2016 (WWF, 2022). In marine environments, although breaks in structural and functional connectivity are less apparent, oceanic features such as upwellings and currents can act as barriers to structural and functional connectivity. For example, Lett et al. (2023) identified several of these barriers to structural and functional connectivity along the coast of South Africa. On a phylogeographic scale, factors like tectonic processes, deglaciation events, and shifting sea levels can determine the genetic connectivity and, consequently, functional connectivity of coastal ecosystems (Parvizi et al., 2022).

Protecting and restoring aquatic connectivity is recognized as a vital action for enhancing species' resilience and reversing declines in aquatic biodiversity (Beger et al., 2022; Thieme et al., 2023; Tickner et al., 2020; Virtanen et al., 2020). Removing physical impediments to dispersal (i.e., improving structural connectivity) has become a key focus of efforts to restore freshwater biodiversity. Construction of fishways and partial or complete removal of barriers can lead to rapid and significant improvements in the abundance and diversity of upstream fish communities (Birnie-Gauvin et al., 2017; Ding et al., 2019) and other aquatic species (Benson et al., 2018). Importantly, the restoration of structural connectivity must be guided by knowledge of functional connectivity to avoid unintentional ecological traps (Pelicice & Agostinho, 2008; Pelicice et al., 2015) while also considering risks associated with unwanted species dispersal (Rahel, 2013; Rahel & McLaughlin, 2018). Likewise, marine spatial planning is advancing to more effectively integrate both structural and functional connectivity (Balbar & Metaxas, 2019; Magris et al., 2014). For instance, marine protected area networks are being designed to explicitly address metapopulation structure and gene flow to ensure the sustainability of protected populations (Weeks, 2017), with these approaches now extended to cross-realm conservation planning (Hermoso et al., 2021).

Human-induced stressors such as the construction of physical barriers are well understood to alter structural and functional connectivity in aquatic ecosystems. While it is easiest to conceive connectivity as a singular threat, the consequences of obstructed movement or inadequate protection become greatly amplified by cumulative effects across space and time (Branco et al., 2016; Carr et al., 2017; Göthe et al., 2019). Since the industrial revolution, increasing greenhouse gas emissions have affected the Earth's temperature regimes, precipitation, wind, and other climate factors to profoundly influence river flows, ocean currents, demand for fresh water, and water quality (O'Reilly et al., 2003). Mounting environmental pressures (i.e., multiple stressors) from climate change impose considerable challenges to fishes already impacted by habitat fragmentation (Bao et al., 2023; Dean et al., 2023; Roberts et al., 2017).

Vulnerable species need to physiologically adapt to changing climate conditions, move to new habitats if possible, or risk extirpation (Andrello et al., 2015; Bice et al., 2023; Crook et al., 2015; Rahel et al., 2008). Experience has shown that conservation plans must be written in consideration of dynamic factors associated with connectivity and climate change, for example changing resource demands, local and regional climate velocity (i.e., pace of climate change), robustness to extreme events, and how increasing temperatures will render conditions favorable to the spread of aquatic invasive species (Bao et al., 2023; Carr et al., 2017; Keeley et al., 2018; Radinger & García-Berthou, 2020; Rahel, 2013; Smith et al., 2023). Although connectivity is crucial for resilient aquatic communities, the associated cumulative effects of climate change add complexity and unknown outcomes that must be addressed to effectively future-proof management plans.

Evaluating how aquatic connectivity and climate change will concomitantly affect fishes is now widely recognized as an essential part of conservation planning and management in both freshwater and marine systems (Beger et al., 2022; Magris et al., 2014; Pittock et al., 2008). While a general approach has been established (e.g., adaptive, integrated, short- and long-term indicators, monitoring, regular oversight and review), in practice the exercise is complicated by short-termism, shifting baselines, status quo bias, political agendas, and uncertainty (Di Bartolomeo et al., 2023; Samuelson & Zeckhauser, 1988). Here, we review how a changing climate has, and is predicted to, alter structural and functional connectivity for fishes across aquatic ecosystems. We then address the challenges of taking a forward-looking approach to managing aquatic connectivity for fishes and strategies to maintain and restore connectivity in a changing climate. Our aim is to synthesize the available research, current practices, and tools for conservation planning at the nexus of aquatic connectivity and climate change. Our goal is to equip resource managers and practitioners with the knowledge to future-proof actions that protect and restore aquatic connectivity, conserve species, and maintain biodiversity in a changing climate.

2 | HOW WILL A CHANGING CLIMATE IMPACT AQUATIC CONNECTIVITY?

To predict the direct and indirect effects of climate change on aquatic connectivity, it is first necessary to characterize how climate will impact fish movements between habitats (Figure 1). Climate-induced changes to the physical linkages of habitat patches will limit where fishes can travel (structural connectivity), while changes in resource availability and species interactions will alter the ability and requirements to access such patches (functional connectivity; Tischendorf and Fahrig, 2000).

2.1 | Structural connectivity

Changes in structural connectivity in aquatic environments will arise both as a direct consequence of climate change modifying the physical environment in aquatic ecosystems, and indirectly through society's actions to mitigate and adapt to a changing climate.

