Human effects on ecological connectivity in aquatic ecosystems: Integrating scientific approaches to support management and mitigation

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HIGHLIGHTS

- Human effects on ecological connectivity in aquatic ecosystems are reviewed.
- Threats include: habitat loss, altered hydrology, invasive species, and climate change.
- Case studies show improved understanding from multi-disciplinary approaches.
- Data on autecology, population structure, movement and physiology are critical.
- Planning requires data synthesis across life histories and temporal/spatial scales.

ARTICLE INFO

ABSTRACT

Understanding the drivers and implications of anthropogenic disturbance of ecological connectivity is a key concern for the conservation of biodiversity and ecosystem processes. Here, we review human activities that affect the movements and dispersal of aquatic organisms, including damming of rivers, river regulation, habitat loss and alteration, human-assisted dispersal of organisms and climate change. Using a series of case studies, we show that the insight needed to understand the nature and implications of connectivity, and to underpin conservation and management, is best achieved via data synthesis from multiple analytical approaches. We identify four key knowledge requirements for progressing our understanding of the effects of anthropogenic impacts on ecological connectivity: autecology; population structure; movement characteristics; and environmental tolerance/phenotypic plasticity. Structuring empirical research around these four broad data requirements, and using this information to parameterise appropriate models and develop management approaches, will allow for mitigation of the effects of anthropogenic disturbance on ecological connectivity in aquatic ecosystems.

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1. Introduction

Animal populations and ecosystems are connected via a range of physical, biological and biochemical pathways. These connections influence biodiversity, productivity, energy fluxes, species assemblage compositions and food web dynamics (Taylor et al., 1993; Lowe and Allendorf, 2010), and define the spatio-temporal scales at which management and conservation initiatives will be most effective (Pringle, 2001; Lindenmayer et al., 2008).

Understanding the drivers and implications of altered ecological connectivity has become a key concern with respect to biodiversity conservation. Globally, few terrestrial and aquatic ecosystems remain unaffected by anthropogenic fragmentation and the resulting loss of connectivity among populations and habitats (Pringle, 2001; Lindenmayer and Fischer, 2006). Humans are fundamentally changing connections within and between ecosystems over a wide range of spatial scales and habitat types. The effects of human activities are not unidirectional, and may result in either increased or decreased levels of connectivity. Such changes can pose direct threats to biota, but may also create novel environments that alter the evolutionary trajectories of populations and species (Allendorf et al., 2013).

In this review, we examine the effects of anthropogenic activities on ecological connectivity as it pertains to the movement and dispersal of aquatic organisms. We recognise, however, the critical importance of other forms of connectivity in aquatic ecosystems that are not specifically considered — for example, the flow of nutrients and energy across space, whether mediated by organisms or physical processes (Polis et al., 2004). Our primary aim is to identify and describe the main anthropogenic effects on ecological connectivity in aquatic ecosystems, and to explore their consequences for biota both within and between populations. A series of case studies illustrates how integration of multiple methodological approaches can increase our understanding of the potential effects of human activity on connectivity in aquatic ecosystems. Based on these considerations, we propose a series of key knowledge requirements for future research in this area.

### 1.1. Movement and dispersal in aquatic ecosystems

Aquatic ecosystems encompass a diverse array of physical configurations, ranging from 'open' systems like oceans, to isolated waterholes in arid landscapes. Based on the spatial structure and physical characteristics of marine, freshwater and estuarine habitats, one might expect different 'rules' for ecological connectivity among ecosystems. The oceans and seas that cover around 70% of the earth's surface provide considerable possibilities for variability in the direction and extent of movement, although factors such as oceanic currents, bathymetry, land boundaries and seabed type can exert strong influences on the movements of many species (Gaspar et al., 2006). Freshwater systems, conversely, cover only ~0.8% of the earth's surface and are typically organised into networks of hierarchically branching streams and rivers, occasionally punctuated by lakes and wetlands (Grant et al., 2007). The complex structure of freshwater ecosystems can create isolation among populations at much smaller spatial scales than would be expected in marine systems; for example, when nearby populations occupy habitats that are not connected via the river network (Hughes et al., 2009). Four general models of ecological connectivity have been proposed to describe the unique constraints imposed by hierarchical network structure in freshwater ecosystems (Text Box 1).

Whilst the different physical attributes of aquatic ecosystems place limitations on the movements of resident organisms, their behavioural responses are not always intuitive with respect to the apparent openness of the environment. For many years, the pelagic larval stages of marine organisms were considered as passive particles that disperse widely under the influence of oceanic currents. This assumption led to a long-held paradigm in which local populations were considered highly mixed and demographically open (Jones et al., 2009). However,

Text Box 1
Models of ecological connectivity in streams.

The *stream hierarchy model* (SHM, Meffe and Vrijenhoek, 1988) predicts that freshwater species will be connected in a way that reflects the dendritic nature of the stream network. Sites within the same stream will be most connected, sites sharing the same subcatchment will be more connected than those in other subcatchments, and so on following the hierarchically branching nature of streams. Under the SHM, zero connectivity would be expected between sites occupying completely isolated stream networks (such as opposite sides of a continental divide). The SHM can apply to animals such as fish, many of which are highly mobile within the water column but have no capacity to move outside of the water column.
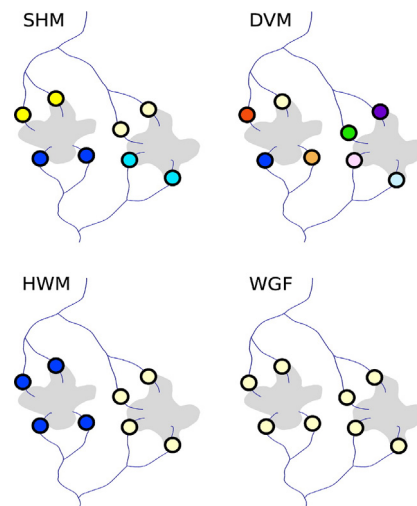
The four models can be visualised as above, with dots of the same colour representing connected populations. Populations occupy four sub-catchments with headwaters in two higher-altitude headwater regions (the grey areas).

The *Death Valley model* (DVM, Meffe and Vrijenhoek, 1988) describes extreme isolation experienced by animals that are similarly restricted to aquatic habitat but are confined to small patches of disconnected habitat. Under the DVM, habitat patches are extremely isolated either physically, due to a permanent lack of hydrological connectivity (e.g., springs in a desert), or functionally, due to a high degree of habitat specialisation for a sparsely distributed habitat type within a river network (e.g., cold headwater streams).

The *headwater model* (HWM, Finn et al., 2007) describes a pattern of ecological connectivity that is essentially opposite to the SHM. The HWM applies to animals that specialise on a particular habitat type, often associated with small headwater streams in a river network, but have some capacity to disperse terrestrially, typically by crawling or weak flight. Animals following the HWM pattern typically disperse readily among nearby headwater streams, whether or not these streams are physically connected in a river network.

Widespread gene flow (WGF) occurs in species that either have a highly mobile terrestrial phase (e.g., many aquatic beetles, Coleoptera) or are adapted to have temporary associations with highly mobile terrestrial animals (e.g., zooplankton attached to birds' legs, Maguire, 1963). For freshwater animals following the WGF pattern, the geometric structure of the river network has little influence on potential ecological connectivity.

more recent studies have demonstrated high levels of larval retention and natal homing for many marine species, even though there appear to be no physical impediments to more widespread dispersal (Jones et al., 1999; Swearer et al., 1999; Gerlach et al., 2007).

In addition to the influence of individual behaviour, morphological and physiological factors across the life-history are major drivers of movement and dispersal. Many aquatic species undergo physical metamorphoses that strongly influence their dispersal characteristics. For example, it is common for aquatic organisms to have a larval stage that is vulnerable to displacement by physical forces, such as river flows and oceanic currents. This passive displacement of larvae acts as an important dispersal mechanism for many species, although this is not always the case. As mentioned above, retention and natal homing by the larvae of some marine species limits their dispersal away from natal habitats. Similarly, many riverine macroinvertebrates and fish undertake 'compensatory' upstream movements at later life-history stages that result in recolonisation of the natal habitat by recruits (Williams and Williams, 1993; Mallen-Cooper and Brand, 2007). The capacity of aquatic organisms to move independently increases with ontogenetic development of locomotory and sensory function, thus reducing the importance of passive dispersal as a driver of ecological connectivity later in the life history (Montgomery et al., 2001).

Directed migration is another important aspect of the life-history of many aquatic species, and is often associated with sexual development and reproduction (Lucas et al., 2001). 'Diadromous' species, for instance, migrate between freshwater and the sea to complete their life cycles: some reproduce in freshwater but require marine habitats for growth ('anadromy', 'amphidromy'), whilst others reproduce in marine habitats but spend most of their lives in freshwater (catadromy) (McDowall, 1988). The catadromous migration of up to 6000 km undertaken by eels (Family Anguillidae) from freshwater rearing habitats to oceanic spawning grounds is a famous example of diadromy (Tesch, 2003). Large-scale migrations are also undertaken by many species within marine and freshwater biomes (e.g., trans-oceanic migrations of bluefin tuna, Block et al., 2001; upstream migrations by giant Mekong catfish *Pangasianodon gigas*, Hogan et al., 2004).

Movement over relatively small spatial scales is also critical for many aquatic organisms. Among its many functions, small-scale movement facilitates alternation between shelter and feeding habitats, access to temporarily or seasonally available resources, avoidance of predators and competitors, and colonisation of new habitat (Lancaster, 1999; Lucas et al., 2001). For example, inshore coastal habitats such as tidal flats and mangroves are highly connected through diel and tidal feeding migrations (Igulu et al., 2013), many fishes move between main channels and inundated floodplains of river systems to forage and breed (Junk et al., 1989; Copp, 1989), and the larval stages of many aquatic insects disperse longitudinally within streams via downstream drifting behaviour (Brittain and Eikeland, 1988).

Patterns of movement and dispersal by individual organisms throughout their life-history, as influenced by the physical and biotic characteristics of the environment, ultimately determine the population structure of a species. Many aquatic species exist as "metapopulations" consisting of spatially separated populations linked by dispersal (Fagan, 2002; Shima et al., 2010). One of the most important functions of such connectivity is to facilitate the movement of individuals between source populations (net exporters of recruits) and sink populations (net importers of recruits), thus preventing demographic decline and extirpation of sink populations (Brown and Kodric-Brown, 1977; Gotelli, 1991). Populations that are connected by dispersal are also likely to possess and maintain higher levels of genetic variability through gene flow, which enhances their long-term viability (Allendorf et al., 2013).

Activities that reduce connectivity in such situations present clear threats to the persistence and genetic integrity of populations and species. However, there are also situations in which artificially increased connectivity may result in deleterious outcomes. For instance, initiating connectivity between populations (e.g., via translocation and stocking)

that have been isolated over evolutionary time may result in the loss of genetic variants uniquely adapted to their local environment or create hybrids with reduced fitness (Allendorf et al., 2001). Given the nuanced outcomes of altered ecological connectivity, a thorough understanding of natural patterns of connectivity – and how they are affected by human activity – is necessary to ensure the long-term viability of populations of aquatic fauna (Fullerton et al., 2010). In the following sections, we examine the key threats posed by human activities with regard to ecological connectivity in aquatic ecosystems.

