

Australian diadromous fishes – challenges and solutions for understanding migrations in the 21st century

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Abstract. Diadromous fishes are a frequent but poorly understood component of coastal riverine fish communities in Australia. There are ~33 diadromous fishes found in Australian waters, mainly catadromous and amphidromous species. An extensive review of the literature identified major information gaps about the lifecycles and ecology of many of these species, with information on facultative diadromy, navigation, marine and early life stages being particularly limited. In many cases, this lack of information has led to poor management decisions and consequently many of the Australian diadromous species are under increasing threat from a range of environmental impacts. Much of the required information is difficult to obtain with traditional field surveys and, as a result, new and improved research tools and technologies, including telemetry, otolith chemistry, stable-isotope analysis (SIA) and functional magnetic resonance imaging (fMRI) are increasingly being applied. Key areas for research on Australian diadromous fishes should involve: (1) use of telemetry and otolith chemistry to determine the level of facultative diadromy and variation in diadromous movements across a species range; (2) use of otolith chemistry and SIA to gain a greater understanding of larval and juvenile marine life stages of catadromous and amphidromous species; and (3) use of fMRI or traditional techniques such as electroolfactogram (EOG) to determine the role of olfaction in spawning and migration, and the impact of impoundments and agricultural run-off on these critical life history stages.

Additional keywords: diadromy, migration, river regulation, threatened.

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Introduction

Anthropogenic influences on the migratory habits of diadromous fishes have resulted in this group of organisms being identified among the most threatened vertebrate species in many parts of the world (Angermeier 1995; Jonsson *et al.* 1999). Despite some species such as salmonids being well studied, in many regions there is still limited information available on the biology of diadromous fish species or on their ecological importance (McDowall 1999). It is therefore difficult to adequately assess the conservation status of many diadromous fishes (McDowall 1988; Jonsson *et al.* 1999; McDowall 1999).

Populations of several Australian diadromous fishes have declined in abundance and distribution since European settlement (Ingram *et al.* 1990; Faragher and Harris 1994). Declines in

the populations of Australian diadromous fishes is extremely concerning, particularly as some fish species that were once plentiful are now rare or locally extinct over parts of their previous range (Faragher and Harris 1994; Allen *et al.* 2002). However, assessing the current status of most Australian diadromous fishes is difficult, as the baseline data needed to understand their lifecycles is not currently available (Koehn and O'Connor 1990; Allen *et al.* 2002; Pusey *et al.* 2004). In response to this obvious knowledge gap and the urgent need for further research and improved management, we have reviewed the information available for the diadromous fish fauna of Australia and highlighted how the application of new and improved technologies and research tools could aid in the understanding of their lifecycles. In particular, the benefits and

pitfalls of many of these techniques for studying the lifecycles of Australian diadromous species are examined and directions for future research have been discussed.

Definitions and usage of diadromous terms

The term ‘diadromy’ was brought into common usage by Myers (1949) and is defined as the life history of ‘truly migratory fishes which migrate between the sea and freshwater’. Diadromy comes in three forms; anadromy, catadromy and amphidromy (see Fig. 1).

Anadromy refers to diadromous fishes which spend most of their lives in the sea but migrate to freshwater to breed (Myers 1949; McDowall 1988). Most of the feeding and growth are in the sea, before migration of fully grown adult fish into freshwater to reproduce. Either there is no subsequent feeding in freshwater, or any feeding is accompanied by little somatic growth. As a result, the principal feeding and growing biome (the sea) differs from the reproductive biome (freshwater) (McDowall 1997a).

Catadromy refers to diadromous fish which spend most of their lives in freshwater and which migrate to the sea to breed (Myers 1949; McDowall 1988). Most of the feeding and growth are in freshwater before migration of fully grown, adult fish to the sea to reproduce. There is either no subsequent feeding by

adults at sea, or any feeding is accompanied by little somatic growth. The principal feeding and growing biome (freshwater) differs from the reproductive biome (the sea) (McDowall 1997a).

Amphidromy refers to diadromous fishes where the migration between both waters is not for the purpose of breeding, but occurs at a defined or regular part of their lifecycle (Myers 1949; McDowall 1988). The migration often involves movement of larval fish to the sea soon after hatching, followed by early feeding and growth at the sea, and then a migration of small postlarval to juvenile fish from the sea back into freshwater. There is a further, prolonged period in freshwater during which most somatic growth from juvenile to adult stages occurs, as well as sexual maturation and reproduction. In this case, the principal feeding biome is the same as the reproductive one (freshwater) (McDowall 1997a). Amphidromy is also thought to occur in a marine form, where spawning is marine, and the larvae and/or juveniles are temporarily in freshwater before returning to the sea to grow to maturity (McDowall 1988) (Fig. 1). Although marine amphidromy has rarely been identified, it has been included in the current review to emphasise the difference between amphidromous and euryhaline species.