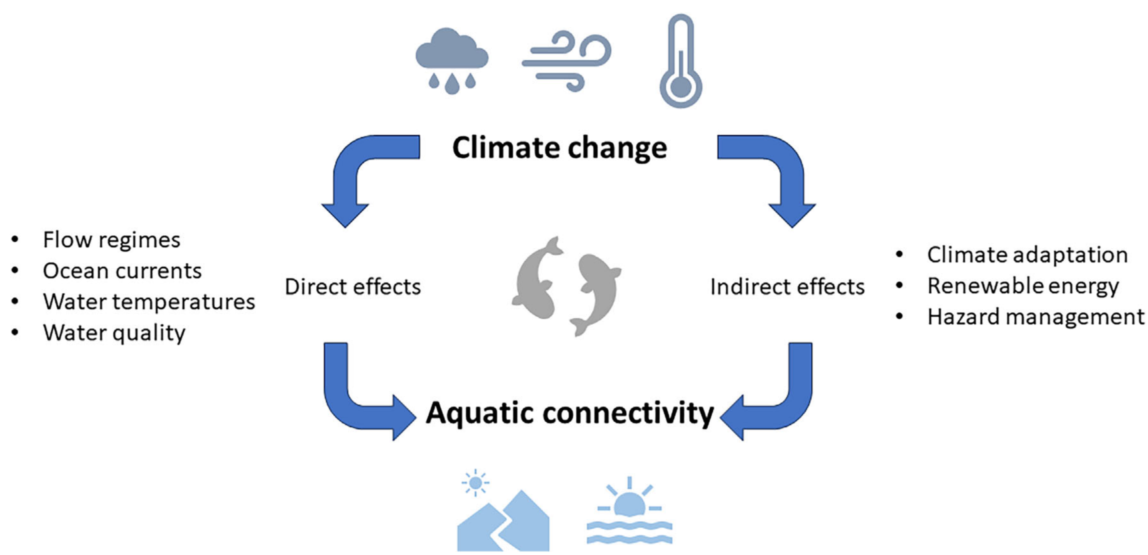

FIGURE 1 Conceptualization of some of the direct and indirect effects of climate change on connectivity in aquatic ecosystems.

2.1.1 | Direct impacts

Climate change is driving shifts in the magnitude, frequency, intensity, and timing of the precipitation, temperature regimes, and wind patterns (Meehl et al., 2000; Stott, 2016) that influence structural connectivity in aquatic ecosystems. For example, flow regimes in rivers and streams are naturally variable, many with large seasonal variations across the year, and with interannual differences in peak flow magnitudes (Poff et al., 1997; Sofi et al., 2020). Ecological communities are adapted to that natural range of flow variability, with key life-history stages dependent on and cued to the occurrence of specific flows (Mims & Olden, 2012; Naiman et al., 2008; Poff et al., 1997). Human alteration of flow regimes, e.g. through the construction of dams, has already been shown to reduce longitudinal, lateral, and vertical connectivity (Palmer & Ruhi, 2019; Thieme et al., 2023). Similarly, climate change is now driving changes in flow regimes, even in minimally disturbed systems, with the timing of peak flows being altered and flow magnitudes changing due to altered precipitation and snow cover, for example (Chalise et al., 2021; Schneider et al., 2013). This may exacerbate the structural disconnect by reducing the inundation frequency of lateral floodplain habitats or increasing the length and duration that river sections are dry and/or intermittent (Datry et al., 2017; Malish et al., 2023). Conversely, increased precipitation in some areas may result in more frequent connections with floodplain habitats, with associated risks of fish becoming stranded (Nagrodski et al., 2012).

In marine environments, structural connectivity and dispersal patterns of marine species, particularly early life stages, are shaped by wind patterns, resulting ocean currents, and features such as eddies and fronts (Wilson et al., 2016). Future climate change scenarios indicate that altered wind patterns will substantially affect the intensity and path of surface currents as well as the position of ocean fronts (Franco et al., 2017; Sorte, 2013). Such a scenario changes connectivity by strengthening, weakening, and modifying the structure and functioning of larval dispersal and migration pathways (Wilson et al., 2016), inducing potential range shifts, and resulting in the redistribution of marine communities (Pecl et al., 2017). Weakening of ocean currents may dampen and/or create new barriers to dispersal (Keith et al., 2011), whereas stronger currents accelerate connectivity of pelagic larvae via faster transport (e.g., western boundary currents in the Southern Ocean; van Gennip et al., 2017).

Climate change is expected to impact physical, chemical, and biological properties of aquatic environments, further amplifying the drivers of water quality degradation (IPCC, 2022). In fresh waters, predicted increases in the magnitude and frequency of floods in some areas may lead to elevated sedimentation and pollution loads, increasing mobilization of contaminants and pathogens (Mishra et al., 2021; Whitehead et al., 2009). Low-flow episodes and droughts are expected to become more prevalent in many regions during summer, increasing contaminant concentrations, toxic algal blooms, and oxygen depletion (Mishra et al., 2021; Mosley, 2015; van Vliet & Zwolsman, 2008). Elevated water temperature will affect chemical reactions and bacteriological processes, with subsequent physiological effects for fish (Schiedek et al., 2007; Whitehead et al., 2009). In marine environments, rising temperatures, acidification, and reduced salinity and oxygen content lead to further deterioration of water quality (Brierley & Kingsford, 2009; Williamson & Guinder, 2021). Altered ocean circulation patterns coupled with increasing temperatures and thermal stratification may reduce subsurface dissolved oxygen levels (Keeling et al., 2010). Oxygen minimum zones, areas of oxygen-deficient waters, have expanded in recent decades and are likely to affect structural connectivity as they form a respiratory barrier to the vertical and horizontal movements of many pelagic and benthic species (Dewitte et al., 2021; Wishner et al., 1995). All this creates unsuitable conditions for a variety of aquatic species and impedes fish movements, with responses varying from avoidance to physiological reactions and direct mortalities (Solomon & Sambrook, 2004; Stramma et al., 2012; Townhill et al., 2017). Interactions between water quality properties can give rise to synergistic effects on aquatic biota in both realms (IPCC, 2022). The challenge will be to disentangle these complex cumulative impacts, especially as climate change will interplay with other stressors across different spatial and temporal scales (Cloern et al., 2016; Lin et al., 2021; Michalak, 2016).

2.1.2 | Indirect impacts

In addition to the direct effects of climate change on the structural connectivity of aquatic habitats, actions to mitigate human impacts on the climate (e.g., the transition to renewable energy sources) and climate adaptation strategies (i.e., responses to the impacts of climate change on society) have the capacity to alter aquatic connectivity.