2. Human effects on aquatic ecological connectivity

2.1. Dams and weirs

It has long been recognised that the abstraction of water for agricultural, industrial and domestic use has wide-ranging effects on aquatic biota (Petts, 1984; Dynesius and Nilsson, 1994). Nevertheless, construction and planning of new dams proceed apace, particularly in developing regions of the world [e.g., Yangtze River, China (Xie, 2003); Lower Mekong Basin, Thailand, Laos, Cambodia (Baran and Myschowoda, 2009)]. Dams and weirs, and the impoundments they form, function as physical and behavioural barriers to longitudinal movement. This fundamentally alters patterns of ecological connectivity in affected river ecosystems (Pringle et al., 2000) and, in many cases, leads to local extinctions of migratory organisms (Warren and Pardew, 1998). According to a recent analysis, nearly 50% of freshwater eco-regions across the world are affected by large and medium sized dams (Liermann et al., 2012; Fig. 1a).

In contrast to terrestrial and marine ecosystems – where multiple pathways for movement exist – the linear or dendritic characteristics of rivers and streams amplify the effects of artificial barriers on the movement of aquatic organisms (Gotelli and Taylor, 1999; Fagan, 2002). As a consequence, minor barriers such as small weirs, road crossings, culverts, and even light from street lamps (Perkin et al., 2011) can significantly constrain the movement of biota in rivers and streams. Small instream barriers are extremely common in many regions of the world. In the Murray-Darling Basin, Australia, for example, there are more than 4000 licensed weirs and numerous unlicensed weirs and other barriers (Fig. 1b). Whilst much management emphasis is placed on mitigating the effects of large dams, the sheer number of small artificial barriers suggests that, collectively, they will have effects on ecological connectivity at least as significant as larger dams.

Fish passage infrastructure (fish ladders) is commonly incorporated into the design and construction of dams and weirs to maintain or restore connectivity between upstream and downstream habitats. However, such structures are typically effective only for allowing upstream passage of a sub-set of fish species (Agostinho et al., 2007), and are generally ineffective at facilitating downstream movement (Baumgartner et al., 2006; Schilt, 2007). Thus, even barriers fitted with fish ladders are likely to exert strong effects on ecological connectivity in rivers and streams. There has been a great deal of research devoted to the design of fish passage infrastructure in recent years (Williams et al., 2012). If appropriately implemented, such designs have the potential to reduce the negative effects of dams and weirs for at least some species.

2.2. River flow regulation

Changes to river flows associated with consumptive human use (potable water supply, irrigation, stock and domestic) can fundamentally alter the nature of hydrological and ecological connectivity in rivers (Bunn and Arthington, 2002). Flow regimes in regulated rivers are characterised by reduced overall discharge, and often have pronounced alterations in flow variability and seasonality due to water storage during periods of high-rainfall and subsequent release during periods of low-rainfall (Maheshwari et al., 1995).
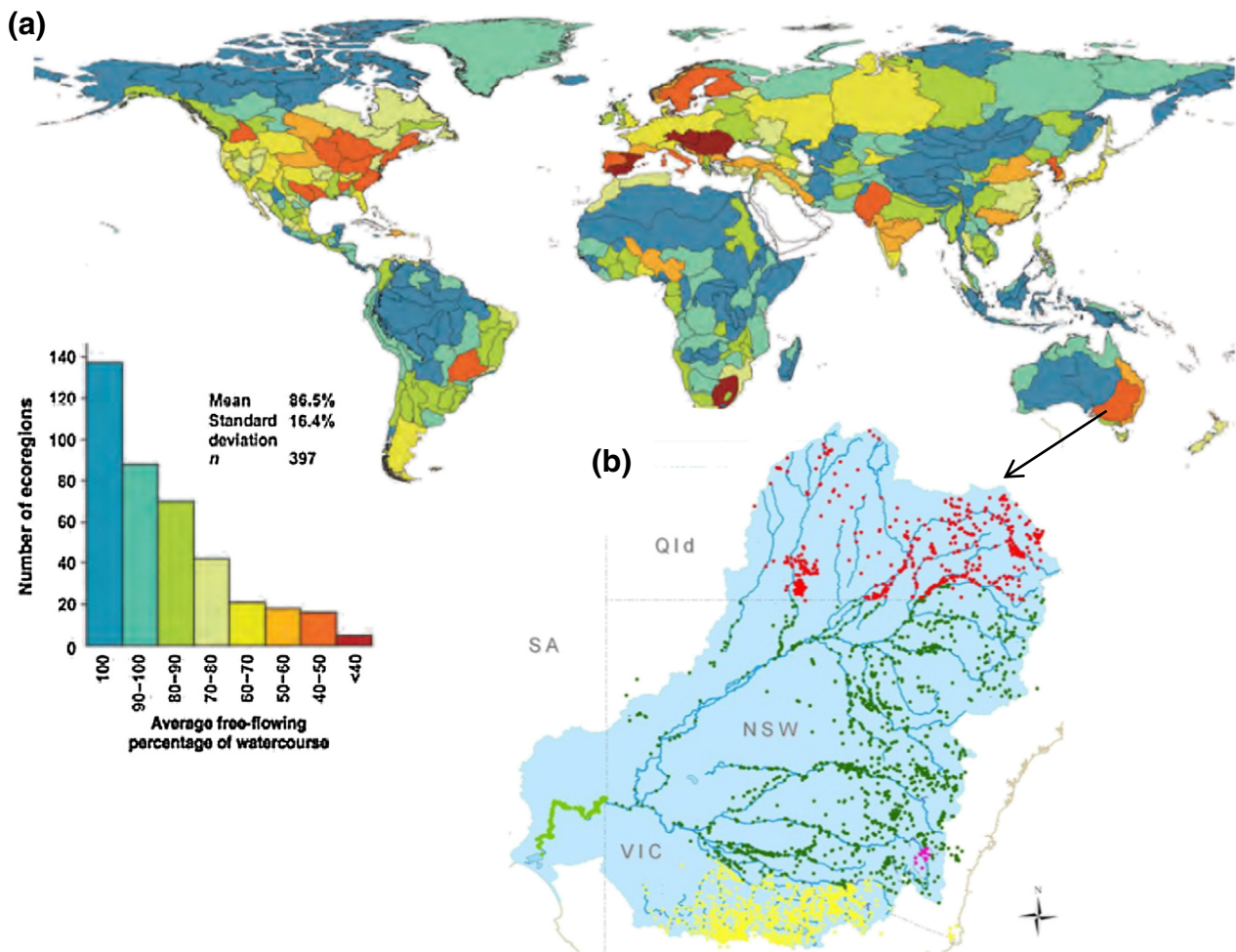
Fig. 1. (a) Average free-flowing percentage of watercourse length among 397 freshwater eco-regions globally. Lower values represent regions with high levels of fragmentation due to the effects of dams (reproduced from Liermann et al., 2012). (b) Distribution of the approx. 4000 licensed dams and weirs in the Murray-Darling Basin in south-eastern Australia. Different coloured dots represent State jurisdictions: red — Queensland (Qld), dark green — New South Wales (NSW), purple — Australian Capital Territory, yellow — Victoria (VIC), and light green — South Australia (SA) (Source: Murray-Darling Basin Commission).

Unnaturally long periods of low flow can sever hydrological connections between critical habitats (e.g., pools), reducing the likelihood of movement by individual organisms between source and sink populations and increasing rates of mortality due to habitat loss and desiccation (Bunn et al., 2006; Scharbert and Borcherding, 2013; Bond et al., in press). By decreasing the magnitude of high flow events, flow regulation can also reduce the frequency and extent of connections between the main channel and floodplain (Ward and Stanford, 1995). Many fishes and other organisms move onto inundated floodplains to breed and/or forage. The transport of assimilated energy and nutrients associated with these movements provides an energetic 'subsidy' that is a critical driver of in-channel secondary productivity in many rivers (Junk et al., 1989; Jardine et al., 2012).

Releases of stored water during periods of low rainfall can artificially increase hydrologic connectivity, rendering naturally ephemeral systems perennial, with resultant effects on the composition on aquatic fauna and the extent of connectivity within meta-populations (Bond et al., 2010). Flow regulation for hydro-electric power can also strongly affect ecological connectivity, with extreme variation in river flow for power generation (hydro-peaking) creating rapid oscillations in hydrological connectivity. Critical habitats, such as riffles, are often successively inundated and dewatered over short periods (i.e., hours). This can result in a loss of access to critical habitat, as well as stranding of organisms in dewatered habitats (Cushman, 1985; Irvine et al., 2009).

Species inhabiting estuaries and coastal marine habitats are not immune to the effects of altered river flows. Estuaries are the dynamic transition zone between freshwater and marine biomes, where productivity and biodiversity are strongly influenced by the salinity gradient formed by the mixing of inflowing freshwater and seawater. In many systems, sand bars are deposited during low flow periods at the mouth of the estuary, resulting in truncation of the salinity gradient and periodic severing of the connection between freshwater and marine biomes (Potter et al., 2010). Such estuaries rely on high riverine discharge to breach the sand bar and re-establish the freshwater–marine connection and the progressive increase in salinity from river to ocean. Anthropogenic reductions in river discharge can result in unnaturally extended periods of estuary mouth closure and reduced flushing of estuaries (Potter et al., 2010; Lloyd et al., 2012). This reduction in connectivity between freshwater habitats and the sea has obvious implications for diadromous species, and may also affect marine species that utilise estuaries as breeding or nursery grounds (Gillanders et al., 2003).

A wide range of management responses have been implemented to mitigate the effects of river flow regulation on ecological connectivity (see Tharme, 2003; Arthington et al., 2006). For example, release of 'environmental flows' from impoundments that augment natural high flow events have been used to restore connectivity between main channel and floodplain habitats (King et al., 2010). Similarly, water releases

may be used to restore longitudinal connectivity by providing sufficient depth for passage of organisms over riffles and other shallow habitats (Arthington et al., 2010) or prevent the accumulation of sand and resultant formation of sand bar barriers across estuary mouths (Lloyd et al., 2012).

2.3. Habitat alteration and loss

Although damming of rivers is the most obvious anthropogenic disruption of connectivity in aquatic ecosystems, the most ubiquitous effects result from physical alteration and loss of habitats. In freshwater, estuarine, and coastal marine ecosystems, large swathes of habitat have been lost or modified by industrial, agricultural, forestry, and urban development (Bunn and Arthington, 2002). Worldwide, many rivers and streams have been leveed, straightened and lined with concrete or stone, thus removing habitat complexity (pool–riffle sequences, in-stream wood) that is essential to support diverse ecological communities (Rabeni and Jacobson, 1993). Many lakes, estuaries, coastal wetlands and mangroves have been supplanted by coastal development of harbours and 'reclaimed' residential areas, with man-made structures and materials replacing natural ones at the water's edge (Fig. 2). These physical alterations to catchment land use, topography, hydrodynamics, riparian vegetation and benthic substrates are often accompanied by increased sediment loads and terrestrially-derived chemical pollutants and nutrients (Drinkwater and Frank, 1994; Allan, 2004).

The effects of physical and chemical alterations to ecosystems have been well documented across the full range of aquatic environments (Malmqvist and Rundle, 2002; Halpern et al., 2008), but the effects on ecological connectivity have only recently begun to be fully appreciated (Bunn and Arthington, 2002; Rolls et al., 2014). Alteration or loss of habitat patches can have spatially extensive effects on meta-population and species assemblage dynamics by influencing rates of dispersal by organisms between interconnected patches (Fullerton et al., 2010).