Several authors have reviewed the use of Myers’ (1949) terms to describe fish migrations (see Lagler *et al.* 1962; Fontaine 1976; Shubnikov 1976; McDowall 1988; McDowall 1992;

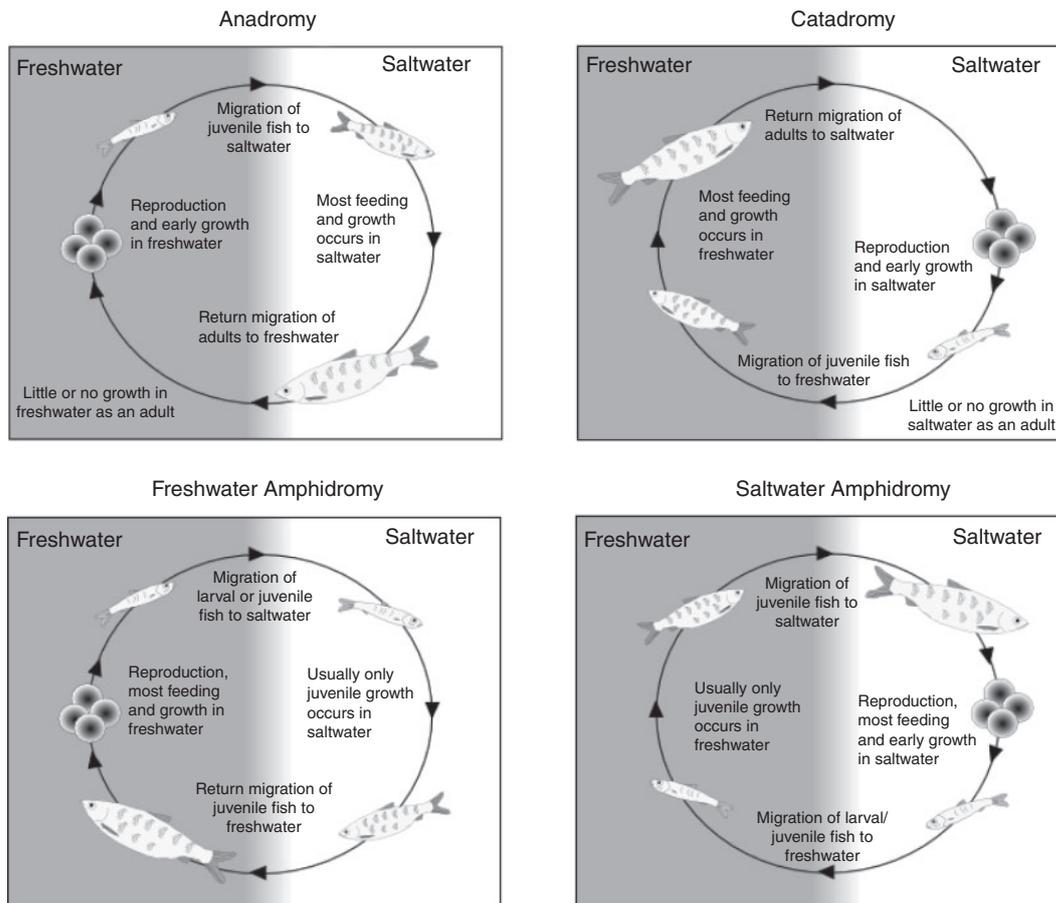


Fig. 1. Migration patterns of diadromous fish between marine and freshwater environments (Myers 1949; McDowall 1988, 1992, 1997a).

Jobling 1995; McDowall 1997b; McDowall 2007). McDowall (1988; 2007) provided a detailed summary of the development and history of these terms and problems with their usage to describe fish migrations. Typically, the reason for past examination, misinterpretation and scrutiny of diadromy and related terms, appears to be mainly due to inherent problems in defining diadromy in fishes and the unclear and/or poorly studied life-cycles of many species (McDowall 1988; McDowall 1997b; McDowall 1999; McDowall 2007). One of the key issues highlighted by McDowall (1988) in his review of the subject, is that diadromy is a specialised form of migration, and the problem of determining diadromy in fishes often relates to the definition of the term 'migration'. The key with these definitions is that the movement should be considered a migration and does not include scenarios where fish may move into other environments in a more sporadic nature. McDowall (2007) suggested that migration refers to movements that are 'regular in terms of season, direction and life stage, and they involve reciprocal movements, so that migratory fish occupy two (or more) distinct and well-separated habitats'. In some species, this migration may require fish to undergo a metamorphosis to overcome the significant physiological and osmoregulatory challenges resulting from the changing environment (McDowall 1988). The key here is that the definition should exclude euryhaline species, such as sea mullet *Mugil cephalus* L. 1778, black bream *Acanthopagrus butcheri* (Houttuyn, 1782) and bull shark *Carcharhinus leucas* (Müller & Henle, 1839), as well as other species which may move between waters of varying salinity in a more sporadic nature.

The lifecycles of some diadromous species are further complicated as they are able to abandon the diadromous lifecycle and establish 'landlocked' or exclusively marine or freshwater populations (McDowall 1988). The occurrence of landlocked populations has led some researchers to further separate fish species which display a primarily diadromous lifecycle into obligatory and facultative diadromous species (e.g. McDowall 1988, 2001). These terms refer to those species which cannot survive unless there is access between marine and freshwater environments (obligatory) and those that usually display a diadromous lifecycle, but abandon it at times (facultative) (McDowall 2001). Facultative diadromy has been defined at two levels (McDowall 2001). First, at the individual level, where some members of a population never leave the birth environment, but others of the same cohort do and second, at the population level, where all individuals fail to leave their birth environments (McDowall 2001).