Pursuit of net zero goals has led to a proliferation of renewable energy development (Greaves et al., 2022; Zarfl et al., 2015). The rapid expansion of offshore wind farms (OWFs) has the potential to alter localized and regional marine hydrodynamics, particularly in seasonally stratified regions such as the North Sea. Beyond impacts of habitat alteration, OWFs may introduce turbulence and wind wake effects, which impact circulation, stratification, and mixing over large spatial areas (Carpenter et al., 2016). Changes to the physical environment by OWFs may, therefore, influence larval transport pathways (van Berkel et al., 2020) and nutrient availability (Floeter et al., 2017), with potential knock-on effects for higher trophic levels. As climate change and large-scale OWFs can act in the same direction (e.g., increasing stratification), there is a growing need to disentangle and quantify such impacts separately, especially in the context of marine spatial planning. Holistic ecosystem modelling approaches should therefore be applied at realistic spatial and temporal scales to further our understanding of such impacts on marine connectivity.

Similarly, in freshwater environments there is an ongoing expansion of hydropower development (Couto & Olden, 2018; Zarfl et al., 2015). The construction of hydropower and its adjacent infrastructure results in disrupted longitudinal river connectivity, habitat fragmentation (Cutler et al., 2020), altered flow regimes (Richter et al., 1996), water loss from evaporation (Friedrich et al., 2018; Zhao & Gao, 2019), thermal alteration (Olden & Naiman, 2010), reduced oxygen levels and conversion of lotic to lentic systems

(Parasiewicz et al., 2023). Dams act as physical barriers that prevent fish from moving upstream and downstream in rivers, disrupting natural migration patterns and restricting access to important spawning and feeding areas (Larinier, 2000). Conversion of upstream reaches to lentic habitats affects migratory fish behavior along a gradient of hydraulic and limnological conditions (Pelicice et al., 2015). For example, this profound habitat conversion has been demonstrated to disorient translocated fish and alter their movement ecology (Lopes et al., 2021, 2024). A global assessment on around 10,000 freshwater fish species and 40,000 existing large dams identified the highest current level of fragmentation present in USA, Europe, South Africa, India, and China (Barbarossa et al., 2020). Consequently, hydropower has been highlighted as a leading factor for the dramatic decrease in migratory fish populations worldwide (Deinet et al., 2020).

Only 37% of rivers longer than 1000 km remain free of hydropower globally (Grill et al., 2019). With the global hydropower sector set to grow at a rate of 4% per year between 2023 and 2030 according to the Net Zero Emissions by 2050 Scenario (International Energy Agency, 2021), the number of free-flowing rivers will likely decrease further, exacerbating the effects on aquatic ecosystems. This threat is particularly great in the tropics, where rivers such as the Congo, Salween, Mekong, and Amazon are expected to experience decreases in connectivity of between 20% and 40% (Barbarossa et al., 2020; Winemiller et al., 2016). There are also proposals emerging to construct floating solar power arrays on hydroelectric reservoirs (Sahu et al., 2016; Vidović et al., 2023). While this has advantages over the expansion of hydroelectric dams with respect to impacts on structural connectivity, the potential impact of this infrastructure on fish movements and habitats remains largely unknown (Almeida et al., 2022a; Nobre et al., 2023).

Climate change is also causing increases in multiple climate hazards, including more intense and frequent extreme rainfall, pluvial, fluvial, and coastal flooding, sea level rise, and storm surges (IPCC, 2022). The physical infrastructure required to mitigate and manage these climate hazards, such as levees, dykes, seawalls, weirs, reservoirs, pumping stations, and flood/tide gates, among others, significantly impacts structural connectivity in multiple dimensions, yet is under-represented in the global literature on aquatic connectivity (Bice et al., 2023; Bolland et al., 2019; Knox et al., 2022; Thieme et al., 2023). Levees and dykes disrupt lateral connectivity between rivers and their floodplains, which provide critical habitats and resources for aquatic biodiversity (Bolland et al., 2012; Knox et al., 2022). Pumping stations and flood/tide gates are critical infrastructure for managing inundation, yet interrupt longitudinal connectivity and significantly alter hydrodynamic and sediment regimes, with consequent impacts on fish dispersal, survival, and habitat availability (Bolland et al., 2019; Buysse et al., 2014; Franklin & Hodges, 2015; Seifert & Moore, 2018; Wright et al., 2016). Likewise, construction of seawalls, breakwaters, and groynes creates disconnections in structure and function both along shorelines and between marine and terrestrial habitats, with subsequent impacts on population processes and geomorphic processes (Bishop et al., 2017; Bulleri & Chapman, 2010). Ongoing expansion of hazard mitigation infrastructure in response to increasing threats to productive land, property, and human life will inevitably magnify impacts on aquatic connectivity. The location of this infrastructure in the lower areas of rivers and estuaries means that it can have a disproportionate impact on overall structural connectivity, reducing movements between marine and freshwater ecosystems, eliminating tidal fluxes, and converting estuarine habitats to freshwater.

2.2 | Functional connectivity

The distributions of many aquatic species are predicted to shift, expand, or contract in response to climate change (Heino et al., 2009; Pinsky et al., 2020). Globally, increasing water temperatures are expected to shift species to higher latitudes or altitudes (in the case of freshwater), or into deeper waters (Alofs et al., 2014; Comte et al., 2013; Dulvy et al., 2008; Fuchs et al., 2020; Perry et al., 2005). Oxygen minimum zones are likely to cause vertical range contraction for species in open waters (Gallo & Levin, 2016; Gilly et al., 2013). Within-species connectivity might be maintained where species range shifts are wholesale, but will be disrupted where some populations have limited scope for range extension due to a lack of suitable habitat, or structural barriers (Carr et al., 2017; Donelson et al., 2019; Hodapp et al., 2023). The colonization of species into new areas will create novel interspecific interactions with native species, particularly at high latitudes (Donelson et al., 2019), contributing to structural and functional reorganization of aquatic life and its connectivity, with consequences for fisheries and management in both marine and freshwater environments (e.g., Free et al., 2019; Maltby et al., 2020).

