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

David A. Crook[1*], Winsor H. Lowe[2], Frederick W. Allendorf[2], Tibor Erős[3], Debra S. Finn[4], Bronwyn M. Gillanders[5], Wade L. Hadwen[6], Chris Harrod[7], Virgilio Hermoso[6], Simon Jennings[8], Raouf W. Kilada[9], Ivan Nagelkerken[5], Michael M. Hansen[10], Timothy J. Page[6], Cynthia Riginos[11], Brian Fry[6], Jane M. Hughes[6]

[1] Research Institute for the Environment and Livelihoods, Charles Darwin University, Darwin, Northern Territory, 0909, Australia.

[2] Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA.

[3] Balaton Limnological Institute, Centre for Ecological Research, Hungarian Academy of Sciences, Tihany, Klebelsberg, K.u. 3., H-8237, Hungary.

[4] Department of Integrative Biology, Oregon State University, Corvallis, Oregon 97331 USA; and Departamento de Recursos Hídricos y Ciencias Ambientales, Universidad de Cuenca, Cuenca, Ecuador.

[5] Southern Seas Ecology Laboratories, School of Biological Sciences and The Environment Institute, DX 650 418, The University of Adelaide, Adelaide, SA 5005, Australia.

[6] Australian Rivers Institute, Griffith University, Nathan, Qld 4111, Australia

[7] Instituto de Ciencias Naturales Alexander Von Humboldt, Universidad de Antofagasta, Avenida Angamos 601, Antofagasta, Chile.

[8] Centre for Environment, Fisheries and Aquaculture Science (CEFAS), Lowestoft Laboratory, Lowestoft, NR33 0HT, UK and School of Environmental Sciences, University of East Anglia, Norwich, NR4 7TJ, UK.

[9] Biology Department, University of New Brunswick (Saint John), Canada.

[10] Department of Bioscience, Aarhus University, Ny Munkegade, Bldg. 1540, DK-8000 Aarhus C, Denmark.

[11] School of Biological Sciences, The University of Queensland, St Lucia, Qld, Australia 4072.

*Corresponding author: Research Institute for the Environment and Livelihoods, Charles Darwin University, Darwin, Northern Territory, 0909. Ph: +61 (8) 8946 6285. (david.crook@cdu.edu.au).

Highlights:

- Human effects on ecological connectivity in aquatic ecosystems are reviewed.
- Threats include: habitat loss, altered hydrology, invasive species, 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.

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.

Keywords: fragmentation; dispersal; migration; meta-population; source-sink; climate change

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 & 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 & 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

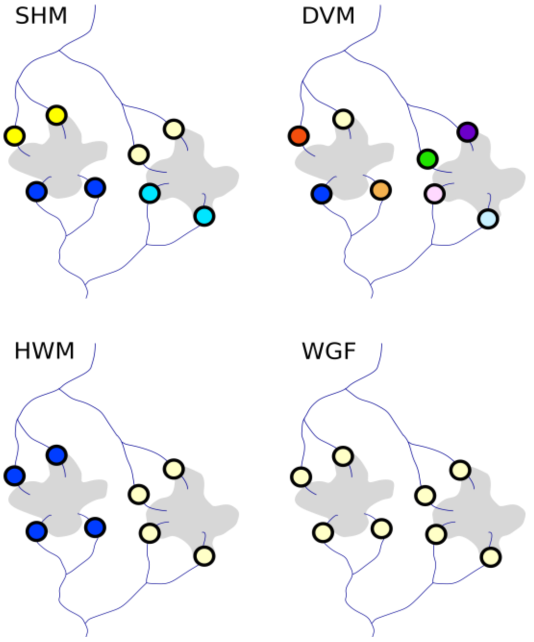
Aquatic ecosystems encompass a diverse array of physical configurations, ranging from ‘open’ systems like oceans, to isolated waterholes in arid landscapes. Based on the spatial structure and physical characteristics of marine, freshwater and estuarine habitats, one might expect different ‘rules’ for 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).

Text box 1

Models of ecological connectivity in streams

The **stream hierarchy model** (SHM, Meffe & 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 **Death Valley model** (DVM, Meffe & 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 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 **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.