Another common problem which seems to arise in the current definition of diadromy relates to the definition of 'sea'. Many fish actually undertake migrations to estuaries, bays and other saline waters (Whitfield *et al.* 2012), which cannot strictly be defined as a sea or ocean (Shubnikov 1976). However, fish migrating between freshwater and marine environments, such as estuaries, bays and other saline waters, still have to overcome the osmotic differences between fresh and saltwater. As such, these fish would appear to have a lifecycle which resembles that of an essentially diadromous species, except that they fail to enter the open ocean. These fish are often described as being 'marginally' diadromous, in that they require saline waters (e.g. salinities >5), but not the open ocean to complete their lifecycle (McDowall 1988). One example is the Australian bass

Macquaria novemaculeata (Steindachner, 1866) which spends the majority of its life in freshwater, but migrates annually to the estuary to breed in water with salinities of ~8–14 (Harris 1986). Sperm vitality experiments in this species showed that sperm were not motile in salinity below 6, but were motile in waters with salinities of up to 35 (Harris 1986). Furthermore, when this migration to saline waters is prevented through the construction of barriers (such as weirs, dams and barrages), the species soon disappears above the obstruction (Harris 1986).

For fish species with life cycles similar to that demonstrated by *M. novemaculeata*, it can be seen that they have an essentially diadromous lifecycles, even though they do not enter the open ocean. Shubnikov (1976) suggested the inclusion of the term 'semi-diadromous', referring to fish that migrate between brackish water and the ocean or brackish and freshwater. Shubnikov (1976) provides examples of species in Siberia, such as inconnu *Stenodus leucichthys* (Güldenstädt, 1772) and omul *Coregonus autumnalis* L. 1758, that travel immense distances (1000–2000km) from estuaries to freshwater to breed. It might therefore be more applicable to investigate whether individuals and/or populations can survive if movement between freshwater and saline waters (oceans, estuaries and brackish water) is prevented or, if freshwater and saline waters are essential for the survival of a different life stages. Such information is critical for the management of these diadromous species, as it immediately identifies threats to their long-term survival. In the current review, the definition of diadromy has included species which migrate into estuaries, but these species have been differentiated by using the term 'marginally' diadromous. Species which are predominantly marine, but stray into freshwaters occasionally or even regularly (but in the most part sporadically) have been excluded from this review, as it is not possible to interpret these movements as migrations or whether these movements are essential for completing their lifecycle or for sustaining their populations.

The problem that obviously arises when examining the lifecycle of a species thought to display a diadromous lifecycle is that the species could also potentially be a freshwater, marine, euryhaline or a facultative individual or population. As a result, a thorough understanding of the lifecycle is required before any accurate classification can be made. Although this review deals with diadromy, the overall goal is not to simply identify fishes as diadromous, but rather to gain knowledge of their lifecycle and behaviour, so that their populations can be adequately assessed and managed. Obviously, it is critical that, if diadromy is evident in the lifecycle of a fish species, then subsequent policy development and management actions aimed at conserving and rebuilding the species' populations should reflect this basic requirement.

Diadromy in Australian fishes

There have been relatively few reviews of diadromy worldwide and particularly for Australian species (McDowall 1988). A review by Miles (2007) indicated that ~33 species of fish found in Australian waters display some form of diadromy in their lifecycle (Table 1). Diadromy in Australian fishes is primarily made up of amphidromous (15) and catadromous (14) species, with relatively few anadromous (4) species (Table 1). However, at this stage, Table 1 should not be considered definitive, as it is likely that several fish species will be added and/or removed from this list as more information is collated on the

Table 1. Summary of available information on the biology of Australian diadromous fish species

NOTES: 'Mostly known' life stages are those species where substantial information is available. 'Mostly unknown' lifecycle stages are those species where little or no information is available. Biological information, such as habitat, migration, diet and changes to the morphology and/or physiology were reviewed and the information for each lifecycle assessed and rated as: 0 – no quantitative data available; 0.5 – some quantitative data available; and, 1 – substantial information available for that stage of the lifecycle. The individual scores for each lifecycle stage were then added to give an overall rating ranging from 0 to 5 corresponding to: 0 – no information; and, 5 – substantial information. E = embryonic, L = larval, J = juvenile, A = adult and S = senescent