Warming, changes in photoperiod, and earlier spring blooms due to increased stratification may induce changes in functional connectivity via phenology, including altered migration timing (Crozier & Hutchings, 2014), spawning onset (Polte et al., 2021), and larval duration (Asch, 2015). Resulting match-mismatch dynamics between, for example, larval stages and plankton peaks (Platt et al., 2003; Polte et al., 2021) can strongly affect recruitment and survival of fishes across all aquatic realms (Beaugrand et al., 2003; Durant et al., 2007). In temperate zones, prolonged mismatches between fish consumers and lower trophic levels are expected under future climate change (Polte et al., 2021). This may induce range shifts in spawning grounds, where species with limited dispersal capacities are most susceptible (Asch et al., 2019), and impact behavioral and physiological responses to altered food availability (e.g., reduced activity and growth) (Illing et al., 2018). In reef ecosystems, warming-induced changes in the pelagic larval duration of reef fish affect dispersal through earlier reef-seeking behavior, changing the spatial scale of connectivity (Munday et al., 2009).

Climate change will drive adaptation in aquatic organisms, with different genetic sub-populations exhibiting greater or lesser ability or propensity to adapt. Maintaining functional genetic connectivity will therefore be essential for supporting the adaptive response of organisms to climate change. For example, Atlantic cod *Gadus morhua* L. populations have different thermal adaptive potential (Oomen &

Hutchings, 2015), and peripheral populations of Pacific cod *Gadus macrocephalus* Tilesius 1810 harbor potentially adaptive loci (Fisher et al., 2022). Relatedly, brown trout *Salmo trutta* L. population connectivity could itself be driven by environmental barriers rather than physical ones (Bekkevold et al., 2020). In a review of likely evolutionary responses to climate change in fish populations, changes in the timing of migration and reproduction, age at maturity, age at juvenile migration, growth, survival, and fecundity were all associated with changes in temperature (Crozier & Hutchings, 2014).

The availability of new genetic techniques (e.g., environmental DNA, transcriptomics) and reduced costs of genome sequencing allow improved understanding of connectivity between populations that go beyond using hypothetically neutral markers for monitoring inbreeding depression and genetic structure from physical specimens (Carvalho & Hauser, 1998). Where genomics or transcriptomics data are available, resources increasingly allow identification of regions of the genome that might be crucial for adaptation to climate change (Bernatchez, 2016) or that can confirm phenotypic and epigenetic changes that identify adaptation (Munday et al., 2017). Using an aquatic landscape and seascape/riverscape genomics approach will be required to understand the genetic components important for populations to adapt in changing climates (Grummer et al., 2019; Oleksiak & Rajora, 2020).

A further impact on functional connectivity can be the creation of ecological traps, where animals choose or are forced to use habitat that ultimately reduces their fitness (Hale & Swearer, 2016). For example, the formation of large reservoirs because of dam construction significantly alters upstream habitats. For some species, these habitats are inappropriate for supporting critical lifecycle requirements such as spawning. Consequently, when ripe fish move upstream via constructed fishways, previously high-quality habitats are no longer available and reproduction is impaired, creating a sink population above the dam (Buderman et al., 2020; Pelicice & Agostinho, 2008).

The existence of ecological traps is understudied in marine environments (Swearer et al., 2021). Current evidence does not indicate that offshore renewables are creating ecological traps (Reubens et al., 2013), but artificial reefs are shown to potentially disrupt functional connectivity by redirecting larvae to poorer quality artificial habitat (Komyakova & Swearer, 2019), indicating that there is the potential for offshore renewables to function similarly. With climate change and other related human-induced changes leading to alterations in habitat quality, movement patterns, and range distributions, ecological traps are likely to become more common (Hale & Swearer, 2016; Komyakova et al., 2022; Pike, 2013). Moreover, climate change refugia could become ecological traps where access to critical habitats is disconnected (Morelli et al., 2020; Vander Vorste et al., 2020).

Increased connectivity of aquatic systems, while generally beneficial for population resilience of native species and ecosystem health, also has undesirable consequences by facilitating the spread of some aquatic invasive species (AIS) (Francis et al., 2019; Manenti et al., 2019). This results in what has been described as a connectivity conundrum (Zielinski et al., 2020). An extreme example occurs when naturally unconnected water bodies are connected by the construction of canals, enabling dispersal of species that then invade communities, or impact populations that have evolved in isolation. Examples include the spread of numerous invertebrates and fish through the European canal network (Alt et al., 2019; Panov et al., 2009), and the transfer of several hundred species from the Red Sea to the Mediterranean Sea through the Suez Canal (Galil et al., 2021). Climate change opens new pathways and leaves communities more vulnerable to invasion by favoring generalist (typically including those with the highest probability of becoming invasive) over specialist species (D'Amen & Azzurro, 2019; Hiddink et al., 2012).

The effects of climate change must be considered when developing strategies to achieve connectivity for native species whilst limiting AIS movement (Hellmann et al., 2008). For example, the efficacy of control measures for AIS (e.g., migratory barriers for sea lamprey *Petromyzon marinus* L. and habitat exclusion gates for common carp *Cyprinus carpio* L.) and the passage effectiveness for native species strongly depend on environmental factors associated with a changing climate (Lennox et al., 2020; Piczak et al., 2023). In the warming Arctic, increased ship traffic will inevitably assist in the transport and establishment of AIS into new ice-free environments (McLachlan et al., 2007), while building new infrastructure for renewable energy increases connectivity for marine AIS by providing "stepping stones" of hard intertidal substrate across shelf seas (Adams et al., 2014; De Mesel et al., 2015). Climate change also reduces dissolved oxygen concentrations (Irby et al., 2018; Mahaffey et al., 2023) to levels tolerable only to adaptable species (Byers et al., 2023; Lagos et al., 2017). The dual objectives of preserving structural connectivity while limiting the spread of AIS under the pressures of rapid climate change present a formidable obstacle for natural resource managers to overcome (Havel et al., 2015; Wallingford et al., 2020).