In riverine ecosystems, the dendritic geometry of connectivity pathways strongly influences the outcomes of different types of habitat disturbance (Fagan, 2002) (Fig. 3). Some disturbances operate within the river channel to reduce or block movement of organisms at discrete points in the river network. For example, channelisation and removal of instream habitat (e.g., woody debris) can create areas of unsuitable
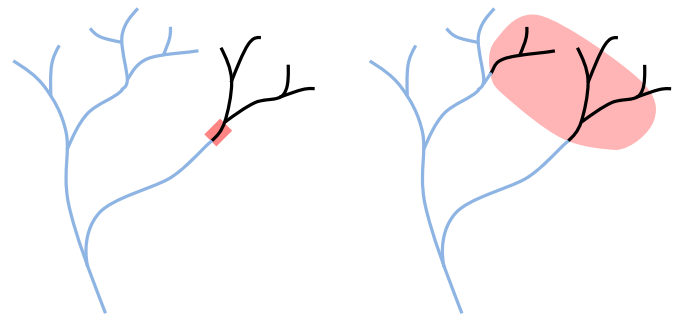
Fig. 3. Schematic of the contrasting effects of within-channel and landscape habitat disturbance on population connectivity for obligate aquatic species in dendritic river networks. The within-channel habitat disturbance (red area on left) isolates a segment of the network (black lines), but does not affect nearby segments. The landscape disturbance (red area on right) is unconstrained by the river network and isolates multiple segments that are in close proximity, but remote in terms of connectivity.

habitat that lead to the fragmentation of segments of river networks (Dodd, 1990) (Fig. 3). Other disturbances, such as fire (Brown et al., 2001) and deforestation (Alexander et al., 2011), occur over areas of the landscape that are not constrained by the dendritic river network. Because the movements of obligate aquatic organisms are constrained to the river channel, these terrestrially based disturbances can lead to a mismatch between the geometry of dispersal pathways and the geometry of landscape disturbances (Fagan, 2002). As a consequence, organisms living in habitat patches at the branch tips of the network may be remote from a connectivity perspective, but have a high correlation in their disturbance-related extinction risk due to their close proximity (Fagan, 2002) (Fig. 3).

Organisms inhabiting marine and larger lentic systems are likely to be more resilient to localised habitat alteration than those inhabiting dendritic streams and rivers due to the existence of multiple possible routes for dispersal and migration. However, the existence of these alternative pathways does not necessarily preclude strong effects on ecological connectivity. For example, Puritz and Toonen (2011) found that point sources of storm and wastewater effluent into coastal waters off California reduced genetic connectivity among populations of the

Fig. 2. Coastline of Curtis Island (Great Barrier Reef World Heritage Area) near Gladstone, Australia. Image on the left from 2005 predates construction of a liquefied natural gas facility and the image on the right is from 2011: the coastline has been straightened, estuaries replaced by reclaimed land, and high suspended sediment loads are evident. Photo credit — Kiwi (Australian Marine Conservation Society Collection).

seastar *Patiria miniata*. There is also increasing evidence that many organisms in marine and lacustrine ecosystems utilise habitat mosaics (rather than single habitat types) on a day-to-day basis, as well as throughout ontogeny (Zamora and Moreno-Amich, 2002; Sheaves, 2005; Verweij and Nagelkerken, 2007). The availability of intact habitat mosaics at scales that match species' home ranges, as well as the maintenance of connectivity pathways within the mosaic, are essential to ensure that specific habitats can be effectively utilised by organisms to perform their ecological functions (e.g., as nurseries and foraging areas) (Sheaves, 2005, 2009; Nagelkerken et al., 2015).
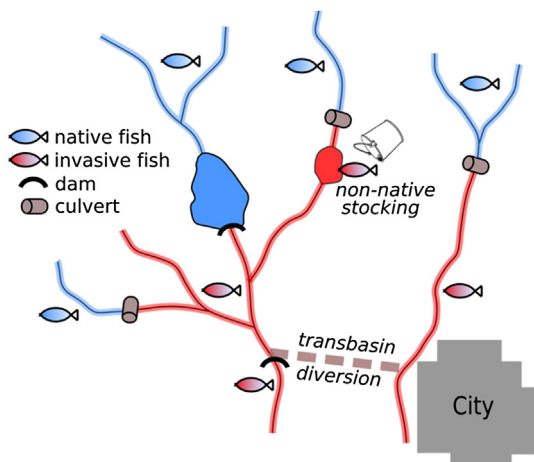
2.4. Human assisted spread of organisms

A number of human activities facilitate movements of organisms that would not occur naturally, altering species assemblages and related ecological processes. Prime examples are the construction of shipping channels (Galil et al., 2007) and the transfer of water across river basin boundaries (Grant et al., 2012) (Fig. 4). Canals now link freshwater and marine water bodies worldwide and their use has increased along with the globalisation of economies and trade (Galil et al., 2007; Rahel, 2007). The Panama and Suez Canals, for example, have re-established links between basins that had been isolated for 3 and 10 million years, respectively (Lessios, 2008; McQuarrie et al., 2003). More than 500 alien species have been recorded in the Mediterranean Sea; the majority originating from the Indo-Pacific or Indian Oceans following opening of the Suez Canal in 1869 (Galil, 2009). Inter-basin transfers of freshwater are increasingly used to help address water supply problems, both in developing and developed countries (Ghassemi and White, 2007; Grant et al., 2012). These transfers of water often facilitate the movement of biota across ancient biogeographical barriers (e.g., Waters et al., 2002). In the U.S. state of Colorado alone there are 30 active inter-basin diversions, artificially connecting major river basins on either side of the continental divide (Colorado Department of Natural Resources, 2014).

Aquatic taxa often have specific habitat requirements that create unconnected and genetically distinct populations within apparently continuous freshwater (Page and Hughes, 2014) and marine environments (Cadrin et al., 2005). As disparate areas are artificially linked via canals, inter-basin diversions and other human activities, previously restricted aquatic species can disperse to new areas, leading to a homogenisation in the species composition of aquatic biota, reduced local biodiversity, and the spread of noxious invasive species (Rahel, 2007). The invasions of the Great Lakes region in Northern America by the sea lamprey (*Petromyzon marinus*) and zebra mussel (*Dreissena polymorpha*) are graphic examples of the ability of invasive species to utilise artificial connectivity pathways, and the devastating consequences this can have on native biota and human values (Smith and Tibbles, 1980; Johnson et al., 2006).

The wave of species invasions resulting from artificial connectivity pathways has been further bolstered by the direct translocation of organisms by humans, including the intentional stocking of exotic sport fishes, escapees from aquaculture (Kochmann et al., 2012), and spread of organisms via ship ballast water and hull fouling (Rahel, 2007). Many of the organisms translocated directly by humans have resulted in major adverse ecological and economic outcomes. The deliberate translocation of the red king crab (*Paralithodes camtschaticus*) from the Bering Sea in the North Pacific Ocean to the Barents Sea in the North Atlantic Ocean during the 1960s, for example, was followed by rapid increases in the range and abundance of this species, and local and regional reductions in the abundance and diversity of indigenous marine fauna (Falk-Petersen et al., 2011). In the freshwater realm, the common carp (*Cyprinus carpio*) has been introduced to all continents except Antarctica and is considered one of the world's most destructive invasive species due to its high rate of spread and negative effects on riverine habitats (Koehn, 2004).

Once invasive species have become established in open systems such as the ocean, little can generally be done to manage connectivity pathways in order to limit their spread. In river networks, a series of management interventions is available, including the installation of artificial barriers at key locations (e.g., Pratt et al., 2009). However, the establishment of invasive species in river networks often creates a conundrum with regard to the management of ecological connectivity. This is particularly the case for populations in small, headwater streams where invasive predators have colonised downstream river reaches (Fig. 4) (Fausch et al., 2009). Small and isolated populations face an inherent extinction risk that could be reduced by removing barriers and re-establishing dispersal and gene flow throughout river networks. However, artificial barriers can prevent invasive predators and/or competitors from interacting with isolated native populations in headwaters (Rahel, 2013) (Fig. 4). Consequently, management decisions must weigh the invasion threat against the demographic and genetic risks of isolation of native populations (Fausch et al., 2009).

2.5. Climate change

Climate change driven by emissions of CO_2 and other greenhouse gases from anthropogenic sources has created widespread and continuing change to the global climate system (IPCC, 2013). These changes are shaping global trends for air and water temperature, oceanic pH, sea level, polar ice cap extent, precipitation (total and seasonal) and extreme events like drought, flood and storms (IPCC, 2013). The implications of climate change for ecological connectivity are pervasive across ecosystems and spatial scales (Krosby et al., 2010).

2.5.1. Hydrologic connectivity
Climate change will significantly alter the hydrology of rivers principally through direct and indirect changes to rainfall, temperature, evapotranspiration rates and soil moisture content (Kundzewicz et al., 2007). In broad terms, changes in hydrology will be most strongly driven by changes in patterns of precipitation and snow/ice melt, and through the strong structural effects of extreme events like droughts and floods (Aldous et al., 2011; Arnell and Gosling, 2013). Whilst changes in precipitation are not unidirectional globally (i.e., some places will get wetter and others will get drier), it is likely that the future climate will promote increased variability in river flows, both through

Fig. 4. Schematic of the interactive effects of artificial increases in aquatic connectivity. 1) Stocking of non-native game fish in a lake indicated by the bucket, 2) inter-basin diversion of stream flow to a city in a neighbouring basin (indicated by broken red/grey line). The introduced species has become invasive in both networks (red-shaded streams and lakes), driving native species to fragment into a series of isolated populations in headwaters (blue-shaded streams) above movement barriers. In this case all barriers are artificial (culverts and dams).

extended periods of low flows and through more frequent and larger flood events (Aldous et al., 2011).

In terms of ecological connectivity, the outcomes of extended periods of low or zero flows due to climate change are likely to be similar to those associated with water abstraction for consumptive use (see Section 2.2). That is, reduced longitudinal connectivity within the river network, increased physiological stress and mortality of biota due to changed physicochemical conditions (e.g., lower dissolved oxygen), and reduced frequency and extent of connectivity between river channels and their floodplains. In contrast, more frequent and extreme flooding events may connect habitats and communities that have been isolated from each other for extended periods of time (Bunn et al., 2006). This increase in connectivity may benefit some organisms (Ilg et al., 2009), but only if the floods are not so frequent and extreme as to be damaging to the newly connected habitats (Sousa et al., 2012). Indeed, because flood flows shape and restructure riverine environments, ecological communities may effectively become less stable and more variable as a consequence of more frequent and extreme flood events (Ilg et al., 2009). The interplay between species traits and adaptability to large and abrupt changes in connectivity is likely to shape the way that aquatic ecosystems and species respond to future climate change (Hadwen and Arthington, 2011).

2.5.2. Species range shifts

Climate change will also affect connectivity by changing the spatial distribution of populations and species. It has been proposed that species distributions are shifting in a generally polewards direction in response to climate change, as the geographic distributions of optimal thermal regimes change with increasing global temperatures (Parmesan and Yohe, 2003). Shifts in the spatial distributions and movement pathways of animals have broad-ranging ecological consequences (Walther et al., 2002). For example, the composition of species assemblages, and ecological interactions (competition, predation, parasitism, etc.) among component species, will be significantly altered (e.g., Winder and Schindler, 2004).

In oceanic regions showing pronounced increases in temperature, numerous range shifts of biota have already been reported (Perry et al., 2005; Last et al., 2011; Large and Yeager, 2012; Jung et al., 2014). For example, fishes with southern affinities have been reported for the first time in northern areas of the northern hemisphere (Beare et al., 2004), whilst changes in the ranges of 72% of species in the North Sea have been linked to increases in sea temperature (Simpson et al., 2011). Ocean warming also has the potential to decrease connectivity in some species. The larval stages of marine organisms tend to develop faster at higher temperatures, leading to reduced pelagic larval duration (Munday et al., 2009) and earlier settlement to benthic habitats. This can increase local retention of pelagic larvae, weaken connectivity between populations, and potentially reduce the replenishment of distant habitats and populations (Figueiredo et al., 2014). It is also likely that changes in the temporal and spatial distributions of food resources will decouple interactions among species within food webs, resulting in perturbations to the flow of energy from lower trophic levels to top order predators (Winder and Schindler, 2004; Fraser and Hoimann, 2003; Fernandes et al., 2013).