Common name	Species name	Mostly known lifecycle stages	Mostly unknown lifecycle stages	Rating (0–5)
<i>Catadromy</i>				
Barramundi	<i>Lates calcarifer</i>	E, L, J, A, S		5
Tarpon	<i>Megalops cyprinoides</i>	L, A	E	2.5
Freshwater anchovy	<i>Thryssa scratchleyi</i>		E, L, S	1
Freshwater Herring	<i>Potamalosia richmondia</i>		E, L, J	1
Freshwater mullet	<i>Myxus petardi</i>		E, L	1
Australian bass	<i>Macquaria novemaculeata</i>	E, L, J, A, S		5
Jungle perch	<i>Kuhlia rupestris</i>	A	L	2.5
Long-spined glassfish	<i>Ambassis interrupta</i>		E, L, S	1
Common jollytail	<i>Galaxias maculatus</i>	E, L, J, A, S		5
Short-finned eel	<i>Anguilla australis</i>	L, J, A, S		4
Indian short-finned eel	<i>Anguilla bicolor</i>	L, J, A, S		4
Pacific short-finned eel	<i>Anguilla obscura</i>	L, J, A, S		4
Long-finned eel	<i>Anguilla reinhardtii</i>	L, J, A, S		4
Tupong/congilli	<i>Pseudaphritis urvillii</i>	J	S	2.5
<i>Anadromy</i>				
Tasmanian whitebait	<i>Lovettia sealii</i>	E, A, S		4
Tasmanian smelt	<i>Retropinna tasmanica</i>	A, S		3
Pouched lamprey	<i>Geotria australis</i>	E, L, J, A, S		5
Short-headed lamprey	<i>Mordacia mordax</i>	E, L, J, A, S		5
<i>Amphidromy</i>				
Australian grayling	<i>Prototroctes maraena</i>	E, S	J	3
Climbing galaxias	<i>Galaxias brevipinnis</i>	E, J, A, S		4.5
Spotted galaxias	<i>Galaxias truttaceus</i>	E, L, J, A, S		5
Australian mudfish	<i>Neochanna cleaveri</i>	J		3
Brown gudgeon	<i>Elotris fusca</i>		E, L, J	1
Ebony gudgeon	<i>Elotris melanosoma</i>		E, L, J	1
Striped gudgeon	<i>Gobiomorphus australis</i>	A	L, J	2.5
Snakehead gudgeon	<i>Giurus margaritacea</i>	A	L, J	2
Greenback gauvina	<i>Bunaka gyrinoides</i>		E, L, J	1
Golden goby	<i>Glossogobius aureus</i>		E, L, J	1
Flathead goby	<i>Glossogobius giurus</i>	A	L	2.5
False Celebes goby	<i>Glossogobius sp.</i>		E, L	1.5
Roman nose goby	<i>Awaous acritosus</i>	A	L, J	2
Pacific mangrove goby	<i>Mugilogobius notospilus</i>		E, L, J	1
Flag-tailed glassfish	<i>Ambassis miops</i>		E, L, J	1

lifecycles of Australia's fish fauna. The changeable nature of this current list of Australian diadromous fish species is highlighted by the non-inclusion of the apparently diadromous populations (or species) of *Retropinna*, identified by Crook *et al.* (2008). This group has not been included as the taxonomy is still uncertain.

Australian diadromous fishes display several significant differences in regional taxonomic composition, as well as basic ecology, compared to those found in other areas of the world. In particular, major diadromous fish groups found in other regions, such as larger salmonids (particularly *Salmo* and *Oncorhynchus* spp.) and the sturgeons (*Acipenser* spp.) are missing (McDowall 1987). Also, 'landlocking' in populations of Australian fish species appears to be less common than elsewhere in the world, and is confined to the galaxiids (McDowall 1988). In fact, even though New Zealand species of *Gobiomorphus* are capable of becoming landlocked, similar Australian species do not establish

self-sustaining landlocked populations (McDowall 1988). Australia also has several endemic diadromous species, including the only apparent diadromous representative of the predominantly marine Antarctic and sub-Antarctic Bovichtidae family and the only surviving member of the grayling (Prototroctidae) family since the extinction of the closely related New Zealand species last century (McDowall 1988; Allen *et al.* 2002). Diadromous fishes which are found elsewhere include: the previously mentioned galaxiids, which are found in New Zealand and South America (McDowall 1988); anguillid eels which are widely distributed throughout the world; and, several families that occur in the northern latitudes of Australia (e.g. Gobiidae and Kuhlidae), also occur in Asia, Africa, New Guinea and other tropical regions (Allen 1991; Skelton 1993; Allen *et al.* 2002).

The majority of Australian diadromous fish fishes have relatively old origins, with several species arising before the

break-up of Gondwana, over 50 million years ago (McDowall 1981; Allen *et al.* 2002). There is increasing evidence that many Australian freshwater fishes are 'secondary' freshwater fishes, having originated from marine species. For example, this marine ancestry has been hypothesised for several diadromous species (Allen *et al.* 2002), including the congolli or tupong, *Pseudaphritis urvillii* (Valenciennes, 1831) which is the only freshwater or diadromous representative of the otherwise exclusively marine Bovichthyidae family (McDowall 1988). Likewise, marine ancestors of the genus *Macquaria*, which contains a range of diadromous, marine and freshwater species currently found in Australian waters, are thought to have been trapped in a large inland sea formed during the end of the vast Cretaceous inundation (75–85 mya) (Musyl and Keenan 1992; Pusey and Kennard 2001). Support for this hypothesis stems from *Macquaria antiquus*, an ancestor of the diadromous *M. novemaculeata*, which are present in Eocene deposits from 45 mya (Hills 1934; Unmack 2001). However, recent work by Feutry *et al.* (2013), who examined the phylogeny of the tropical genus *Kuhlia* which inhabit northern Australia and the Indo-Pacific region, found a more convoluted evolutionary history, with catadromous species probably giving rise to marine species. In fact, it is thought that ~70% of freshwater species occurring in Australia have strong affiliations with Indo-Pacific marine species (Allen *et al.* 2002). As a result, the role of diadromy in the evolution of Australian fish fauna appears complex and requires further research (McDowall 1997a; Tsukamoto and Aoyama 1998; Feutry *et al.* 2013).

No Australian diadromous fish are thought to have gone extinct since European settlement, although three species are currently listed as threatened with extinction. Threatened species include: the Australian grayling *Prototroctes maraena* Gunther, 1860, which is listed as endangered by the IUCN, vulnerable by the Australian Society for Fish Biology, and threatened by both Victorian and Tasmanian governments; and, the Australian mudfish *Nechanna cleaveri* Scott, 1934 and the freshwater herring *Potamalosa richmondia* (Macleay, 1879), which are both listed as endangered in parts of their range by the Victorian government. The percentage of diadromous fish listed as threatened in Australia (~9%) is comparatively low compared to the percentage throughout the remainder of the world, which is ~18% (Jonsson *et al.* 1999; McDowall 1999). However, the limited number of diadromous species listed as threatened in Australia may be more a reflection of the lack of available information on the lifecycles and status of these and other Australian fish species compared to many other regions of the world.