(Colour figure print and electronic)

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, 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 or 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 & 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 fresh water and the sea to complete their life cycles: some reproduce in freshwater but require marine habitats for growth (‘anadromy’, ‘amphidromy’), while others reproduce in marine habitats but spend most of their lives in fresh water (‘catadromy’) (McDowall, 1988). The catadromous migration of up to 6,000 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 & 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 & 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 or 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 regards 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 & Nielsen 1994). Nevertheless, construction and planning of new dams proceeds apace, particularly in developing regions of the world [e.g. Yangtze River, China (Xie 2003); Lower Mekong Basin, Thailand, Laos, Cambodia (Baran & 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 & 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 & 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 4,000 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 & 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).

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 & 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 & 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 fresh water 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 & 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 & 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 & 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 & Rundle 2002; Halpern et al. 2008), but the effects on ecological connectivity have only recently begun to be fully appreciated (Bunn & 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 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 & Toonen (2011) found that point sources of storm and wastewater effluent into coastal waters off California reduced genetic connectivity among populations of the 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 & Moreno-Amich 2002; Sheaves 2005; Verweij & 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 or 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 & 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 & 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 & 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 regards 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 & 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 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 above). 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 & 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 & 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 & 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 & 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 & Schindler 2004; Fraser & 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, while 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 stream reaches (e.g., by adding wood, boulders, etc.) 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 time frames (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 time frames, 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 south-eastern Australia. The only other member of the genus, the New Zealand grayling *P. oxyrhynchus*, became extinct in the 1920s or 1930s, possibly due to predation by 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 & Bell 1978; Berra 1982). Berra (1982) observed spent adults in freshwater river reaches and noted the appearance of 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 & 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. 2010). 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).

While 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 & Bell

(1978), Berra (1982) and Bacher & 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. (2010) 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 & Hughes 2006, Boersma & Lytle *in press*). 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 *Abedus 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 & 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 & Lytle *in press*). 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 & 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 & 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 & 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 & 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 & 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 & 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 not only shows the value of multiple methods 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 modeling, 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 Anglestam 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:

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.

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 modeling, 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).

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 & 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.

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 & 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.

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References

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

Aldous, A., Fitzsimons, J., Richter, B. & Bach, L. Droughts, floods and freshwater ecosystems: evaluating climate change impacts and developing adaptation strategies. Marine and Freshwater Research 2011; 62: 223-231.

Alexander, L. C., Hawthorne, D. J., Palmer, M. A., & Lamp, W. O. Loss of genetic diversity in the North American mayfly *Ephemerella invaria* associated with deforestation of headwater streams. Freshwater Biology 2011; 56: 1456-1467.

Allan, J.D. Landscapes and riverscapes: the influence of land use on stream ecosystems. Annual Review of Ecology and Systematics 2004; 35: 257-284.

Allendorf, F.W., Leary, R.F., Spruell, P. & Wengurg, J.K. The problems with hybrids: setting conservation guidelines. Trends in Ecology and Evolution 2001; 16: 613-622.

Allendorf, F.W., Luikart, G.H. & Aitken, S.N. Conservation and the Genetics of Populations. 2013; 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. Considering spatial and temporal scale in landscape-genetic studies of gene flow. Molecular Ecology2010; 19: 3565-3575.

Arnell, N. W. & Gosling, S. N. The impacts of climate change on river flow regimes at the global scale. Journal of Hydrology 2013; 486: 351-364.

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

Arthington, A.H., Naiman, R. J. McClain, M. E. & Nilsson, C. Preserving the biodiversity and ecological services of rivers: new challenges and research opportunities. Freshwater Biology 2010; 55: 1-16.

Bacher, G. J. & O'Brien, T. A. Salinity tolerance of the eggs and larvae of the Australian grayling, *Prototroctes maraena* Günther (Salmoniformes: Prototroctidae). Australian Journal of Marine and Freshwater Research 1989; 40: 227-230.

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

Baran, E. & Myschowoda, C. Dams and fisheries in the Mekong Basin. Aquatic Ecosystem Health & Management 2009; 12: 227-234.