3 | CHALLENGES AND SOLUTIONS FOR MANAGING AQUATIC CONNECTIVITY IN A CHANGING CLIMATE

Resilience of populations, communities, and ecosystems depends on several factors (Bolnick et al., 2003; Campana et al., 2023; de la Vega et al., 2023), but generally, biological diversity can stabilize system processes and buffer environmental change (Schindler et al., 2010). Conserving or reestablishing functional and structural connectivity has the potential to retain and restore intraspecific diversity (Limburg et al., 2001) and food web complexity (LeCraw et al., 2014), and enable portfolio effects (Schindler et al., 2010), thus future-proofing conservation efforts (Lynch et al., 2023b). However, such actions may involve ecological and socio-economic trade-offs (Walter et al., 2021).

In the following sections we identify some of the key challenges and solutions for managing aquatic connectivity in a changing climate. These different actions were identified by participants in a thematic workshop at the Fisheries Society of the British Isles annual conference at the University of Essex in 2023. The list is not considered exhaustive, but represents what participants felt were some of the critical challenges for managing connectivity in the context of a changing climate based on their diverse experiences.

3.1 | Defining objectives under a shifting baseline

Conroy and Peterson (2013) define objectives as "specific, quantifiable outcomes that reflect the values of decision makers and stakeholders and relate directly to the management decisions." Clear objectives are integral to designing management interventions and for developing performance standards against which the effectiveness of interventions such as restoring aquatic connectivity can be evaluated (O'Connor et al., 2022; Pressey et al., 2021). Historical reference states have often been used as a basis for defining management objectives. Identifying and following these reference states or baselines comes with their own philosophical and logistic challenges. Philosophically, the idea of "baseline" is intricately linked with ideas like "pristine/untouched nature" and "climax community", both of which have been challenged in contemporary ecology (e.g., Denevan, 2011). Determining the pristine reference state can be impossible because of data limitations. Logistically, restoring to the reference state may become unrealistic or even irrelevant in an era of shifting baselines due to climate change (Acreman et al., 2014; Alleway et al., 2023; Tonkin et al., 2019). Despite these challenges and limitations, there is value in using past or contemporary conditions to support more informed decisions about how to respond to potential future states. Future-proofing efforts to protect and restore aquatic connectivity will require decision-makers to anticipate future changes in baseline state and to define objectives and design interventions accordingly (Lynch et al., 2023b).

Defining future-proof objectives will require that researchers and practitioners adopt biological models based on processes and mechanisms that enable them to forecast changes in response to unprecedented conditions (Tonkin et al., 2019). It will also be necessary to recognize that aquatic habitats are often considered resources by people and exist as part of complex socio-ecological systems (Baldwin-Cantello et al., 2023; Birnie-Gauvin et al., 2023). As such, objectives for restoring aquatic connectivity to preserve future ecosystem health will involve balancing trade-offs with global efforts to future-proof human society in the face of climate change (see Section 3.2). Objectives will also need to allow for uncertainty in predictions. Given that new information will become available through time, objectives must be part of a larger adaptive management framework for flexible and progressive refinement (see Section 3.6).

3.2 | The need for nature-positive climate adaptation

Balancing climate change mitigation and adaptation strategies with aquatic connectivity is a growing challenge. As efforts to address climate change intensify, necessary trade-offs will likely become more apparent. However, the public may not readily observe the impact of these adaptations on biodiversity. Currently, there is an urgent need to reshape society's relationship with nature (sensu Birnie-Gauvin et al., 2023). By underscoring the important role that aquatic biodiversity plays in supporting human society (Lynch et al., 2023a; Worm et al., 2006), actions in response to climate change can be designed to be "nature positive" (Bull et al., 2020; Maron et al., 2020).

As discussed above, the pursuit of net zero emissions objectives and the associated expansion of renewable energy present a direct challenge to maintaining and restoring aquatic connectivity. The installation of fishways is a common solution in fresh waters to facilitate movement past hydropower plants. However, fishway effectiveness is neither guaranteed nor universal across species or sites (Hershey, 2021; Silva et al., 2018). Nonetheless, a baseline understanding of site-specific habitat and species-specific passage effectiveness can inform and potentially serve to minimize the impacts of hydropower on aquatic connectivity (Calles et al., 2021; Nyqvist et al., 2017). Furthermore, strategic spatial planning (see Section 3.3 for further discussion) of new hydropower development, including repurposing existing dams that are currently not used for energy production (e.g., used instead for irrigation) and/or improving the efficiency of existing energy production, can lessen the impact on aquatic biodiversity (Almeida et al., 2022b; Couto et al., 2021; Garrett et al., 2021; Thieme et al., 2023). Strategic spatial planning of offshore wind farms can achieve similar win–win benefits, as discussed further in Section 3.3.

Likewise, status quo bias in efforts to protect property and lives from climate hazards sees conventional practice dominated by hard engineering approaches that sever connectivity at the terrestrial–aquatic interface, with negative outcomes for aquatic habitats and biodiversity. There is a need for a more nature-centric approach to infrastructure design that meets society's needs for a livable world, while also maintaining and enhancing biodiversity. Reimagining infrastructure so that biodiversity and ecosystem services become a central objective of civil engineering (van Rees et al., 2023a) offers the opportunity to rethink how aquatic ecosystems fit within the landscape, accommodating nature within the climate adaptation process. Nature-based solutions (Seddon et al., 2021), such as making room for rivers (Bogdan et al., 2022; Rijke et al., 2012), an approach to flood mitigation that involves reconnecting rivers with their floodplains, managed coastal retreat (Fouqueray et al., 2018; Powell et al., 2019), or barrier removal, offer excellent potential for enhancing aquatic connectivity and mitigating the effects of climate change on human infrastructure (Newbury, 2013; van Rees et al., 2023b).