In addition to the direct effects of altered thermal regimes, climate-related changes in global topography strongly influence patterns of ecological connectivity. Long-term reductions in Arctic sea-ice cover are increasing the connectivity between the Pacific and Atlantic Oceans. Regular satellite monitoring of sea-ice extent shows that, since 2010, the minimum and maximum seasonal extents have been at or close to the lowest recorded values (National Snow and Ice Data Center, 2014). The Northeast and/or Northwest Passages between the Atlantic and Pacific Oceans have opened regularly for part of the summer since 2005 and 2007 respectively (Fig. 5). The observed trends in ice cover are expected to continue, exacerbated by the presence of younger and thinner ice (Maslanik et al., 2007).

Increases in the exchange of fauna between the Pacific and Atlantic Oceans – ranging from phytoplankton to marine mammals – have been reported in recent decades. The discovery of the Pacific diatom *Neodenticula seminae* in the North Atlantic, an area where it had been extinct for approximately 800,000 years, is believed to be linked to sea-ice retreat from the coasts of Alaska and Canada in the late 1990s (Reid et al., 2007). In the Northwest Passage, Heide-Jørgensen et al. (2012) recently documented the overlap between Atlantic and Pacific bowhead whales (*Balaena mysticetus*). A grey whale (*Eschrichtius robustus*) was also sighted in the Mediterranean Sea in 2010, when the species had not been recorded in the North Atlantic since the 1700s. Scheinina et al. (2011) concluded that this whale was most likely a member of the large North Pacific grey whale population that crossed the Arctic Ocean in the summer months following sea ice retreat. As more species move between the Atlantic and Pacific Oceans with sea-ice retreat, it is reasonable to expect that a proportion of these species will flourish in their new environments, with potential ramifications for ecosystem structure and function. In this respect, the effects of sea-ice retreat are analogous to those of the artificial connectivity pathways created by shipping canals and inter-basin water diversions (see Section 2.4).

In freshwater and estuarine ecosystems, there are fewer examples of species range shifts that can be attributed directly to the effects of climate change (Booth et al., 2011). However, as mentioned above, the potential effects of altered hydrological regimes (e.g., increased frequency of drought) and higher temperatures are well documented, and are likely drivers of change in species distributions. Statistical models linking historical and current distributional information to hydro-climatic and catchment data in freshwater ecosystems have predicted general shifts in species distributions towards higher altitudes and higher latitudes (e.g., Bond et al., 2011). This has serious implications for high-altitude endemic species, as their habitat diminishes and potential competitors and predators invade from lower altitudes (Dirnböck et al., 2011).

In comparison to more open oceanic environments, the complex topography of freshwater and estuarine ecosystems restricts the pathways through which species range shifts can occur. For example, optimal temperatures for growth of golden perch *Macquaria ambigua* in south-eastern Australia are predicted to shift southwards under the effects of climate change, yet a range shift via natural dispersal is not possible for this species due to the presence of a large mountain range that forms a major biogeographic barrier (Morrongiello et al., 2011). Whilst the effects of climate change on the distributions of freshwater and estuarine fauna are likely to be considerable, the complexity of dispersal pathways, coupled with strong interactions among species, makes accurate prediction of future range shifts particularly difficult in freshwater and estuarine ecosystems (Heino et al., 2009; Booth et al., 2011; Gillanders et al., 2011).

3. Towards an operational understanding of the outcomes of altered connectivity

Scientific understanding of the movement behaviours, dispersal patterns, and genetic structuring of populations of aquatic organisms has increased greatly over recent decades, as has our knowledge of the spatial arrangement and dynamics of aquatic habitats (Kool et al., 2013) (Text Box 1). However, whilst we can point to specific impacts of altered connectivity for particular systems (e.g., extirpation of diadromous species above dams), information on the broader effects on ecosystem processes and population viability is often lacking. This makes it difficult to assess the efficacy of potential mitigation activities and often results in sub-optimal management responses (Fullerton et al., 2010).

Stream restoration activities, for example, rarely apply a network based perspective, but often focus instead on small scale projects (Hermoso et al., 2012a) that enhance structural complexity at isolated
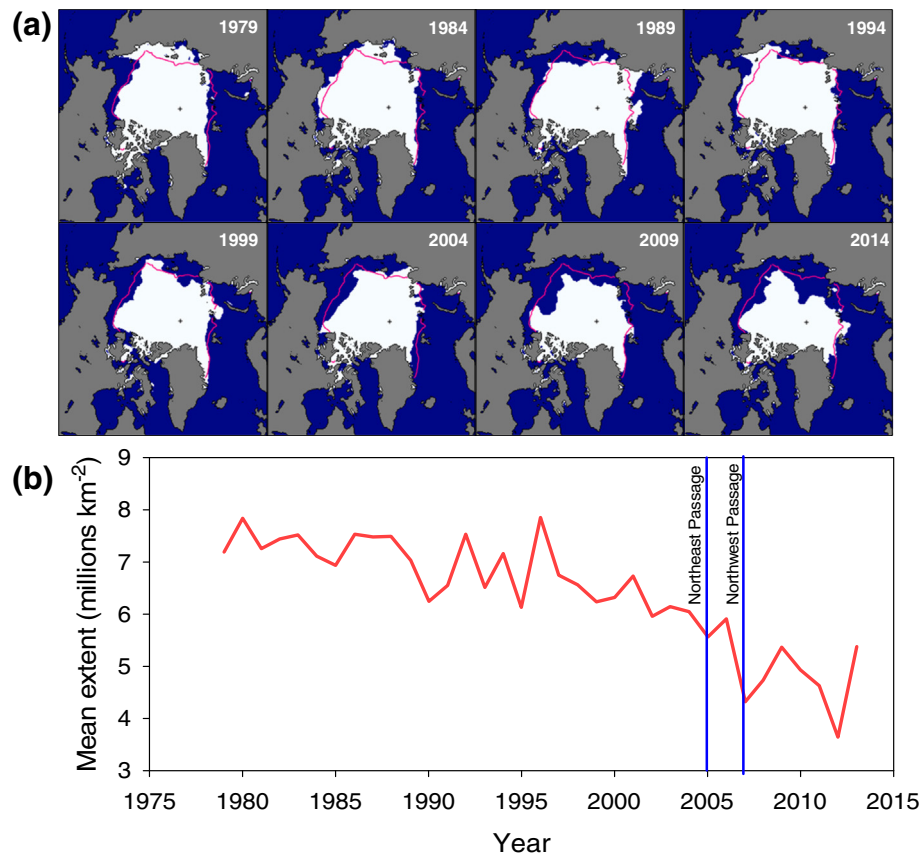
Fig. 5. (a) Five-yearly September sea ice extent (white areas) for the Arctic from 1979 to 2014. Pink line shows median ice extent from 1978 to present; (b) Mean Arctic sea-ice extent from 1979 to present. The years when the Northeast and Northwest passages between the Atlantic and Pacific Oceans were first observed to be ice-free for part of the year are shown with vertical bars. Mean extent in September is displayed because it is the month during which sea-ice extent attains its annual minimum.
Data is from the National Snow and Ice Data Center, University of Colorado, USA.

stream reaches (e.g., by adding wood and boulders) or remove physical barriers (e.g., weirs). Removal of barriers has been effective for restoring migration of many fish species (Bednarek, 2001), but will only be successful in the long-term if colonising organisms can find suitable habitats for feeding, breeding and refuge. Similarly, restoration projects that increase habitat complexity may fail to show significant improvement in stream biodiversity if planning and implementation do not account for the protection of migration routes, availability of source areas for recolonisation, and habitat conditions outside the focal reach (Lepori et al., 2005; Palmer et al., 2010).

A wide spectrum of logistical and technical challenges must be overcome to gain operational understanding of the effects of anthropogenic alterations to ecological connectivity (see Kool et al., 2013). Nonetheless, rapid methodological advances are meeting these challenges. The range of relevant techniques includes methods to elucidate the movements of individuals over relatively short timeframes (i.e., within individual lifetimes), such as mark–recapture, acoustic and radio telemetry, micro-chemical analysis of hard body parts (e.g., fish otoliths, mollusc shells), and stable isotope analysis of soft tissues. Over longer timeframes, molecular genetic techniques have been widely used to infer population connectivity from intergenerational (e.g., parentage analysis) to evolutionary (e.g., phylogenetic analysis) time scales.

Rather than being limited by the available technology, we contend that the greatest impediment to our understanding is the fact that the outcomes of altered connectivity are influenced by behavioural, developmental, physiological and environmental factors that act – and often interact – simultaneously over a wide range of spatial and temporal scales (Cowen et al., 2000; Anderson et al., 2010). In contrast,

empirical aquatic research to date has often focused on discipline- or method-specific approaches capable of addressing one or two factors at limited temporal and spatial scales. Integration of information from methods that can be applied across multiple spatial and temporal scales is the most promising way forward for understanding ecological connectivity (Fullerton et al., 2010; Kool et al., 2013). But how does this look in practice? In the following section, we use three case studies to demonstrate how the integration of complementary methods can increase the inference available from research on connectivity in aquatic ecosystems.

3.1. The Australian grayling

The Australian grayling *Prototroctes maraena* (Fig. 6) is a threatened species of diadromous fish found in coastal rivers and streams in southeastern Australia. The only other member of the genus, the New Zealand grayling *Prototroctes oxyrhynchus*, became extinct in the 1920s or 1930s, possibly due to predation by the introduced brown trout *Salmo trutta* and habitat degradation (McDowall, 2006). The distribution and abundance of Australian grayling have declined substantially since European settlement of Australia and, given the rapid extinction of its sister species, there is a very strong focus on management actions to prevent further decline (e.g., Backhouse et al., 2008).

Anecdotal observations of migration by Australian grayling were reported in the late 19th century (Saville-Kent, 1885). However, its diadromous habits were only revealed by systematic field surveys in the 1970s (Bishop and Bell, 1978; Berra, 1982). Berra (1982) observed spent adults in freshwater river reaches and noted the appearance of

Fig. 6. The three case study species. The Australian grayling *Prototroctes maraena* (left), the giant water bug *Abedus herberti* (middle) and the bull trout *Salvelinus confluentus*. Photographs: Wayne Koster (left), Michael Bogan (middle), Jason Dunham (right).

juveniles in freshwater 4–6 months after spawning, whereas larvae were never collected in freshwater, despite considerable effort. Subsequent laboratory experiments demonstrated that newly hatched larvae failed to develop in freshwater, but survived in saline water (Bacher and O'Brien, 1989). An otolith chemistry study later confirmed that all individuals spend their early life in saline water and suggested that populations from different rivers share a common marine recruitment source (Crook et al., 2006). This latter finding was subsequently supported by an analysis of inter-population variability in microsatellite and mitochondrial DNA, which reported complete genetic mixing among river systems separated by more than 400 km of coastline (Schmidt et al., 2011). Most recently, acoustic telemetry and larval drift sampling showed that adults undertake large-scale migrations from freshwater reaches to spawn in the lower reaches immediately upstream of the estuary (Koster et al., 2013).