Challenges and opportunities

Knowledge gaps

Although there has been no recent detailed review specifically focussed on Australian diadromous fishes, the earlier studies of McDowall (1988) and other researchers (e.g. Harris 1984; Faragher and Harris 1994) identified the need for further research on many aspects of the life history of several Australian fish species. Despite more than 20 years since the publication of McDowall's major work on diadromy (McDowall 1988), major knowledge gaps remain for many diadromous species in Australia. A summary of the current biological information

and knowledge gaps for Australian diadromous species has been provided in Table 1. Only three species (or ~9%) have lifecycles which are known in detail, while 10 species (or ~30%) have lifecycles which are mostly unknown. In general, the species with mostly unknown lifecycles, only have information available for their adult phase and the related habitats (Table 1). The limited amount of information available on the biology of most Australian diadromous species creates enormous difficulties in the assessment of the current status of these populations, as well as identifying potential threats and appropriate management for their conservation.

One of the key threats to many diadromous fishes is river regulation, the impacts of which have been investigated for some species and for some coastal regions of Australia (Harris 1984; Stuart and Mallen-Cooper 1999; Morgan and Beatty 2006; Reinfelds *et al.* 2012; Walsh *et al.* 2012). While the majority of these studies have focused on disruption to the migrational patterns or function of fishways, river regulation is likely to have many other significant impacts on diadromous fishes. For example, apart from disruption to migrations, impoundment of coastal catchments may cause changes to the environmental cues (temperatures and flows) for diadromous and riverine fish (Harris 1984; Quinn and Adams 1996; Walsh *et al.* 2012). Australian species such as the striped gudgeon *Gobiomorphus australis* (Krefft, 1864) and the Australian grayling *Prototroctes maraena* are two species that may be particularly impacted by impoundments and the associated changes in flow regime, temperature and chemical compositions of the water, as they spawn in freshwater and rely on flows to help transport larvae to marine environments (Harris 1984). Further, many other Australian amphidromous and catadromous species are thought to rely heavily on flood events for either the downstream drift of juveniles from freshwater to marine habitats or as a migrational cue (Koehn and O'Connor 1990; O'Connor and Koehn 1998; Pusey *et al.* 2004). As a result of river regulation, these events may be reduced or occur at the incorrect times, meaning larvae or juveniles are less likely to survive while attempting to reach the nursery grounds (Harris 1984). Although no case studies of such impacts have been examined in detail in Australia, Quinn and Adams (1996) have reported that in north-western America half the population of American shad *Alosa sapidissima* (Wilson, 1811) in the Columbia River now migrate more than a month earlier than in 1938, probably due to decreased flows and changes in temperature. The potential impacts of river regulation are of particular concern along the east coast of Australia, as there are over 290 dams and weirs between southern Queensland and northern Victoria, many of which could have significant but undocumented impacts on diadromous fishes, beyond forming physical barriers to migration (Harris 1984).

The lack of information on many Australian diadromous species probably relates to difficulties in studying many aspects of their lifecycles. Diadromous fishes can be particularly difficult to study as several species have complicated life cycles which include complex migratory patterns, such as migrating larval and/or juvenile stages. These can be difficult to detect in the wild, due to their patchy distribution, small size and often unpigmented and transparent bodies (McDowall 1988; Closs *et al.* 2003; Keith 2003; Pusey *et al.* 2004). However, recent

advances in the available technologies have resulted in a range of new and improved research tools and techniques that are increasingly being used to study the lifecycle and ecology of migratory fishes (e.g. Cooke *et al.* 2008; Elsdon *et al.* 2008; Ueda 2012). This includes a variety of techniques which can be used to gain a better understanding of migratory patterns and habitat use (e.g. through use of telemetry, otolith chemistry and stable isotope analyses), mechanisms behind migration (e.g. through physiological, telemetry and olfaction based studies) and connectivity between populations and dispersion (e.g. through GIS, data modelling and molecular ecology). The focus of the remainder of this review will be the potential of these new and improved technologies, in particular telemetry, otolith chemistry, stable isotope analyses (SIA) and the study of olfaction, which are the methods most likely to address the previously identified information gaps in the biology and ecology of Australian diadromous fishes (Table 1).

Telemetry

Determining the movement patterns of diadromous fish is fundamental to understanding their ecological and migratory requirements, as well as for the design of effective conservation and resource management strategies (Miles *et al.* 2009; Crook *et al.* 2010; Reinfelds *et al.* 2012; Walsh *et al.* 2012). In a global context, up until the 1950s, studies of fish movements were based on direct observational studies or via the use of a variety of mark-recapture techniques (Wydoski and Emery 1983). Whilst these methods offered valuable insights into the movement of fish, the activities of individuals in the period between tagging and recapture, were largely unknown (Lucas and Baras 2000). This has changed dramatically with the development of new and improved biotelemetry techniques, which have supplied the means to understand the way fish move and behave to a much greater extent. The 'real time' data provided by biotelemetry has provided researchers with the opportunity to gain an insight into the behaviour and habitat requirements of fishes, including information on the cues, timing, and location of specific life history events, such as spawning (Douglas *et al.* 2009; Reinfelds *et al.* 2012; Walsh *et al.* 2012).