3.3 | The importance of strategic spatial planning

While global biodiversity goals emphasize the importance of connectivity (CBD, 2022), it is often only superficially considered within spatial management and related objectives (Balbar & Metaxas, 2019; Beger et al., 2022; Hermoso et al., 2021; Linke et al., 2012; Magris et al., 2014). There is an urgent need to implement strategic spatial planning to help ensure that structural and functional connectivity, and hence aquatic biodiversity, is maintained now and into the future (Hermoso et al., 2021; Jonsson et al., 2021; Magris et al., 2014; Virtanen et al., 2020).

Considering connectivity in spatial planning requires information about animal movement and how this might alter under a changing climate or with climate adaptations. Depending on the spatiotemporal scale, movement data can be collected using biotelemetry technology (Breen et al., 2015; Dunn et al., 2019), microchemistry (Chang & Geffen, 2013), or genetics (Riginos & Beger, 2022). Movement data can additionally be used for statistical analyses such as species distribution models (Hodapp et al., 2023) or simulation-based tools, such as individual-based models (Xuereb et al., 2021), to understand and predict movements in changing climates. Such tools and derived metrics (Keeley et al., 2021) can contribute to setting quantifiable objectives for ecological connectivity and help to provide more impact-focused assessments of management tools and climate adaptations, helping to achieve global conservation goals (Beger et al., 2022; Heino et al., 2017; Magris et al., 2018; Pressey et al., 2021). However, the integration of tools (e.g., individual-based models) into policy and management is currently lacking in some systems and there is a need for the resulting model outputs to be made accessible and communicated to policy makers in a relevant and credible way that explicitly acknowledges uncertainty (Blastland et al., 2020; Gray et al., 2023; Saltelli et al., 2020).

With climate change shifting distributions and species interactions, spatial management must be increasingly adaptive. Area-based management tools (ABMTs), such as marine protected areas, already face challenges from implementation gaps (Gill et al., 2017) and will need further adaptions with a changing climate. Specifically, ABMTs will need to be designed in a more flexible and interconnected manner to account for future range shifts and migration corridors, as well as to avoid a mismatch of management efforts and remaining biological resources (Almany et al., 2009; Weeks, 2017).

Development of renewable energy infrastructure in both marine and freshwater environments should occur strategically to help optimize the trade-offs between the need to achieve net zero goals and mitigating their impacts on aquatic connectivity (Bao et al., 2023). For instance, offshore wind farms have been suggested as important stepping stones facilitating connectivity (Adams et al., 2014; Bishop et al., 2017), but can also serve as barriers to animal movement (Bishop et al., 2017). In the absence of adequate baselines, assessing the impacts of such structures on connectivity is difficult and requires operational assessment tools of connectivity, which are so far lacking for marine environments (Balbar & Metaxas, 2019; Beger et al., 2022; Magris et al., 2014). The benefits of strategic spatial planning of hydropower development have already been highlighted, assisting decision-makers in comparing the benefits of building dams against their socio-environmental impacts (Almeida et al., 2022b). Couto et al. (2021), for example, were able to demonstrate that strategic planning of future small hydropower construction could halve the number of hydropower plants required, while simultaneously resulting in lower river fragmentation and protecting numerous undammed basins in Brazil.

The meta-ecosystem framework (Gounand et al., 2018; Loreau et al., 2003) is a powerful tool to investigate the dynamics of aquatic ecosystems and carry out appropriate strategic spatial planning. The meta-ecosystem framework advances the concepts of meta-populations (Hanski, 1998) and meta-communities (Leibold et al., 2004), which are focused on spatial flows of organisms, to also incorporate flows of material and energy. Biodiversity and ecosystem functioning in aquatic environments arise from the interaction between regional and local scale processes (Scherer-Lorenzen et al., 2022). Understanding regional processes occurring at different levels of organization (i.e., meta-population, meta-community, and meta-ecosystem) is crucial for managing aquatic connectivity and for guiding effective management and policy recommendations for aquatic ecosystems (Cid et al., 2022). Practices that focus only on the local scale cannot achieve the desired ecological outcomes for connectivity restoration since environmental challenges, such as climate change, are not restricted to ecosystem boundaries and can act at regional or global scales (Cañedo-Argüelles et al., 2023; Cid et al., 2022; Schiesari et al., 2019).

3.4 | Addressing the connectivity conundrum

Confronting the key conservation challenges of habitat fragmentation and species invasions together is essential because these issues are intrinsically linked. While mangers aim to increase and restore connectivity between native populations, such interventions can ultimately facilitate movements of invasive species between locations, creating a connectivity conundrum (Rahel & McLaughlin, 2018; Zielinski et al., 2020).

Restoring aquatic connectivity has become an increasingly important goal for the sustainable recovery of aquatic biodiversity, particularly in fresh waters (Thieme et al., 2023; Tickner et al., 2020). The impacts of riverine infrastructure on fish communities have long been recognized and there is a lengthy history of attempts to restore connectivity at culverts, dams, and weirs (Katopodis & Williams, 2012). Ensuring that objectives for maintaining migratory pathways are incorporated at the outset of project design rather than retrospectively would likely improve outcomes (Katopodis & Williams, 2012; van Rees et al., 2023a). For example, engineering erosion-resistant culverts that also mimic natural conditions should be viewed as feasible and valuable goals for habitat restoration. The underwhelming performance of some fishways has led to an increasing focus on barrier removal as a strategy for reconnecting waterways, with positive outcomes for fish communities (e.g., Bubb et al., 2021; Sun et al., 2021; Weigel et al., 2013). Likewise, replacement of poorly designed structures with more "fish friendly" options has proven effective for improving fish movements (Timm et al., 2017), but also for increasing the resilience of infrastructure to extreme events (Gillespie et al., 2014), creating a win–win scenario in a changing climate.