Whilst each of these studies provides a partial picture of Australian grayling biology, the likely implications of altered connectivity only become apparent when results of the studies are considered collectively. The direct observations of Bishop and Bell (1978), Berra (1982) and Bacher and O'Brien (1989) made it clear that connectivity between the freshwater adult habitat and the sea is essential to the viability of the species, whilst the observations of Koster et al. (2013) demonstrate the importance of maintaining connectivity between upstream adult habitats and the spawning grounds in the lower freshwater reaches. The whole-of-lifetime salinity histories inferred using otolith chemistry analysis confirmed that diadromy is obligatory, thus explaining why Australian grayling do not occur above major instream barriers (Gehrke et al., 2002). Finally, the population genetics analysis of Schmidt et al. (2011) showed that populations within coastal catchments are highly connected over large temporal and spatial scales via dispersal of larvae/juveniles in the sea, suggesting that a meta-population approach to management may be appropriate for this species.

3.2. The giant water bug (Abedus herberti)

The most ubiquitous animals in river networks are invertebrates. River macroinvertebrates are dominated numerically by insects in most regions, although crustaceans attain high biomass and diversity in many tropical streams. Most aquatic insects have a terrestrial adult stage, and many crustaceans and insects without specifically terrestrial life stages can survive in the terrestrial environment at least for brief periods during some life stages (e.g., Ponniah and Hughes, 2006; Boersma and Lytle, 2015). When aquatic animals have the ability to move successfully outside of the aquatic environment, the concept of ecological connectivity changes (i.e., HWM/WGF versus SHM/DVM; Text Box 1), but the strategy of integrating information from multiple methodologies still applies.

The giant water bug *A. herberti* (Fig. 6) is an indicator species of permanent aquatic habitat in arid regions of the southwestern United States and northern Mexico (Bogan and Lytle, 2007). The species requires surface water to complete all life stages, and it lacks the ability to fly (Bogan and Boersma, 2012). However, *A. herberti* is an adept crawler, and it can survive in the terrestrial environment for up to 2 days (Christine L. Goforth, personal communication), which is long enough to migrate overland several kilometres (Lytle, 1999; Boersma and Lytle, 2015). Whilst drying of a local habitat patch is a cue for this species to crawl across terrestrial landscape, experimental manipulations of heavy "rainfall" (i.e., water sprayed from a hose onto stream pools, Lytle, 1999; Lytle et al., 2008) suggest that *A. herberti* may also crawl on the land in order to escape impending flash floods. Hence, these experimental manipulations initially suggested that *A. herberti* populations occupying neighbouring, but hydrologically unconnected, streams could be ecologically connected via overland crawling.

Traditional population genetic methods confirmed that *A. herberti* tends to fit the headwater connectivity model (HWM, Text Box 1) (Finn et al., 2007). This result is consistent with the experimental demonstration of rainfall response behaviour and the localisation of permanent aquatic habitat in headwater areas. Furthermore, a landscape genetics approach testing several models of spatial connectivity revealed that landscape concavity – including dry sections of streambed or gullies and low passes or saddles between drainages – was the best predictor of limited gene flow between populations (Phillipsen and Lytle, 2013). This combination of autecological studies of the species' basic biology, direct observations of movement behaviour, application of genetics to determine population structure across the landscape, and finer-scaled genetic studies to infer movement pathways, provides a unified picture of natural connectivity patterns for *A. herberti*.

Based on this understanding of the species' dispersal patterns and population structure, the biggest threat to the long-term viability of *A. herberti* appears to be the reduction in total area of permanent aquatic habitat in the already arid environment. Increasing frequency and severity of drought due to climate change, and intensified groundwater pumping, are converting perennial habitat into intermittent aquatic habitat. Both direct long-term monitoring of *A. herberti* populations (e.g., Bogan and Lytle, 2011) and genetic inference of population demographic stability (Finn et al., 2009) suggest that these changing conditions are driving bottlenecks and local extinctions. With decreasing habitat and more sparsely distributed populations, the already naturally low ecological connectivity will decrease further, perhaps leading to a shift from the HWM to the Death Valley model (DVM) for this species.

3.3. Native and invasive trout in western North America

Research on the threatened bull trout (*Salvelinus confluentus*) (Fig. 6) in the western USA illustrates how demographic and genetic methods complement one another to provide a full picture of the importance of connectivity for species persistence (Lowe and Allendorf, 2010). In an Idaho watershed, analytical models based on a temporal sequence of redd (spawning nests laid in gravel) counts determined that isolated headwater populations were too small to prevent impending

extinction (Rieman and McIntyre, 1993). Furthermore, genetic analysis of five populations in the 220-km^2 watershed suggested that all populations were strongly isolated from one another (Spruell et al., 1999). However, the total genetic diversity across populations was similar to healthy bull trout populations elsewhere in the species range, suggesting that increasing connectivity in this system could enhance long-term survival probability.

The invasive species of greatest concern across the bull trout's native range is the brook trout (*Salvelinus fontinalis*; native to eastern North America). In the Idaho system, however, harmful effects of brook trout appear to be minimal, according to two key observations (Neraas and Spruell, 2001). First, evidence from radio telemetry showed some bull trout juveniles from populations upstream of dams out-migrate through the dams to overwinter in downstream lakes (Swanberg, 1997; Flatter, 1998). As adults, many of these individuals return to congregate at the base of impassable dams in an upstream spawning migration, having successfully reached maturity in sympatry with downstream brook trout. Further, genetic analysis also demonstrated minimal hybridisation of bull and brook trout in this system (Neraas and Spruell, 2001). These observations, achieved by a combination of methods, suggest that increasing connectivity is a worthy conservation objective for bull trout in this watershed.

In stark contrast to the Idaho system, reducing brook trout encroachment from downstream reaches was critical to the recovery of a bull trout population in Crater Lake National Park, Oregon. Buktenica et al. (2013) studied a remnant population of bull trout in Sun Creek, a second-order headwater stream, which was found to be threatened with extinction due to competition and hybridisation with brook trout. To save the bull trout population, managers used artificial barriers, electrofishing, and piscicide applications between 1992 and 2005 to remove brook trout from a 14.6 km section of the stream and prevent further invasion from downstream reaches. Thanks to this multi-pronged effort, brook trout have not been detected in the study reach since 2005. By 2010, bull trout abundance had increased by tenfold and distribution had expanded from 1.9 km to 11.2 km of stream length. In combination, this body of work shows the value of multiple methods not only for assessing the role of connectivity in species conservation, but also for actively managing connectivity to promote recovery.

4. Key knowledge requirements

As the above discussion and case studies demonstrate, the effects of human-altered connectivity are numerous, complex, and often highly specific to the species and environment of concern. Despite rapid advances in methodologies for data gathering and modelling, there is unlikely to ever be a single approach for effective mitigation of these effects. Even when 'umbrella' or 'focal species' approaches are employed to direct conservation strategies (e.g., Lambeck, 1997; Roberge and Angelstam, 2004), each situation will require a specific integration of the most pertinent available evidence. Nonetheless, we suggest that there are four key areas of knowledge that are generally necessary, regardless of taxon, environment or methodological approach:

4.1. Autecology

Whilst autecological research may struggle to attract the interest of funding agencies and editors of high-impact journals, empirical information on the interactions between individual species and their habitats (e.g., habitat requirements, reproductive behaviour, spatial patterns in demography) is nonetheless essential for providing the building blocks upon which the taxon-specific and assemblage-level implications of altered connectivity can be explored. As a case in point, it is impossible to predict how the meta-population dynamics of a species will be affected by the destruction of habitat (e.g., mangroves in coastal areas, Fig. 2) without a thorough knowledge of their habitat

requirements across the life history. Similarly, our understanding of the spatial distributions of species within river networks – and thus how they will respond to changes in connectivity – is highly dependent on knowledge of species-specific habitat preferences in relation to the availability of habitat across the riverscape.

4.2. Population structure

Information on the spatial arrangement of populations, and the degree to which they are connected over space and time, provides the spatial template upon which alterations to pathways of ecological connectivity can be interpreted. This is traditionally the domain of population genetics research (and increasingly genomics), but is also informed by species distribution data, habitat suitability modelling, and other types of spatially explicit information. Studies of population structure have underpinned the development of conceptual models of ecological connectivity in river networks, including the Stream Hierarchy and Death Valley models (Text Box 1). Information on population structure is also critical for examining the genetic implications of linking populations via translocation and artificial connectivity pathways. For example, genetic analyses found that artificial translocation of shrimp (*Paratya australiensis*) between subcatchments resulted in the extinction of a monophyletic lineage of the species in the receiving subcatchment within 7 years (Hughes et al., 2003). This effect was attributed to a mating preference by all females (resident and translocated) for translocated males and low viability of crosses between resident females and translocated males (Hughes et al., 2003).

4.3. Movement characteristics

Movement of individual organisms is the mechanism that drives connectivity at population/meta-population scales. Without understanding when, why and how individuals move, it is difficult to develop targeted strategies to mitigate the effects of altered ecological connectivity (Lowe and McPeek, 2014). Conceptual and quantitative models utilising information on movement characteristics have been widely used to explain and/or predict changes in species distributions resulting from altered ecological connectivity. For example, a range of quantitative models have been used to predict the invasion trajectory of zebra mussels in the Great Lakes of North America (e.g., Bossenbroek et al., 2001) and rates of change in species dispersal characteristics resulting from ocean warming (e.g., O'Connor et al., 2007). As the Australian grayling case-study shows, even very basic information on movement requirements – such as whether diadromous migration is obligate – can provide critical information on the likely outcomes of altered connectivity.

4.4. Environmental tolerances/phenotypic plasticity

Information on the environmental tolerances of animals and the degree to which they are able to alter their physiology, morphology and behaviour in response to environmental change (i.e., phenotypic plasticity) is crucial for predicting their responses to altered ecological connectivity. Species with limited dispersal potential and low resilience to changing environmental conditions are particularly vulnerable to human disturbance (Crook et al., 2010). For example, in streams subject to increased drought frequency or high levels of water abstraction, species with limited ability to rapidly disperse or withstand desiccation (e.g., the giant water bug) are prone to population bottlenecks and localised extinctions (Finn et al., 2009). On the other hand, many invasive species (e.g., common carp) have very wide physiological tolerances, flexible behaviours and high dispersal ability. Such species tend to be powerful invaders of newly available habitat and often dominate in heavily disturbed environments (Koehn, 2004).

5. Conclusions

By structuring empirical research around these four broad data requirements, then using this information to parameterise appropriate models and develop management approaches (e.g., spatially explicit individual based models, Perry and Bond, 2009; graph theory networks, Erős et al., 2011, 2012; systematic conservation planning, Hermoso et al., 2012b), the field of aquatic ecology can deliver the information required to mitigate anthropogenic disturbance of ecological connectivity. Ideally, this would proceed via a strategic approach to research, with a priori objectives specifically designed to fill the most significant knowledge gaps as they emerge. In practice, the scientific process is more haphazard than this, with researchers collecting relevant data for reasons that may or may not relate to ecological connectivity, and with their own preferred methods.

Given the strong culture of individualism in science, we see integration of empirical information from multiple methodologies (telemetry, genetics, otolith chemistry, stable isotope analysis, etc.) as the most promising way to develop an empirical understanding of ecological connectivity across temporal and spatial scales (Kool et al., 2013). However, as our case studies show, the relevant data are often scattered throughout the scientific literature and must be actively assembled into coherent conceptual and quantitative frameworks. Putting the pieces of the puzzle together to develop such frameworks represents a difficult challenge — but one with exciting possibilities into the future.

References

Agostinho, A.A., Marques, E.E., Agostinho, C.S., Almeida, D.A.D., Oliveira, R.J.D., Melo, J.R.B.D., 2007. Fish ladder of Lajeado Dam: migrations on one-way routes? Neotrop. Ichthyol. 5, 121–130.

Aldous, A., Fitzsimons, J., Richter, B., Bach, L., 2011. Droughts, floods and freshwater ecosystems: evaluating climate change impacts and developing adaptation strategies. Mar. Freshw. Res. 62, 223–231.