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

Beare, D.J., Burns, F., Greig, A., Jones, E.G. Peach, K., Kienzle, M., McKenzie, E. & Reid, D.G. Long-term increases in prevalence of North Sea fishes having southern biogeographic affinities. Marine Ecology Progress Series 2004; 284: 269–278.

Bednarek, A.T. Undamming rivers: a review of the ecological impacts of dam removal. Environmental Management 2001; 27: 803-814.

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

Bishop, K.A. & Bell, J.D. Aspects of the biology of the Australian grayling *Prototroctes maraena* Günther (Pisces : Prototroctidae). Australian Journal of Marine and Freshwater Research 1978; 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. Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. Science 2001; 293 1310-1314.

Boersma, K.S., & D.A. Lytle. Overland dispersal and drought escape behavior in a flightless aquatic insect, *Abedus herberti* (Hemiptera: Belostomatidae). Southwestern Naturalist, *in press*.

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

Bogan, M.T. & Lytle, D.A. Severe drought drives novel community trajectories in desert stream pools. Freshwater Biology 2011; 56: 2070-2081.

Bogan, M.T. & Boersma, K.S. Aerial dispersal of aquatic invertebrates along and away from arid-land streams. Freshwater Science 2012; 31: 1131-1144.

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

Bond, N., Thomson, J, Reich, P., & Stein, J. Using species distribution models to infer potential climate change-induced range shifts of freshwater fish in south-eastern Australia. Marine and Freshwater Research 2011; 62, 1043–1061.

Bond, N.R., Balcombe, S.R., Crook, D.A., Marshall, J.C., Menke, N. & Lobegeiger, J.S. Fish population persistence in hydrologically variable landscapes. Ecological Applications *in press*; http://dx.doi.org/10.1890/14-1618.1

Booth, D.J., Bond, N.R. & Macreadie, P. Detecting range shifts among Australian fishes in response to climate change. Marine and Freshwater Research 2011; 62: 1027-1042.

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

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

Brown, D.K., Echelle, A.A. Propst, D.L. Brooks, J.E. & Fisher, W.L. Catastrophic wildfire and number of populations as factors influencing risk of extinction for Gila trout. Western North American Naturalist 2001; 6: 139–148.

Brittain, J. & Eikeland, T. Invertebrate drift — A review. Hydrobiologia 1988; 166: 77-93.

Buktenica, M.W., Hering, D.K., Girdner, S.F., Mahoney, B.D., & Rosenlund, B.D. Eradication of nonnative brook trout with electrofishing and antimycin-A and the response of a remnant bull trout population. North American Journal of Fisheries Management 2013; 33: 117–129.

Bunn, S.E., Thoms, M.C., Hamilton, S.K. & Capon, S.J. Flow variability in dryland rivers: boom, bust and the bits in between. River Research and Applications 2006; 22: 179-186.

Bunn, S.E., & AH. Arthington. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environmental Management 2002; 30: 492–507.

Cadrin, S.X., Friedland, K.D., & Waldman, J. (eds). Stock identification methods: applications in fishery science. 2005. 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. The habitat diversity and fish reproductive function of floodplain ecosystems. Environmental Biology of Fishes 1989; 26: 1-27.

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

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

Crook, D.A., Bond, N.R. Reich, P., McMaster, D., Lake, P.S. & Koehn. J.D. Using biological information to support proactive strategies for managing freshwater fish during drought. Marine and Freshwater Research 2010; 61, 379-387.

Cushman, R. M. Review of ecological effects of rapidly varying flows downstream from hydroelectric facilities. North American Journal of Fisheries Management 1985; 5: 330-339.

Dirnböck, T., Essl, F. & Rabitsch, W. Disproportional risk for habitat loss of high-altitude endemic species under climate change. Global Change Biology 2011; 17: 990–996.

Dodd Jr, K. Effects of habitat fragmentation on a stream-dwelling species, the flattened musk turtle *Sternotherus depressus*. Biological Conservation 1990; 54: 33-45.

Drinkwater, K.F. & Frank, K.T. Effects of river regulation and diversion on marine fish and invertebrates. Aquatic Conservation: Freshwater and Marine Ecosystems 1994; 4: 135.141.