Despite the success of these early studies and the development of smaller and longer lasting acoustic and radio-tags, it was not until the 1990s that the first fish movement study using biotelemetry was undertaken in Australia. In this study, Koehn *et al.* (2009) used radio-tags to quantify the movement and habitat preference of the Murray cod, *Maccullochella peelii* (Mitchell, 1839), in the Murray River over a three year period. Single movements of ~90 km were recorded by several individuals and all of the tagged fish displayed a preference for large woody debris. Radio-tags continued to be employed throughout the 1990s and 2000s to study freshwater fish movement (e.g. Butler 2001; Crook 2004; Ebner *et al.* 2007), while acoustic tags have been used to study several mainly marine species (e.g. Simpfendorfer *et al.* 2010).

Few studies have directly employed radio-tags to specifically study the movement of diadromous fishes in Australia. This is most likely because radio waves are attenuated at salinities of 600 EC or greater, potentially creating long periods of time during which little or no information about tagged fish is provided (Koehn 2000). Therefore, hypotheses about the life

history of diadromous species have historically been predominantly based on limited biological knowledge, traditionally attained through: examination of spatio-temporal trends in population abundances; tag and recapture studies; creel surveys; and anecdotal evidence from commercial and recreational fishers (Bishop and Bell 1978; Harris 1986; Miles 2007). By contrast, Gehrke *et al.* (2001) implanted a small number of *M. novemaculeata* and *M. cephalus* with radio-tags to monitor movements below an impoundment in the Shoalhaven River in southern New South Wales and recorded small localised movements for both species, with sporadic upstream and downstream movements of >35 km undertaken by some individuals. One of the tagged *M. cephalus* moved out of the river into the ocean and migrated north ~300 km, however this particular fish was positioned by a tag return from a fisher, rather than by active tracking.

There has been a considerable increase in the use of acoustic telemetry across Australia in recent years. The integration of passive acoustic telemetry techniques to determine the distribution and movement behaviour of diadromous fishes has not only validated important aspects of their life history (e.g. spawning, refuge and feeding) but also highlighted previously unknown information in respect to their biology and ecology (Crook *et al.* 2010; Walsh *et al.* 2012; Koster *et al.* 2013). For example, in a two year study undertaken on a large tidal river in south-eastern Australia, Walsh *et al.* (2012) confirmed the existing hypothesis that *M. novemaculeata* exhibited high site fidelity, but the study also found that the 'catadromous' life cycle previously postulated for this species, with a freshwater residency phase and an annual spawning migration, may not be obligatory for all individuals. Likewise, telemetry on tupong, *Pseudaphritis urvillii* (Valenciennes, 1831), provided data that supported the diadromous lifecycle previously suggested, but also found that movements were typically associated with relatively high river discharges; and, that movement from the estuary to the sea tended to occur most frequently during intermediate moon phases (Crook *et al.* 2010). In addition to determining diadromous movements, telemetric techniques provide more detailed information about the importance of environmental and anthropogenic effects, such as the role of temperature, salinity and river discharge, on the instream distribution and initiation of important spawning and post-spawning migrations (Crook *et al.* 2010; Reinfelds *et al.* 2012; Koster *et al.* 2013).

Recent advances in acoustic receiver and transmitter technology further highlight the future utility of telemetry for research on diadromous fishes. In particular, receiver units have become more affordable, longer lasting, and when combined with wireless and satellite downloading make long-term remote deployment a more realistic proposition (Heupel and Webber 2012). Moreover, the evolution of smaller sized transmitters (<0.5 g), with longer battery life and sophisticated tag programming makes it increasingly possible to monitor the movements of juvenile fish, as well as small bodied species. This has important implications for diadromous fish research in Australia considering that many species are less than 300 mm total length (Allen *et al.* 2002; Pusey *et al.* 2004) and ~88% of species are amphidromous or catadromous (Table 1), meaning that they have substantial migrations occurring during the larval and juvenile stages. In addition, longer lasting tags mean that it is

now possible to carry out studies across longer temporal scales. Therefore seasonal, annual and even decadal trends in fish population distribution and movement may potentially be correlated with long-term anthropogenic induced and environmental effects, such as river regulation and climate change.

Another area of telemetry that has proven useful in understanding the lifecycles of diadromous fishes is the use of tags with physiological or environmental sensors (Cooke *et al.* 2008). The use of these tags on Australian species has been limited, despite the important information that could be gained on migration, such as the physiological costs of these migrations to individuals (see Cooke *et al.* 2008). For example, advances in physiological sensor technology now allow telemetry studies to collect data on fish physiologically through the measurement of heart rate, opercular rate, or some indicator of locomotion (e.g. electromyogram [EMG], accelerometer, tail beat) (Cooke *et al.* 2004; Cooke *et al.* 2008). Tags with EMG transmitters have been widely used outside of Australia, for example in the recent research undertaken in Canada and Japan on salmon (Ueda 2004; Makiguchi *et al.* 2007; Cooke *et al.* 2008; Makiguchi *et al.* 2008). These studies have found that swimming speeds, swimming pattern, and energy use of migrating fishes vary with environmental and biological factors. Tags can now also be fitted with sensors to measure water temperature, depth, dissolved oxygen, and salinity (Cooke *et al.* 2004; Cooke *et al.* 2008). These can be used to understand migration patterns in relation to environmental factors and the potential consequences of environmental changes, such as increased mortality associated with high temperatures (Cooke *et al.* 2008). In regards to Australian diadromous fishes, tags fitted with physiological and environmental sensors will prove useful for understanding the impacts of river regulation and associated changes in the thermal regime of the river on the migration of larger catadromous species such as barramundi *Lates calcarifer* (Bloch, 1790), jungle perch *Kuhlia rupestris* (Lacépède, 1802) and *M. novemaculeata*.