Alexander, L.C., Hawthorne, D.J., Palmer, M.A., Lamp, W.O., 2011. Loss of genetic diversity in the North American mayfly *Ephemerella invaria* associated with deforestation of headwater streams. Freshw. Biol. 56, 1456–1467.

Allan, J.D., 2004. Landscapes and riverscapes: the influence of land use on stream ecosystems. Annu. Rev. Ecol. Syst. 35, 257–284.

Allendorf, F.W., Leary, R.F., Spruell, P., Wenburg, J.K., 2001. The problems with hybrids: setting conservation guidelines. Trends Ecol. Evol. 16, 613–622.

Allendorf, F.W., Luikart, G.H., Aitken, S.N., 2013. Conservation and the Genetics of Populations. Wiley-Blackwell, Chichester, UK.

Anderson, C.D., Epperson, B.K., Fortin, M.J., Holderegger, R., James, P., Rosenberg, M.S., Scribner, K.T., Spear, S., 2010. Considering spatial and temporal scale in landscape-genetic studies of gene flow. Mol. Ecol. 19, 3565–3575.

Arnell, N.W., Gosling, S.N., 2013. The impacts of climate change on river flow regimes at the global scale. J. Hydrol. 486, 351–364.

Arthington, A.H., Bunn, S.E., Poff, N.L., Naiman, R.J., 2006. The challenge of providing environmental flow rules to sustain river ecosystems. Ecol. Appl. 16, 1311–1318.

Arthington, A.H., Naiman, R.J., McClain, M.E., Nilsson, C., 2010. Preserving the biodiversity and ecological services of rivers: new challenges and research opportunities. Freshw. Biol. 55, 1–16.

Bacher, G.J., O'Brien, T.A., 1989. Salinity tolerance of the eggs and larvae of the Australian grayling, *Prototroctes maraena* Günther (Salmoniformes: Prototroctidae). Aust. J. Mar. Freshwat. Res. 40, 227–230.

Backhouse, G., Jackson, J., O'Connor, J., 2008. National Recovery Plan for the Australian Grayling *Prototroctes maraena*. Victorian Department of Sustainability and Environment, Melbourne.

Baran, E., Myschowoda, C., 2009. Dams and fisheries in the Mekong Basin. Aquat. Ecosyst. Health Manag. 12, 227–234.

Baumgartner, L.J., Reynoldson, N., Gilligan, D.M., 2006. Mortality of larval Murray cod (*Maccullochella peelii peelii*) and golden perch (*Macquaria ambigua*) associated with passage through two types of low-head weirs. Mar. Freshw. Res. 57, 187–191.

Beare, D.J., Burns, F., Greig, A., Jones, E.G., Peach, K., Kienzle, M., McKenzie, E., Reid, D.G., 2004. Long-term increases in prevalence of North Sea fishes having southern biogeographic affinities. Mar. Ecol. Prog. Ser. 284, 269–278.

Bednarek, A.T., 2001. Undamming rivers: a review of the ecological impacts of dam removal. Environ. Manag. 27, 803–814.

Berra, T.M., 1982. Life history of the Australian grayling, *Prototroctes maraena* (Salmoniformes: Prototroctidae) in the Tambo River, Victoria. Copeia 795–805.

Bishop, K.A., Bell, J.D., 1978. Aspects of the biology of the Australian grayling *Prototroctes maraena* Günther (Pisces: Prototroctidae). Aust. J. Mar. Freshwat. Res. 29, 743–761.

Block, B.A., Dewar, H., Blackwell, S.B., Williams, T.D., Prince, E.D., Farwell, C.J., Boustany, A., Teo, S.L.H., Seitz, A., Walli, A., Fudge, D., 2001. Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. Science 293, 1310–1314.

Boersma, K.S., Lytle, D.A., 2015. Overland dispersal and drought escape behavior in a flightless aquatic insect, *Abedus herberti* (Hemiptera: Belostomatidae). Southwest. Nat. 59, 301–302.

Bogan, M.T., Boersma, K.S., 2012. Aerial dispersal of aquatic invertebrates along and away from arid-land streams. Freshw. Sci. 31, 1131–1144.

Bogan, M.T., Lytle, D.A., 2007. Seasonal flow variation allows "time-sharing" by disparate aquatic insect communities in montane desert streams. Freshw. Biol. 52, 290–304.

Bogan, M.T., Lytle, D.A., 2011. Severe drought drives novel community trajectories in desert stream pools. Freshw. Biol. 56, 2070–2081.

Bond, N., McMaster, D., Reich, P., Thomson, J.R., Lake, P.S., 2010. Modelling the impacts of flow regulation on fish distributions in naturally intermittent lowland streams: an approach for predicting restoration responses. Freshw. Biol. 55, 1997–2010.

Bond, N., Thomson, J., Reich, P., Stein, J., 2011. Using species distribution models to infer potential climate change-induced range shifts of freshwater fish in south-eastern Australia. Mar. Freshw. Res. 62, 1043–1061.

Bond, N.R., Balcombe, S.R., Crook, D.A., Marshall, J.C., Menke, N., Lobegeiger, J.S., 2015. Fish population persistence in hydrologically variable landscapes. Ecol. Appl. http://dx.doi.org/10.1890/14-1618.1 (in press).

Booth, D.J., Bond, N.R., Macreadie, P., 2011. Detecting range shifts among Australian fishes in response to climate change. Mar. Freshw. Res. 62, 1027–1042.

Bossenbroek, J.M., Kraft, C.E., Nekola, J.C., 2001. Prediction of long-distance dispersal using gravity models: zebra mussel invasion of inland lakes. Ecol. Appl. 11, 1778–1788.

Brittain, J., Eikeland, T., 1988. Invertebrate drift — a review. Hydrobiologia 166, 77–93.

Brown, J.H., Kodric-Brown, A., 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58, 445–449.

Brown, D.K., Echelle, A.A., Propst, D.L., Brooks, J.E., Fisher, W.L., 2001. Catastrophic wildfire and number of populations as factors influencing risk of extinction for Gila trout. W. N. Am. Nat. 6, 139–148.

Buktenica, M.W., Hering, D.K., Girdner, S.F., Mahoney, B.D., Rosenlund, B.D., 2013. Eradication of nonnative brook trout with electrofishing and antimycin-A and the response of a remnant bull trout population. N. Am. J. Fish Manag. 33, 117–129.

Bunn, S.E., Arthington, A.H., 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environ. Manag. 30, 492–507.

Bunn, S.E., Thoms, M.C., Hamilton, S.K., Capon, S.J., 2006. Flow variability in dryland rivers: boom, bust and the bits in between. River Res. Appl. 22, 179–186.

Cadrin, S.X., Friedland, K.D., Waldman, J. (Eds.), 2005. Stock Identification Methods: Applications in Fishery Science. Elsevier-Academic Press, New York.

Colorado Department of Natural Resources, 2014. http://water.state.co.us/SurfaceWater/SWRights/WaterDiagrams/Pages/TransbasinDiversions.aspx (accessed 27 July, 2014).

Copp, G., 1989. The habitat diversity and fish reproductive function of floodplain ecosystems. Environ. Biol. Fish 26, 1–27.

Cowen, R.K., Lwiza, K.M., Sponaugle, S., Paris, C.B., Olson, D.B., 2000. Connectivity of marine populations: open or closed? Science 287, 857–859.

Crook, D.A., Macdonald, J.I., O'Connor, J.P., Barry, B., 2006. Use of otolith chemistry to examine patterns of diadromy in the threatened Australian grayling (*Prototroctes maraena*). J. Fish Biol. 69, 1330–1344.

Crook, D.A., Bond, N.R., Reich, P., McMaster, D., Lake, P.S., Koehn, J.D., 2010. Using biological information to support proactive strategies for managing freshwater fish during drought. Mar. Freshw. Res. 61, 379–387.

Cushman, R.M., 1985. Review of ecological effects of rapidly varying flows downstream from hydroelectric facilities. N. Am. J. Fish Manag. 5, 330–339.

Dirnböck, T., Essl, F., Rabitsch, W., 2011. Disproportional risk for habitat loss of high-altitude endemic species under climate change. Glob. Chang. Biol. 17, 990–996.

Dodd Jr., K., 1990. Effects of habitat fragmentation on a stream-dwelling species, the flattened musk turtle *Sternotherus depressus*. Biol. Conserv. 54, 33–45.

Drinkwater, K.F., Frank, K.T., 1994. Effects of river regulation and diversion on marine fish and invertebrates. Aquat. Conserv. Freshwat. Mar. Ecosyst. 4, 135.141.

Dynesius, M., Nilsson, C., 1994. Regulation of river systems in the northern third of the world. Science 266, 753–762.

Erős, T., Schmera, D., Schick, R.S., 2011. Network thinking in riverscape conservation — a graph-based approach. Biol. Conserv. 144, 184–192.

Erős, T., Olden, J.D., Schick, R.S., Schmera, D., Fortin, M.-J., 2012. Characterizing connectivity relationships in freshwaters using patch-based graphs. Landsc. Ecol. 27, 303–317.

Fagan, W.F., 2002. Connectivity, fragmentation, and extinction risk in dendritic metapopulations. Ecology 83, 3243–3249.

Falk-Petersen, J., Renaud, P., Anisimova, N., 2011. Establishment and ecosystem effects of the alien invasive red king crab (Paralithodes camtschaticus) in the Barents Sea — a review. ICES J. Mar. Sci. 68, 479–488.

Fausch, K.D., Rieman, B.E., Dunham, J.B., Young, M.K., Peterson, D.P., 2009. Invasion versus isolation: trade-offs in managing native salmonids with barriers to upstream movement. Conserv. Biol. 23, 859–870.

Fernandes, J.A., Cheung, W.W.L., Jennings, S., Butenschön, M., de Mora, L., Frölicher, T.L., Barange, M., Grant, A., 2013. Modelling the effects of climate change on the distribution and production of marine fishes: accounting for trophic interactions in a dynamic bioclimate envelope model. Glob. Chang. Biol. 19, 2596–2607.

Figueiredo, J., Baird, A.H., Harii, S., Connolly, S.R., 2014. Increased local retention of reef coral larvae as a result of ocean warming. Nat. Clim. Chang. 4, 498–502.

Finn, D.S., Blouin, M.S., Lytle, D.A., 2007. Population genetic structure reveals terrestrial affinities for a headwater stream insect. Freshw. Biol. 52, 1881–1897.

Finn, D.S., Bogan, M.T., Lytle, D.A., 2009. Demographic stability metrics for conservation prioritization of isolated populations. Conserv. Biol. 23, 1185–1194.

Flatter, B., 1998. Life history and population status of migratory bull trout (Salvelinus confluentus) in Arrowrock Reservoir, Idaho. Final Report to the U.S. Department of Interior, Bureau of Reclamation, Pacific Northwest Region. Idaho Department of Fish and Game, Boise.

Fraser, W.R., Hoimann, E.E., 2003. A predator's perspective on causal links between climate change, physical forcing and ecosystem response. Mar. Ecol. Prog. Ser. 265, 1–15.

Fullerton, A.H., Burnett, K.M., Steel, E.A., Flitcroft, R.L., Pess, G.R., Feist, B.E., Torgersen, C.E., Miller, D.J., Sanderson, B.L., 2010. Hydrological connectivity for riverine fish: measurement challenges and research opportunities. Freshw. Biol. 55, 2215–2237.

Galil, B.S., 2009. Taking stock: inventory of alien species in the Mediterranean Sea. Biol. Invasions 11, 359–372.