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

Erős, T., Schmera, D., & Schick, R.S. Network thinking in riverscape conservation–a graph-based approach. Biological Conservation 2011; 144: 184-192.

Erős, T., Olden, J.D., Schick, R.S., Schmera, D., & Fortin, M-J. Characterizing connectivity relationships in freshwaters using patch-based graphs. Landscape Ecology 2012; 27: 303-317.

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

Falk-Petersen, J., Renaud, P., & Anisimova, N. Establishment and ecosystem effects of the alien invasive red king crab (*Paralithodes camtschaticus*) in the Barents Sea – a review. ICES Journal of Marine Science 2011; 68: 479-488.

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

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

Figueiredo, J., Baird, A.H., Harii, S., & Connolly, S.R. Increased local retention of reef coral larvae as a result of ocean warming. Nature Climate Change 2014; 4: 498-502

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

Finn, D.S., Bogan, M.T., & Lytle, D.A. Demographic stability metrics for conservation prioritization of isolated populations. Conservation Biology 2009; 23: 1185–1194.

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

Fraser, W.R., & Hoimann, E.E. A predator's perspective on causal links between climate change, physical forcing and ecosystem response. Marine Ecology Progress Series 2003; 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. Hydrological connectivity for riverine fish: measurement challenges and research opportunities. Freshwater Biology 2010; 55: 2215–2237.

Galil, B.S., Nehring, S., & Panov, V. Waterways as invasion highways - impact of climate change and globalization. 2007. *In:* Nentwig W. (ed). Biological Invasions. Springer Berlin, 59-74.

Galil, B.S. Taking stock: inventory of alien species in the Mediterranean sea. Biological Invasions 2009; 11, 359-372.

Gaspar, P., Georges, J.Y., Fossette, S., Lenoble, A., Ferraroli, S., & Le Maho, Y. Marine animal behaviour: neglecting ocean currents can lead us up the wrong track. Proceedings of the Royal Society B: Biological Sciences 2006; 273: 2697-2702.

Gehrke, P.C., Gilligan, D.M., & Barwick, M. Changes in fish communities of the Shoalhaven River 20 years after construction of Tallowa Dam, Australia. River Research and Applications 2002; 18: 265-286.

Gerlach, G., Atema, J., Kingsford, M.J., Black, K.P., & Miller-Sims, V. Smelling home can prevent dispersal of reef fish larvae. Proceedings of the National Academy of Sciences of the United States of America 2007; 104, 858-863.

Ghassemi, F, & White, I. Inter-basin water transfer: case studies from Australia, United States, Canada, China, and India. 2007. Cambridge University Press, Cambridge.

Gillanders, B.M., Able, K.W., Brown, J.A., Eggleston, D.B. & Sheridan, P.F. Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. Marine Ecology Progress Series 2003; 247: 281-295.

Gillanders, B.M., Elsdon, T.S., Halliday, I.A., Jenkins, G.P., Robins, J.B., & Valesini, F.J. Potential effects of climate change on Australian estuaries and fish utilising estuaries: a review. Marine and Freshwater Research 2011; 62: 1115-1131.

Gotelli, N.J. Metapopulation models: the rescue effect, the propagule rain, and the core-satellite hypothesis. American Naturalist 1991; 138: 768-776.

Gotelli, N.J., & Taylor, C.M. Testing metapopulation models with stream-fish assemblages. Evolutionary Ecology Research 1999; 1:835–845.

Grant, E.H.C., Lowe, W.H. & Fagan, W.F. Living in the branches: population dynamics and ecological processes in dendritic networks. Ecology Letters 2007; 10: 165-175.

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

Hadwen, W.L. & Arthington, A.H. Visitor impacts and climatic variability will shape the future ecology of Fraser Island's perched dune lakes. Proceedings of the Royal Society of Queensland 2011; 117: 485-495.

Halpern, B. S., Walbridge, S., Selkoe, K. A., & 16 other authors. A global map of human impact on marine ecosystems. Science 2008; 319: 948-952.

Heide-Jørgensen, M.P., Laidre, K.L., Quakenbush, L.T., & Citta, J.J. The Northwest Passage opens for bowhead whales. Biology Letters 2012; 8: 270–273.