One area that requires particular attention when using telemetry to examine diadromous fish migration is the effects that tagging has on fish health, physiology and behaviour (Bridger and Booth 2003; Cooke *et al.* 2011). Most of the studies on tagging effects for diadromous species have been undertaken on northern hemisphere species such as salmonids, with the majority of studies not detecting any differences in growth, physiology, swimming performance or behaviour between tagged and untagged fish, especially over long time periods (Bridger and Booth 2003; Cooke *et al.* 2011). However, Butler *et al.* (2009) examined the retention of tags and impacts on fish health of four Australian native species including two diadromous species and suggested that, whenever possible, the individuals being tagged should be allowed to recover under controlled conditions before release. Butler *et al.* (2009) also identified post-operative complications in some individuals despite being held under controlled and optimal conditions. This suggests that longer term studies on the effect of tagging may be required for some species, especially where tagged individuals are failing to undertake expected migrations. While most studies do not have the opportunity to conduct extensive, long-term 'tag-effect' trials, the potential interference with maturation and migration in diadromous fishes does need to be considered. In particular,

trials need to be undertaken on the effects of tagging for each species and these studies should consider the long-term effects on fish health, biology, physiology, behaviour and ultimately, for diadromous species, the spawning and migratory ability (Bridger and Booth 2003; Butler *et al.* 2009; Cooke *et al.* 2011).

The effects of tagging should be a primary consideration in any study of diadromous fishes, as the level of facultative diadromy at the individual and population level for most Australian diadromous species is poorly understood. Landlocking or facultative diadromy in Australian fishes appears to be most prominent in the galaxiids, but telemetry evidence has suggested that other species, such as *M. novemaculeata*, may undertake less regular migrations than previously hypothesised (McDowall 1988; Walsh *et al.* 2012). Identifying facultative diadromy is difficult, as landlocking appears sporadic through most genera (McDowall 1988). For example, although species of *Gobiomorphus* such as *Gobiomorphus cotidianus* McDowall, 1975 readily established landlocked populations within its natural range in New Zealand, the Australian species *Gobiomorphus australis* (Krefft, 1864) is not found above migrational barriers (McDowall 1988; Rowe 1999; Gehrke *et al.* 2002). Facultative diadromy at the individual level (where only some fish in the population don't migrate) needs particular attention in relation to telemetry research because most studies have been based on 30–50 fish from a few catchments throughout their range (Crook *et al.* 2010; Walsh *et al.* 2012; Koster *et al.* 2013). The importance of considering facultative diadromy and tagging effects is demonstrated in Koster *et al.* (2013) where only a small proportion of *P. maraena* were recorded migrating, possibly due to poor tag retention.

Overall, the potential for variations in lifecycles and diadromous movements demonstrates the need for extensive telemetry studies throughout the range of each species. This can be overcome by setting up large networks of receivers, which has become one of the fastest growth areas in acoustic telemetry research over recent times in Australia (Heupel and Webber 2012). Several large networks of monitoring systems have now been deployed across Australia, involving regional groups of collaborating scientists. In New South Wales alone there are now ~250 acoustic receivers deployed throughout the river systems and oceanic waters along the coastline. The Commonwealth funded Australian Animal Tagging and Monitoring System (AATMS) (<http://imos.org.au/aatams.html>), which is part of the internationally coordinated Marine Animal Tracking program, has ~500 acoustic stations deployed in curtain and clumped arrays at various locations along Australia's coastline, allowing researchers access to a vast network of stations as well as a free database through which data can be accessed. The benefit of user networking is potentially 2-fold. First, large scale movements of diadromous fish extending outside their initial telemetry array can now be detected by offshore receivers and/or those in other river systems (Walsh, C., unpubl. data). Second, a collaborative approach lends itself to the sharing of study costs, as well as providing better leverage for funding. Both these benefits are of particular importance for Australia's diadromous fishes, as the life history of many species are still yet to be determined, including many species that are poorly studied as they are considered to have little or no food or sporting value, and therefore are of no interest to commercial or recreational

fishers or related management bodies. Utilisation of the existing networks has already made an important contribution to the understanding of the movements of Australian diadromous fishes (Walsh *et al.* 2012). It is perhaps this collaborative use of acoustic telemetry technology that will ultimately provide the most significant benefit in better understanding the migratory life histories of this unique group of fishes.

Otolith chemistry

In recent years, otolith chemistry has proved useful in many regions of the world in providing information on the migratory history of fishes (e.g. Kalish 1990; Tzeng *et al.* 2005; Arai 2006). Gillanders (2005) provided a detailed review on the use of otolith chemistry for diadromous fishes, but given the knowledge gaps identified in the current review the specific application of otolith chemistry for Australian diadromous fishes warrants further discussion. Furthermore, as outlined above, many Australian diadromous species have lifecycles that are not easily investigated using techniques like telemetry, fish counters or mark–recapture studies. However, recent advances and reduction in costs of analytical techniques such as laser ablation inductively coupled plasma mass spectrometry (LA-ICPMS) have enabled detailed information on the movements of fish to be collected.