Galil, B.S., Nehring, S., Panov, V., 2007. Waterways as invasion highways — impact of climate change and globalization. In: Nentwig, W. (Ed.), Biological Invasions. Springer, Berlin, pp. 59–74.

Gaspar, P., Georges, J.Y., Fossette, S., Lenoble, A., Ferraroli, S., Le Maho, Y., 2006. Marine animal behaviour: neglecting ocean currents can lead us up the wrong track. Proc. R. Soc. B Biol. Sci. 273, 2697–2702.

Gehrke, P.C., Gilligan, D.M., Barwick, M., 2002. Changes in fish communities of the Shoalhaven River 20 years after construction of Tallowa Dam, Australia. River Res. Appl. 18, 265–286.

Gerlach, G., Atema, J., Kingsford, M.J., Black, K.P., Miller-Sims, V., 2007. Smelling home can prevent dispersal of reef fish larvae. Proc. Natl. Acad. Sci. U. S. A. 104, 858–863.

Ghassemi, F., White, I., 2007. Inter-basin Water Transfer: Case Studies from Australia, United States, Canada, China, and India. Cambridge University Press, Cambridge.

Gillanders, B.M., Able, K.W., Brown, J.A., Eggleston, D.B., Sheridan, P.F., 2003. Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. Mar. Ecol. Prog. Ser. 247, 281–295.

Gillanders, B.M., Elsdon, T.S., Halliday, I.A., Jenkins, G.P., Robins, J.B., Valesini, F.J., 2011. Potential effects of climate change on Australian estuaries and fish utilising estuaries: a review. Mar. Freshw. Res. 62, 1115–1131.

Gotelli, N.J., 1991. Metapopulation models: the rescue effect, the propagule rain, and the core–satellite hypothesis. Am. Nat. 138, 768–776.

Gotelli, N.J., Taylor, C.M., 1999. Testing metapopulation models with stream-fish assemblages. Evol. Ecol. Res. 1, 835–845.

Grant, E.H.C., Lowe, W.H., Fagan, W.F., 2007. Living in the branches: population dynamics and ecological processes in dendritic networks. Ecol. Lett. 10, 165–175.

Grant, E.H.C., Lynch, H.J., Muneepeerakul, R., Arunachalam, M., Rodriguez-Iturbe, I., Fagan, W.F., 2012. Interbasin water transfer, riverine connectivity, and spatial controls on fish biodiversity. PLoS ONE 7, e34170.

Hadwen, W.L., Arthington, A.H., 2011. Visitor impacts and climatic variability will shape the future ecology of Fraser Island's perched dune lakes. Proc. R. Soc. Queensland 117, 485–495.

Halpern, B.S., Walbridge, S., Selkoe, K.A., et al., 2008. A global map of human impact on marine ecosystems. Science 319, 948–952.

Heide-Jørgensen, M.P., Laidre, K.L., Quakenbush, L.T., Citta, J.J., 2012. The Northwest Passage opens for bowhead whales. Biol. Lett. 8, 270–273.

Heino, J., Virkkala, R., Toivonen, H., 2009. Climate change and freshwater biodiversity: detected patterns, future trends and adaptations in northern regions. Biol. Rev. 84, 39–54.

Hermoso, V., Pantus, F., Olley, J., Linke, S., Mugodo, J., Lea, P., 2012a. Systematic planning for river rehabilitation: integrating multiple ecological and economic objectives in complex decisions. Freshw. Biol. 57, 1–9.

Hermoso, V., Kennard, M.J., Linke, S., 2012b. Integrating multidirectional connectivity requirements in systematic conservation planning for freshwater systems. Divers. Distrib. 18, 448–458.

Hogan, Z.S., Moyle, P.B., May, B., Vander Zanden, M.J., Baird, I.G., 2004. The imperiled giants of the Mekong. Am. Sci. 92, 228–237.

Hughes, J.M., Goudkamp, K., Hurwood, D., Hancock, M., Bunn, S., 2003. Translocation causes extinction of a local population of the freshwater shrimp Paratya australiensis. Conserv. Biol. 17, 1007–1012.

Hughes, J.M., Schmidt, D.J., Finn, D.S., 2009. Genes in streams: using DNA to understand the movement of freshwater fauna and their riverine habitat. Bioscience 59, 573–583.

Igulu, M.M., Nagelkerken, I., van der Velde, G., Mgaya, Y.D., 2013. Mangrove fish production is largely fuelled by external food sources: a stable isotope analysis of fishes at the individual, species, and community levels from across the globe. Ecosystems 16, 1336–1352.

Ilg, C., Foeckler, F., Deichner, O., Henle, K., 2009. Extreme flood events favour floodplain mollusc diversity. Hydrobiologia 621, 63–73.

International Panel on Climate Change (IPCC), 2013. Climate Change 2013: The Physical Science Basis. Fifth Assessment Report of the International Panel on Climate Change Working Group, Stockholm.

Irvine, R.L., Oussoren, T., Baxter, J.S., Schmidt, D.C., 2009. The effects of flow reduction rates on fish stranding in British Columbia, Canada. River Res. Appl. 25, 405–415.

Jardine, T.D., Pusey, B.J., Hamilton, S.K., Petit, N.E., Davies, P.M., Douglas, M.M., Sinnamon, V., Halliday, I.A., Bunn, S.E., 2012. Fish mediate high food web connectivity in the lower reaches of a tropical floodplain river. Oecologia 168, 829–838.

Johnson, L.E., Bossenbroek, J.M., Kraft, C.K., 2006. Patterns and pathways in the post-establishment spread of non-indigenous aquatic species: the slowing invasion of North American inland lakes by the zebra mussel. Biol. Invasions 8, 475–489.

Jones, G.P., Milicich, M.J., Emslie, M.J., Lunow, C., 1999. Self-recruitment in a coral reef fish population. Nature 402, 802–804.

Jones, G.P., Almany, G.R., Russ, G.R., Sale, P.F., van Steneck, R.S., Oppen, M.J.H., Willis, B.L., 2009. Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. Coral Reefs 28, 307–325.

Jung, S., Pang, I.-C., Lee, J., Cha, H.K., 2014. Latitudinal shifts in the distribution of exploited fishes in Korean waters during the last 30 years: a consequence of climate change. Rev. Fish Biol. Fish. 24, 443–462.

Junk, W.J., Bayley, P.B., Sparks, R.E., 1989. The flood pulse concept in river–floodplain systems. Can. Spec. Publ. Fish. Aquat. Sci. 106, 110–127.

King, A.J., Ward, K.A., O'Connor, P., Green, D., Tonkin, Z., Mahoney, J., 2010. Adaptive management of an environmental watering event to enhance native fish spawning and recruitment. Freshw. Biol. 55, 17–31.

Kochmann, J., Carlsson, J., Crowe, T.P., Mariani, S., 2012. Genetic evidence for the uncoupling of local aquaculture activities and a population of an invasive species — a case study of Pacific oysters (Crassostrea gigas). J. Hered. 103, 661–671.

Koehn, J.D., 2004. Carp (Cyprinus carpio) as a powerful invader in Australian waterways. Freshw. Biol. 49, 882–894.

Kool, J.T., Moilanen, A., Treml, E.A., 2013. Population connectivity: recent advances and new perspectives. Landsc. Ecol. 28, 165–185.

Koster, W.M., Dawson, D.R., Crook, D.A., 2013. Downstream spawning migration by the amphidromous Australian grayling (Prototroctes maraena) in a coastal river in southeastern Australia. Mar. Freshw. Res. 64, 31–41.

Krosby, M., Tewksbury, J., Haddad, N.M., Hoekstra, J., 2010. Ecological connectivity for a changing climate. Conserv. Biol. 24, 1686–1689.

Kundzewicz, Z.W., Mata, L.J., Arnell, N.W., Döll, P., Kabat, P., Jiménez, B., Miller, K.A., Oki, T., Sen, Z., Shiklomanov, I.A., 2007. Freshwater resources and their management. In: Parry, M.L., Canziani, O.F., Palutikof, J.P., van der Linden, P.J., Hanson, C.E. (Eds.), Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK, pp. 173–210.

Lambeck, R.J., 1997. Focal species: a multi-species umbrella for nature conservation. Conserv. Biol. 11, 849–856.

Lancaster, J., 1999. Small-scale movements of lotic macroinvertebrates with variations in flow. Freshw. Biol. 41, 605–619.

Large, W.G., Yeager, S.G., 2012. On the observed trends and changes in global sea surface temperature and air–sea heat fluxes (1984–2006). J. Clim. 25, 6123–6135.

Last, P.R., White, W.T., Gledhill, D.C., Hobday, A.J., Brown, R., Edgar, G.J., Pecl, G., 2011. Long-term shifts in abundance and distribution of a temperate fish fauna: a response to climate change and fishing practices. Glob. Ecol. Biogeogr. 20, 58–72.

Lepori, F., Palm, D., Brännäs, E., Malmqvist, B., 2005. Does restoration of structural heterogeneity in streams enhance fish and macroinvertebrate diversity? Ecol. Appl. 15, 2060–2071.

Lessios, H.A., 2008. The Great American Schism: divergence of marine organisms after the rise of the Central American isthmus. Annu. Rev. Ecol. Syst. 39, 63–91.

Liermann, C.R., Nilsson, C., Robertson, J., Ng, R.Y., 2012. Implications of dam obstruction for global freshwater fish diversity. Bioscience 62, 539–548.

Lindenmayer, D.B., Fischer, J., 2006. Habitat Fragmentation and Landscape Change: An Ecological and Conservation Synthesis. Island Press, Washington, DC.

Lindenmayer, D., Hobbs, R.J., Montague-Drake, R., et al., 2008. A checklist for ecological management of landscapes for conservation. Ecol. Lett. 11, 78–91.

Lloyd, L.N., Anderson, B.G., Cooling, M., Gippel, C.J., Pope, A.J., Sherwood, J.E., 2012. Estuary Environmental Flows Assessment Methodology for Victoria. Victorian Government Department of Sustainability and Environment, Melbourne, Victoria, Australia.

Lowe, W.H., Allendorf, F.W., 2010. What can genetics tell us about population connectivity? Mol. Ecol. 19, 3038–3051.

Lowe, W.H., McPeek, M.A., 2014. Is dispersal neutral? Trends Ecol. Evol. 29, 444–450.

Lucas, M.C., Baras, E., Thom, T.J., Duncan, A., Slavík, O., 2001. Migration of Freshwater Fishes. Blackwell Science, Oxford.

Lytle, D.A., 1999. Use of rainfall cues by Abedus herberti (Hemiptera: Belostomatidae): a mechanism for avoiding flash floods. J. Insect Behav. 12, 1–12.

Lytle, D.A., Bogan, M.T., Finn, D.S., 2008. Evolution of aquatic insect behaviours across a gradient of disturbance predictability. Proc. R. Soc. B Biol. Sci. 275, 453–462.

Maguire Jr., B., 1963. The passive dispersal of small aquatic organisms and their colonization of isolated bodies of water. Ecol. Monogr. 33, 161–185.

Maheshwari, B.L., Walker, K.F., McMahon, T.A., 1995. Effects of regulation on the flow regime of the River Murray, Australia. Regul. Rivers Res. Manag. 10, 15–38.

Mallen-Cooper, M., Brand, D.A., 2007. Non-salmonids in a salmonid fishway: what do 50 years of data tell us about past and future fish passage? Fish. Manag. Ecol. 14, 319–332.

Malmqvist, B., Rundle, S., 2002. Threats to the running water ecosystems of the world. Environ. Conserv. 29, 134–153.