Heino, J., Virkkala, R., & Toivonen, H. Climate change and freshwater biodiversity: detected patterns, future trends and adaptations in northern regions. Biological Reviews 2009; 84: 39-54.

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

Hermoso, V., Kennard, M.J., & Linke, S. Integrating multidirectional connectivity requirements in systematic conservation planning for freshwater systems. Diversity and Distributions 2012b; 18: 448-458.

Hogan, Z.S., Moyle, P.B., May, B., Vander Zanden, M.J. & Baird, I.G. The imperiled giants of the Mekong. American Scientist 2004; 92, 228-237.

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

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

Igulu, M.M., Nagelkerken, I., van der Velde, G., & Mgaya, Y.D. 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 2013; 16: 1336-1352.

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

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

Irvine, R. L., Oussoren, T., Baxter, J. S., & Schmidt, D. C. The effects of flow reduction rates on fish stranding in British Columbia, Canada. River Research and Applications 2009; 25: 405-415.

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

Johnson, L.E., Bossenbroek, J.M. & Kraft, C.K. 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. Biological Invasions 2006; 8, 475-489.

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

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

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

Junk, W.J., Bayley, P.B., & Sparks, R.E. The flood pulse concept in river-floodplain systems. Canadian Special Publication of Fisheries and Aquatic Sciences 1989; 106: 110-127.

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

Kochmann, J., Carlsson, J., Crowe, T.P., & Mariani, S. Genetic evidence for the uncoupling of local aquaculture activities and a population of an invasive species-a case study of pacific oysters (*Crassostrea gigas*). Journal of Heredity 2012; 103: 661-671.

Koehn, J.D. Carp (*Cyprinus carpio*) as a powerful invader in Australian waterways. Freshwater Biology 2004; 49, 882-894.

Kool, J.T., Moilanen, A., & Treml, E.A. Population connectivity: recent advances and new perspectives. Landscape Ecology 2013; 28: 165-185.

Koster, W.M., Dawson, D.R., & Crook, D.A. Downstream spawning migration by the amphidromous Australian grayling (*Prototroctes maraena*) in a coastal river in south-eastern Australia. Marine and Freshwater Research 2013; 64: 31-41.

Krosby, M., Tewksbury, J., Haddad, N. M., & Hoekstra, J. Ecological connectivity for a changing climate. Conservation Biology 2010; 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. Freshwater resources and their management. Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. 2007. Parry, M.L., Canziani, O.F., Palutikof, J.P., van der Linden, P.J., & Hanson, C.E. (eds). Cambridge University Press: Cambridge, UK; 173–210.

Lambeck, R.J. Focal species: a multi-species umbrella for nature conservation. Conservation Biology 1997; 11: 849-856.

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

Large, W.G. & Yeager, S.G. On the observed trends and changes in global sea surface temperature and air-sea heat fluxes (1984–2006). Journal of Climate 2012; 25: 6123–6135.

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

Lepori, F., Palm, D., Brännäs, E., & Malmqvist, B. Does restoration of structural heterogeneity in streams enhance fish and macroinvertebrate diversity? Ecological Applications 2005; 15: 2060-2071.

Lessios, H.A. The Great American schism: Divergence of marine organisms after the rise of the Central American isthmus. Annual Review of Ecology and Systematics 2008; 39: 63-91.

Liermann, C.R., Nilsson, C., Robertson, J., & Ng, R.Y. Implications of dam obstruction for global freshwater fish diversity. BioScience 2012; 62: 539-548.

Lindenmayer, D.B., & Fischer, J. Habitat fragmentation and landscape change: an ecological and conservation synthesis. 2006. Island Press, Washington DC.

Lindenmayer, D., Hobbs, R.J., Montague-Drake, R.& 34 other authors. A checklist for ecological management of landscapes for conservation. Ecology Letters 2008; 11: 78-91.

Lloyd, L.N., Anderson, B.G., Cooling, M., Gippel, C.J., Pope, A.J. & Sherwood, J.E. Estuary environmental flows assessment methodology for Victoria. 2012. Victorian Government Department of Sustainability and Environment, Melbourne, Victoria, Australia.