The counter to the benefits of restoring connectivity is the increased dispersal of invasive species. The magnitude of this conundrum will only intensify with climate-induced range shifts in both marine and freshwater environments (Rahel et al., 2008; Wallingford et al., 2020). To efficiently restore aquatic connectivity, it will be essential to balance the costs and benefits of invasion control measures against those of restored connectivity (Milt et al., 2018; Walter et al., 2021). To do so, once potential invasives have been identified (e.g., following risk assessments; Andersen et al., 2004), managers need to understand aquatic invasive species movement and dispersal patterns (and how climate change will moderate them), as well as their interactions and effects on native species (e.g., following network theory; Haak et al., 2017). Subsequent management strategies will ultimately depend on the scale and type of connectivity restoration, and the impacts of the invasive(s), but should involve plans to monitor the presence and abundance of invasives over time and space (e.g., through environmental DNA [Robson et al., 2016], visual/mark-recapture surveys [Larson et al., 2020; Christy et al., 2010]) and, where necessary, consider control methods (e.g., genetic engineering [Thresher et al., 2014], natural predators [Mumby et al., 2011], or creating selective barriers/routes [Pratt et al., 2009; Zielinski et al., 2020]).

3.5 | Measuring success

Measuring what does (and does not) work is essential for supporting evidence-based practice and ensuring that efforts to restore aquatic connectivity in a changing climate are successful. However, success can be defined in multiple ways. This presents practitioners with a challenge when identifying appropriate performance measures and implementing effective monitoring, particularly in an era of shifting baselines. Consequently, there is a need to explicitly consider both the fundamental objectives (aspects that a decision-maker truly values and strives to achieve) and means objectives (a way to achieve fundamental objectives) (sensu Conroy & Peterson, 2013) for a project to ensure that measures of success accurately reflect the desired outcomes (Figure 2).

Meeting predefined objectives (see Section 3.1) is a basic prerequisite of success for any management intervention. Efforts to restore connectivity often center on re-establishing physical or structural connectivity relative to a historic baseline state. This focus is appealing to practitioners as it is straightforward to justify (restoring physical access to required habitats is good), intuitive and easy for stakeholders to understand (fewer barriers is good), and there are many existing metrics of structural connectivity (e.g., Cote et al., 2009; Segurado et al., 2013) making changes straightforward to quantify. While an important measure of success, a narrow focus on simply measuring increases in structural connectivity risks neglecting the many nuances of how aquatic organisms respond to changes in structural connectivity (e.g., Wilkes et al., 2019) and the wider importance of functional connectivity (Figure 2). Furthermore, challenges remain with defining baseline conditions and accounting for shifting baselines (Alleway et al., 2023), and quantifying connectivity across scales (Magris et al., 2014).

Measures of success must, therefore, be multifaceted and aligned with achieving the overall restoration objectives. This may include, for example, consideration of the number and frequency of individuals moving between localities, the size of species able to move successfully, delays in movement, the degree of larval dispersal, long-term maintenance of viable populations, and/or genetic affinity between subpopulations (Green et al., 2015; O'Mara et al., 2021; Pompeu et al., 2012; Wilkes et al., 2019). As these processes operate over different scales, so do the requirements for monitoring and the ability to measure success from actions to restore aquatic connectivity. Success is also dependent on the sustainability of conservation objectives as they interact with wider socio-economic needs, such as the use of aquatic systems as a source of water, food, or energy, natural disaster mitigation, and leisure (Baldwin-Cantello et al., 2023).

Measuring the success of connectivity restoration is, therefore, an overarching process with adaptable objectives that must occur over biologically/ecologically informed timeframes (e.g., based on a species' generation time or phenotypic plasticity) and consider how management interventions affect other organisms/ecosystems and people whose livelihoods are intricately linked with these systems.

3.6 | The need for adaptive management

Maintaining connectivity is an essential element of climate adaptation strategies (Reside et al., 2018), although it is rarely included under the existing policies given incomplete knowledge, resource limitations, and trade-offs with conflicting developments (Thieme et al., 2023). Robust knowledge underpins successful management of ecosystems, yet understanding all the complex interactions under a changing climate is difficult, given various levels of uncertainties, and hinders decision-making (Heller & Zavaleta, 2009; Polasky et al., 2011). However, this should not limit the ability to act based on the best available information within appropriate frameworks for decision-making (Heller & Zavaleta, 2009;Mawdsley, 2011; Polasky et al., 2011).

When faced with high uncertainty, adaptive management can guide decision-making through an iterative and structured process (Mawdsley, 2011; Polasky et al., 2011) that should account for economic, environmental, and social drivers and incorporate new information as it becomes available (Tear et al., 2005; Thieme et al., 2023). Key uncertainties around conservation measures should be made transparent, with measures to reduce them set under a robust monitoring program and re-evaluation cycle (Tear et al., 2005). There is a plethora of methods developed to address decision-making under uncertainty, with many based on evaluating multiple options to reach the optimal choice using computer models and incorporating adaptive management (Polasky et al., 2011; Siders & Pierce, 2021). However, there is a lack of guidance for choosing the right tool and evidence of their efficacy and suitability for climate change decisions (Siders & Pierce, 2021). All decision-making will be context dependent, but choosing more robust approaches (Dittrich et al., 2016) as well as combining multiple methods may be most beneficial when dealing with deep uncertainty (Polasky et al., 2011; Siders & Pierce, 2021).