Maslanik, J.A., Fowler, C., Stroeve, J., Drobot, S., Zwally, J., Yi, D., Emery, W., 2007. A younger, thinner Arctic ice cover: increased potential for rapid, extensive sea-ice loss. Geophys. Res. Lett. 34, L24501.

McDowall, R.M., 1988. Diadromy in Fishes: Migrations between Freshwater and Marine Environments. Croom Helm, London.

McDowall, R.M., 2006. Crying wolf, crying foul, or crying shame: alien salmonids and a biodiversity crisis in the southern cool-temperate galaxioid fishes? Rev. Fish Biol. Fish. 16, 233–422.

McQuarrie, N., Stock, J.M., Verdel, C., Wernicke, B.P., 2003. Cenozoic evolution of Neotethys and implications for the causes of plate motions. Geophys. Res. Lett. 30, 2036.

Meffe, G.K., Vrijenhoek, R.C., 1988. Conservation genetics in the management of desert fishes. Conserv. Biol. 2, 157–169.

Montgomery, J.C., Tolimieri, N., Haine, O.S., 2001. Active habitat selection by pre-settlement reef fishes. Fish Fish. 2, 261–277.

Morrongiello, J.R., Crook, D.A., King, A.J., Ramsey, D.S., Brown, P., 2011. Impacts of drought and predicted effects of climate change on fish growth in temperate Australian lakes. Glob. Chang. Biol. 17, 745–755.

Munday, P.L., Crawley, N.E., Nilsson, G.E., 2009. Interacting effects of elevated temperature and ocean acidification on the aerobic performance of coral reef fishes. Mar. Ecol. Prog. Ser. 388, 235–242.

Nagelkerken, I.A., Sheaves, M., Baker, R., Connolly, R.M., 2015. The seascape nursery: a novel spatial approach to identify and manage nurseries for coastal marine fauna. Fish Fish. http://dx.doi.org/10.1111/faf.12057.

National Snow and Ice Data Center, 2014. http://nsidc.org/data/seaice_index/ (Accessed 15th October 2014).

Neraas, L.P., Spruell, P., 2001. Fragmentation of riverine systems: the genetic effects of dams on bull trout (Salvelinus confluentus) in the Clark Fork River system. Mol. Ecol. 10, 1153–1164.

O'Connor, M.I., Bruno, J.F., Gaines, S.D., Halpern, B.S., Lester, S.E., Kinlan, B.P., Weiss, J.M., 2007. Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. Proc. Natl. Acad. Sci. U. S. A. 104, 1266–1271.

Page, T.J., Hughes, J.M., 2014. Contrasting insights provided by single and multi-species data in a regional comparative phylogeographic study. Biol. J. Linn. Soc. 111, 554–569.

Palmer, M.A., Menninger, H.L., Bernhardt, E., 2010. River restoration, habitat heterogeneity and biodiversity: a failure of theory or practice? Freshw. Biol. 55, 205–222.

Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421, 37–42.

Perkin, E.K., Hölker, F., Richardson, J.S., Sadler, J.P., Wolter, C., Tockner, K., 2011. The influence of artificial light on stream and riparian ecosystems: questions, challenges, and perspectives. Ecosphere 2, 122.

Perry, G.L.W., Bond, N.R., 2009. Spatially explicit modeling of habitat dynamics and fish population persistence in an intermittent lowland stream. Ecol. Appl. 19, 731–746.

Perry, A.L., Low, P.J., Ellis, J.R., Reynolds, J.D., 2005. Climate change and distribution shifts in marine fishes. Science 308, 1912–1915.

Petts, G.E., 1984. Impounded Rivers: Perspectives for Ecological Management. John Wiley, Chichester, UK.

Phillipsen, I.C., Lytle, D.A., 2013. Aquatic insects in a sea of desert: population genetic structure is shaped by limited dispersal in a naturally fragmented landscape. Ecography 36, 731–743.

Polis, G.A., Power, M.E., Huxel, G.R. (Eds.), 2004. Food Webs at the Landscape Level. University of Chicago Press, Chicago, Illinois, USA.

Ponniah, M.H., Hughes, J.M., 2006. The evolution of Queensland spiny mountain crayfish of the genus Euastacus. II. Investigating simultaneous vicariance with intraspecific genetic data. Mar. Freshw. Res. 57, 349–362.

Potter, I.C., Chuwen, B.M., Hoeksema, S.D., Elliott, M., 2010. The concept of an estuary: a definition that incorporates systems which can become closed to the ocean and hypersaline. Estuar. Coast. Shelf Sci. 87, 497–500.

Pratt, T.C., O'Connor, L.M., Hallett, A.G., McLaughlin, R.L., Katopodis, C., Hayes, D.B., Bergstedt, R.A., 2009. Balancing aquatic habitat fragmentation and control of invasive species: enhancing selective fish passage at sea lamprey control barriers. Trans. Am. Fish. Soc. 138, 652–665.

Pringle, C.M., 2001. Hydrologic connectivity and the management of biological reserves: a global perspective. Ecol. Appl. 11, 981–998.

Pringle, C.M., Freeman, M.C., Freeman, B.J., 2000. Regional effects of hydrologic alterations on riverine macrobiota in the New World: tropical–temperate comparisons. Bioscience 50, 807–823.

Puritz, J.B., Toonen, R.J., 2011. Coastal pollution limits pelagic larval dispersal. Nat. Commun. 2, 226.

Rabeni, C.F., Jacobson, R.B., 1993. The importance of fluvial hydraulics to fish-habitat restoration in low-gradient alluvial streams. Freshw. Biol. 29, 211–220.

Rahel, F.J., 2007. Biogeographic barriers, connectivity and homogenization of freshwater faunas: it's a small world after all. Freshw. Biol. 52, 696–710.

Rahel, F.J., 2013. Intentional fragmentation as a management strategy in aquatic systems. Bioscience 63, 362–372.

Reid, P.C., Johns, D.G., Edwards, M., Starr, M., Poulin, M., Snoeijs, P., 2007. A biological consequence of reducing Arctic ice cover: arrival of the Pacific diatom Neodenticula seminae in the North Atlantic for the first time in 800,000 years. Glob. Chang. Biol. 13, 1910–1921.

Rieman, B.E., McIntyre, J.D., 1993. Demographic and habitat requirements for conservation of bull trout. General Technical Report INT-302. US Forest Service Intermountain Research Station, Ogden, Utah, USA.

Roberge, J.M., Angelstam, P., 2004. Usefulness of the umbrella species concept as a conservation tool. Conserv. Biol. 18, 76–85.

Rolls, R., Stewart-Koster, B., Ellison, T., Faggotter, S., Roberts, D., 2014. Multiple factors determine the effect of anthropogenic barriers to connectivity on riverine fish. Biodivers. Conserv. 23, 2201–2220.

Saville-Kent, W., 1885. Report for the year terminating 31st July, 1885. Tasmanian Parliamentary Paper No. 90, Hobart, Tasmania, Australia. Fisheries Department.

Scharbert, A., Borcherding, J., 2013. Relationships of hydrology and life-history strategies on the spatio-temporal habitat utilisation of fish in European temperate river floodplains. Ecol. Indic. 29, 348–360.

Scheinina, A.P., Kerema, D., MacLeoda, C.D., Gazoa, M., Chicotea, C.A., Castellotea, M., 2011. Gray whale (Eschrichtius robustus) in the Mediterranean Sea: anomalous event or early sign of climate-driven distribution change? Mar. Biodivers. Rec. 4, e28.

Schilt, C.R., 2007. Developing fish passage and protection at hydropower dams. Appl. Anim. Behav. Sci. 104, 295–325.

Schmidt, D.J., Crook, D.A., O'Connor, J.P., Hughes, J.M., 2011. Genetic analysis of threatened Australian grayling Prototroctes maraena suggests recruitment to coastal rivers from an unstructured marine source population. J. Fish Biol. 78, 98–111.

Sheaves, M., 2005. Nature and consequences of biological connectivity in mangrove systems. Mar. Ecol. Prog. Ser. 302, 293–305.

Sheaves, M., 2009. Consequences of ecological connectivity: the coastal ecosystem mosaic. Mar. Ecol. Prog. Ser. 391, 107–115.

Shima, J.S., Noonburg, E.G., Phillips, N.E., 2010. Life history and matrix heterogeneity interact to shape metapopulation connectivity in spatially structured environments. Ecology 91, 1215–1224.

Simpson, S.D., Jennings, S., Johnson, M.P., Blanchard, J.L., Schon, P.-J., Sims, D.W., Genner, M.J., 2011. Continental shelf-wide response of a fish assemblage to rapid warming of the sea. Curr. Biol. 21, 1565–1570.

Smith, B.R., Tibbles, J.J., 1980. Sea lamprey (Petromyzon marinus) in Lakes Huron, Michigan, and Superior: history of invasion and control, 1936–78. Can. J. Fish. Aquat. Sci. 37, 1780–1801.

Sousa, R., Varandas, S., Cortes, R., Teixeira, A., Lopes-Lima, M., Machado, J., Guilhermino, L., 2012. Massive die-offs of freshwater bivalves as resource pulses. Int. J. Limnol. 48, 105–112.

Spruell, P., Rieman, B.E., Knudsen, K.L., Utter, F.M., Allendorf, F.W., 1999. Genetic population structure within streams: microsatellite analysis of bull trout populations. Ecol. Freshw. Fish 8, 114–121.

Swanberg, T.R., 1997. Movements of and habitat use by fluvial bull trout in the Blackfoot River, Montana. Trans. Am. Fish. Soc. 126, 735–746.

Swearer, S.E., Caselle, J.E., Lea, D.W., Warner, R.R., 1999. Larval retention and recruitment in an island population of a coral-reef fish. Nature 40, 799–802.

Taylor, P.D., Fahrig, L., Henein, K., Merriam, G., 1993. Connectivity is a vital element of landscape structure. Oikos 68, 571–572.

Tesch, F.-W., 2003. The Eel. Blackwell Science, Oxford.

Tharme, R.E., 2003. A global perspective on environmental flow assessment: emerging trends in the development and application of environmental flow methodologies for rivers. River Res. Appl. 19, 397–441.

Verweij, M.C., Nagelkerken, I., 2007. Short and long-term movement and site fidelity of juvenile Haemulidae in back-reef habitats of a Caribbean embayment. Hydrobiologia 592, 257–270.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J., Fromentin, J.-M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. Nature 416, 389–395.

Ward, J.V., Stanford, J.A., 1995. Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. Regul. Rivers Res. Manag. 11, 105–119.

Warren, M.L., Pardew, M.G., 1998. Road crossings as barriers to small-stream fish movements. Trans. Am. Fish. Soc. 127, 637–644.

Waters, J.M., Shirley, M., Closs, G.P., 2002. Hydroelectric development and translocation of Galaxias brevipinnis: a cloud at the end of the tunnel? Can. J. Fish. Aquat. Sci. 59, 49–56.

Williams, D.D., Williams, N.E., 1993. The upstream/downstream movement paradox of lotic invertebrates: quantitative evidence from a Welsh mountain stream. Freshw. Biol. 30, 199–218.

Williams, J.G., Armstrong, G., Katopodis, C., Larinier, M., Travade, F., 2012. Thinking like a fish: a key ingredient for development of effective fish passage facilities at river obstructions. River Res. Appl. 28, 407–417.

Winder, M., Schindler, D.E., 2004. Climate change uncouples trophic interactions in an aquatic ecosystem. Ecology 85, 2100–2106.

Xie, P., 2003. Three-Gorges Dam: risk to ancient fish. Science 302, 1149.

Zamora, L., Moreno-Amich, R., 2002. Quantifying the activity and movement of perch in a temperate lake by integrating acoustic telemetry and a geographic information system. Hydrobiologia 483, 209–218.