Lowe, W.H., & Allendorf, F.W. What can genetics tell us about population connectivity? Molecular Ecology 2010; 19: 3038-3051.

Lowe, W.H., & McPeek, M.A. Is dispersal neutral? Trends in Ecology and Evolution 2014; 29: 444-450.

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

Lytle, D.A. Use of rainfall cues by *Abedus herberti* (Hemiptera : Belostomatidae): A mechanism for avoiding flash floods. Journal of Insect Behavior 1999; 12: 1–12.

Lytle, D.A., Bogan, M.T., & Finn, D.S. Evolution of aquatic insect behaviours across a gradient of disturbance predictability. Proceedings of the Royal Society B-Biological Sciences 2008; 275: 453-462.

Maguire, B. Jr. The passive dispersal of small aquatic organisms and their colonization of isolated bodies of water. Ecological Monographs 1963; 33: 161-185.

Maheshwari, B.L., Walker, K.F., & McMahon, T.A. Effects of regulation on the flow regime of the River Murray, Australia. Regulated Rivers: Research and Management 1995; 10: 15-38.

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

Malmqvist, B. & Rundle, S. Threats to the running water ecosystems of the world. Environmental Conservation 2002; 29: 134-153.

Maslanik, J.A., Fowler, C. Stroeve, J. Drobot, S. Zwally, J. Yi, D. & Emery, W. A younger, thinner Arctic ice cover: Increased potential for rapid, extensive sea-ice loss. Geophysical Research Letters 2007; 34: L24501.

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

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

McQuarrie, N., Stock, J.M., Verdel, C., & Wernicke, B.P. Cenozoic evolution of Neotethys and implications for the causes of plate motions. Geophysical Research Letters 2003; 30: 2036.

Meffe, G.K. & Vrijenhoek, R.C. Conservation genetics in the management of desert fishes. Conservation Biology 1988; 2: 157–169.

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

Morrongiello, J.R., Crook, D.A., King, A.J., Ramsey, D.S., & Brown, P. Impacts of drought and predicted effects of climate change on fish growth in temperate Australian lakes. Global Change Biology 2011; 17: 745-755.

Munday, P.L., Crawley, N.E., & Nilsson, G.E. Interacting effects of elevated temperature and ocean acidification on the aerobic performance of coral reef fishes. Marine Ecology Progress Series 2009; 388: 235-242.

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

National Snow and Ice Data Center, 2012 (http://nsidc.org/data/seaice_index/). Accessed 15th October 2014.

Neraas, L.P., & Spruell, P. Fragmentation of riverine systems: the genetic effects of dams on bull trout (*Salvelinus confluentus*) in the Clark Fork River system. Molecular Ecology 2001; 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. Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. Proceedings of the national Academy of Sciences of the United States of America 2007; 104, 1266-1271.

Page, T.J., & Hughes, J.M. Contrasting insights provided by single and multi-species data in a regional comparative phylogeographic study. Biological Journal of the Linnean Society 2014; 111: 554–569.

Palmer, M.A., Menninger, H.L., & Bernhardt, E. River restoration, habitat heterogeneity and biodiversity: a failure of theory or practice? Freshwater Biology 2010; 55: 205-222.

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

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

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

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

Petts, G.E. Impounded rivers: perspectives for ecological management. 1984. John Wiley, Chichester, UK.

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

Polis, G.A., Power, M.E. & Huxel, G.R. (Eds). Food webs at the landscape level. 2004. University of Chicago Press, Chicago, Illinois, USA.

Ponniah, M.H., & Hughes, J.M.,. The evolution of Queensland spiny mountain crayfish of the genus *Euastacus*. II. Investigating simultaneous vicariance with intraspecific genetic data. Marine and Freshwater Research 2006; 57: 349–362.

Potter, I.C., Chuwen, B.M., Hoeksema, S.D., & Elliott, M. The concept of an estuary: A definition that incorporates systems which can become closed to the ocean and hypersaline. Estuarine and Coastal Shelf Science 2010; 87: 497-500.