4 | CONCLUSIONS

The recent Kunming–Montreal Global Biodiversity Framework sets ambitious targets to reverse declines in global biodiversity through restoration to enhance ecosystem functions and services, ecological

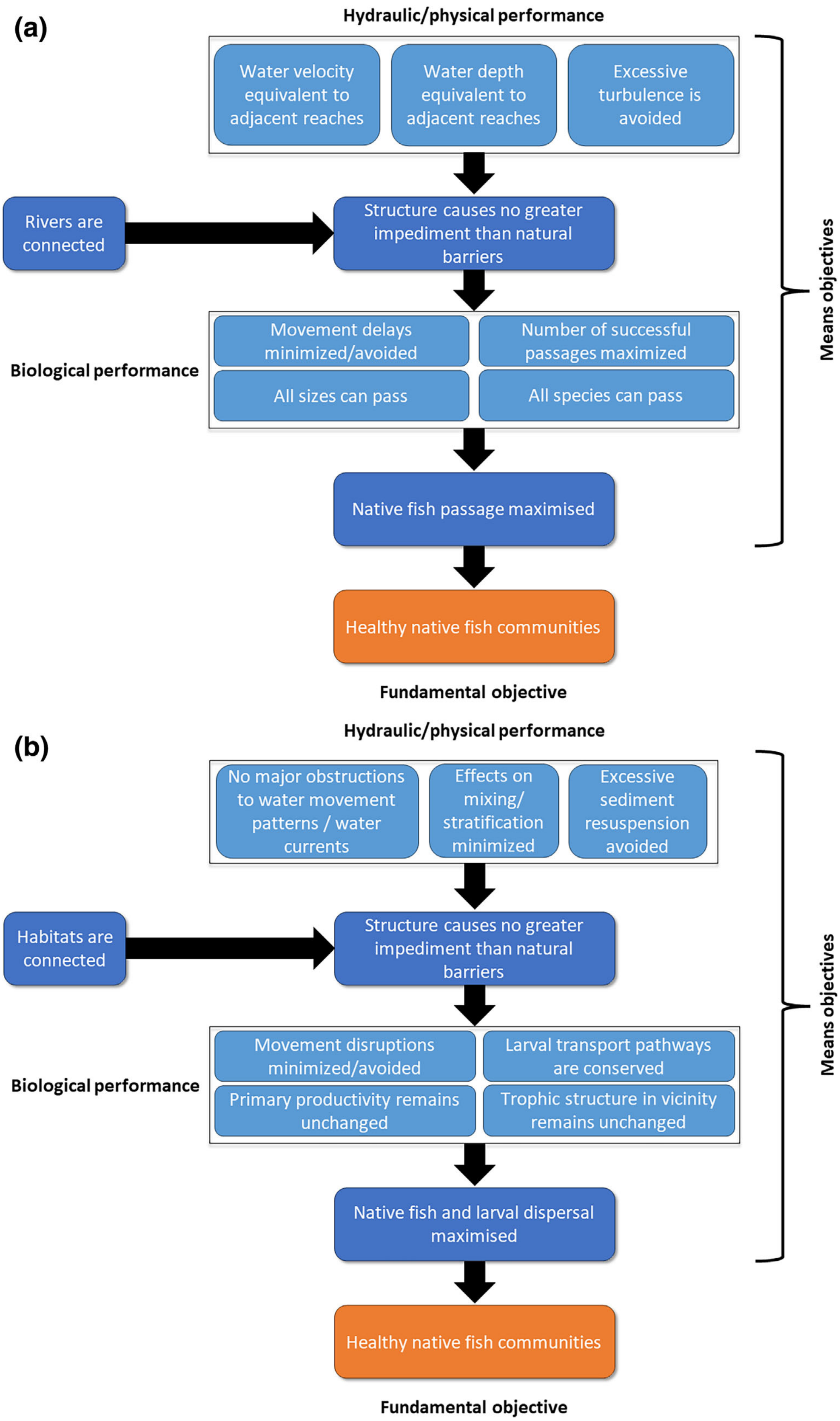

FIGURE 2 Examples of simplified objectives networks for restoring connectivity in freshwater (a) and marine (b) environments. Note how means objectives contribute to achieving the overall fundamental objective. Measures of success must recognize and reflect the diversity of objectives. Means objectives can often also serve as performance measures for evaluating success.

integrity, and connectivity. The framework also recognizes the need to minimize the effects of climate change through mitigation, adaptation, and disaster reduction actions. Indeed, the escalating effects of climate change on aquatic ecosystems require urgent, strategic, and adaptive responses to manage and preserve aquatic connectivity. Finding the balance between bolstering ecosystem resilience through enhanced connectivity and reducing the risk of aquatic invasive species spread is a complex challenge, exacerbated by climate change. Effective management must navigate these intricacies and take a nuanced approach that considers the multifactorial and dynamic nature of ecosystems, cumulative stressors, societal needs, and the pressing imperative to mitigate climate impacts.

Key strategies should focus on future-proofing conservation efforts, embracing nature-positive climate adaptation, and committing to strategic spatial planning. These approaches necessitate setting clear yet flexible objectives that adjust to shifting baselines, while being informed by robust scientific models and an understanding of socio-ecological systems. Renewable energy development, including hydropower, must be planned strategically to minimize negative impacts on connectivity, with an emphasis on modifying existing infrastructure to enhance passage for indigenous aquatic species.

As habitats and species distributions transform under climate pressures, the creation of ecological traps and the spread of aquatic invasive species must be vigilantly monitored and managed. This includes employing innovative monitoring techniques such as environmental DNA and leveraging predictive tools for decision-making. The complexity of these issues calls for an adaptive management framework that integrates economic, environmental, and social considerations, and is receptive to emerging data and evolving scenarios. Through collaborative efforts, informed by interdisciplinary research and stakeholder engagement, it will be possible to forge pathways towards resilient, connected aquatic ecosystems capable of withstanding the uncertainties of a changing climate.

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