Pratt, T.C., O'Connor, L.M., Hallett, A.G., McLaughlin, R.L., Katopodis, C., Hayes, D.B., & Bergstedt, R.A. Balancing aquatic habitat fragmentation and control of invasive species: enhancing selective fish passage at sea lamprey control barriers. Transactions of the American Fisheries Society 2009; 138, 652-665.

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

Pringle, C.M. Hydrologic connectivity and the management of biological reserves: a global perspective. Ecological Applications 2001; 11: 981-998.

Puritz, J.B., & Toonen, R.J. Coastal pollution limits pelagic larval dispersal. Nature Communications 2011; 2: 226.

Rabeni, C.F., & Jacobson, R.B. The importance of fluvial hydraulics to fish-habitat restoration in low-gradient alluvial streams. Freshwater Biology 1993; 29: 211-220.

Rahel, F.J. Biogeographic barriers, connectivity and homogenization of freshwater faunas: it's a small world after all. Freshwater Biology 2007; 52: 696-710.

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

Reid, P.C., Johns, D.G., Edwards, M., Starr, M., Poulin, M. & Snoeijs, P. 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. Global Change Biology 2007; 13: 1910-1921.

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

Roberge, J. M., & Angelstam, P. Usefulness of the umbrella species concept as a conservation tool. Conservation Biology 2004; 18: 76-85.

Rolls, R., Stewart-Koster, B., Ellison, T., Faggotter, S. & Roberts, D. Multiple factors determine the effect of anthropogenic barriers to connectivity on riverine fish. Biodiversity and Conservation 2014; 23: 2201-2220.

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

Scharbert, A. & Borcherding, J. Relationships of hydrology and life-history strategies on the spatio-temporal habitat utilisation of fish in European temperate river floodplains. Ecological Indicators 2013; 29: 348-360.

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

Schilt, C.R. Developing fish passage and protection at hydropower dams. Applied Animal Behaviour Science 2007; 104: 295–325.

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

Sheaves, M. Nature and consequences of biological connectivity in mangroves systems. Marine Ecology Progress Series 2005; 302: 293-305.

Sheaves, M. Consequences of ecological connectivity: the coastal ecosystem mosaic. Marine Ecology Progress Series 2009; 391: 107-115.

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

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

Smith, B.R. & Tibbles, J.J. Sea lamprey (*Petromyzon marinus*) in Lakes Huron, Michigan, and Superior: history of invasion and control, 1936–78. Canadian Journal of Fisheries and Aquatic Sciences 1980; 37, 1780-1801.

Sousa, R., Varandas, S., Cortes, R., Teixeira, A., Lopes-Lima, M., Machado, J. & Guilhermino, L. Massive die-offs of freshwater bivalves as resource pulses. International Journal of Limnology 2012; 48: 105-112.

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

Swanberg, T.R. Movements of and habitat use by fluvial bull trout in the Blackfoot River, Montana. Transactions of the American Fisheries Society 1997; 126: 735-746.

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

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

Tesch, F-W. The eel. 2003; Blackwell Science, Oxford.

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

Verweij, M.C., & Nagelkerken, I. Short and long-term movement and site fidelity of juvenile Haemulidae in back-reef habitats of a Caribbean embayment. Hydrobiologia 2007; 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. Ecological responses to recent climate change. Nature 2002; 416: 389-395.

Ward, J.V. & Stanford, J.A. Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. Regulated Rivers: Research & Management 1995; 11: 105-119.

Warren, M.L., & Pardew, M.G. Road crossings as barriers to small-stream fish movements. Transactions of the American Fisheries Society 1998; 127: 637-644.

Williams, D.D. & Williams, N. E. The upstream/downstream movement paradox of lotic invertebrates: quantitative evidence from a Welsh mountain stream. Freshwater Biology 1993; 30, 199-218.

Williams, J.G., Armstrong, G., Katopodis, C., Larinier, M., & Travade, F. Thinking like a fish: a key ingredient for development of effective fish passage facilities at river obstructions. River Research and Applications 2012; 28: 407-417.

Waters, J.M., Shirley, M. & Closs, G.P. Hydroelectric development and translocation of *Galaxias brevipinnis*: a cloud at the end of the tunnel? Canadian Journal of Fisheries and Aquatic Sciences 2002; 59, 49-56.

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

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

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