The examination of fish movements between marine and freshwaters is now possible by measuring the concentrations of trace elements in the otolith. The key elements used for diadromous fishes are strontium (Sr) and barium (Ba), as these elements are found in different concentrations in seawater and freshwater (Kalish 1990; Secor and Rooker 2000; Gillanders 2005; Crook *et al.* 2006). As a result, otolith layers formed in marine waters typically exhibit higher ratios of Sr : Ca and lower ratios of Ba : Ca than layers formed in freshwater (Milton *et al.* 2000; Crook *et al.* 2006). Therefore, otolith chemistry analyses has already proven to be a valuable tool for examining and understanding the lifecycles and movements of riverine species of south-eastern Australia (Crook *et al.* 2006; Crook *et al.* 2008; Miles *et al.* 2009). Diadromous lifecycles previously hypothesised for a few Australian species (e.g. *P. maraena* and *G. australis*) have now been confirmed (Crook *et al.* 2006; Miles *et al.* 2009) through the use of otolith chemistry while, conversely, data collected for other species has suggested a different lifecycle strategy to that previously hypothesised (Crook *et al.* 2008; Miles *et al.* 2009).

While otolith chemistry has proved useful in understanding the lifecycle of diadromous fishes, the results obtained through these analyses must be carefully interpreted to ensure the correct conclusions are reached. This is especially important for species where certain biological factors (e.g. facultative diadromy and rapid migrations or movements) may influence elemental uptake (Elsdon and Gillanders 2003). For example, otolith chemistry has indicated evidence of amphidromy in some individuals of freshwater mullet *Myxus petardi* (Castelnau, 1875) (Miles *et al.* 2009). However, recent telemetry studies suggest that catadromous movements have been made by tagged individuals and that the length of time of these movements have been very rapid (<1 week) (G. Butler and C. Walsh unpublished data). Given the short-term nature of the migrations, an analytical signature highlighting these movements would not be

easily detected using otolith chemistry analyses (Elsdon and Gillanders 2003). Moreover, this data also highlights the importance of examining a large number of samples across a relatively large proportion of the distribution of the species. Most studies are currently limited to a few catchments and typically less than 40 individuals (Crook *et al.* 2006; Crook *et al.* 2008; Miles *et al.* 2009), however more detailed analyses is most likely required to fully understand patterns of diadromy across the entire range of the species. Walther and Limburg (2012) highlight the importance of carrying out wide-ranging studies of otolith chemistry when attempting to describe the range of behaviours which can occur within particular diadromous fish populations. For example, Walther and Limburg (2012) refer to the findings of numerous otolith chemistry studies where individuals were examined in supposedly diadromous populations of Anguilliformes, Salmoniformes and Perciformes and the results showed that many never truly migrated between fresh and saline water. In similarity to telemetry, large sample sizes, which provide extensive coverage of the distribution of each species, are required so that any instances of facultative diadromy or other factors which may influence migration can be fully considered.

In addition to movement between marine and freshwater, otolith chemistry has also proved useful for examining finer scale habitat use in Australian marine environments (Gillanders & Kingsford, 1996; 2000; Patterson *et al.*, 2005). For example, otolith chemistry analyses have been used to: (1) detect differences in otolith chemistry of fishes based on inhabitation in estuarine and reef environments (Gillanders and Kingsford 1996); (2) determine nursery habitats of fish in estuaries (Gillanders and Kingsford 2000); and, (3) provide evidence of different natal habitats for coral reef fish (Patterson *et al.* 2005). Given the information obtained from these studies, it is likely that otolith chemistry could be used to provide important data on the location of spawning sites and feeding grounds of the larval and marine life stages of several Australian diadromous species. Furthermore, as this method is not reliant on dietary intake (Elsdon and Gillanders 2003), it would be especially useful for understanding movements of catadromous species which may not feed during their spawning migration. Further detailed quantification of otolith and water chemistry is required to clarify the migrations of many of the Australian diadromous species (Miles *et al.* 2009). This includes detailed studies of the chemistry of water during flood events, as well as of tidal waters, to allow a better understanding of the complex movement patterns displayed by euryhaline and catadromous species (Crook *et al.* 2006; Miles *et al.* 2009).

Stable isotope analysis (SIA)

Stable isotope analysis (SIA) has been used over the past 20 years to study the movements of fishes (Hobson 1999). In regards to diadromy, SIA has been shown to be especially useful as ratios of stable carbon (C; $\delta^{13}\text{C}$), nitrogen (N; $\delta^{15}\text{N}$) and sulphur (S; $\delta^{34}\text{S}$) are higher in marine derived food sources compared to freshwater food sources (Doucett *et al.*, 1999; Swanson *et al.*, 2010). As a result, SIA has been used to distinguish migratory patterns of several northern hemisphere species (Doucett *et al.* 1999; Swanson *et al.* 2010). More research is required to validate the relationship between ratios of stable carbon, nitrogen and sulphur in marine and freshwater

environments before the method can be widely used to understand movements and habitat use of Australian diadromous fishes (Elsdon *et al.* 2010).

In northern Australia, SIA has been used to determine stock structure of an estuarine species (Newman *et al.* 2010). However, despite the apparent opportunities of this method in identifying potential feeding grounds of juveniles and larvae of catadromous and amphidromous species, little other work has been undertaken. A good example of where SIA has proven valuable for understanding the life histories of diadromous fishes has been the research undertaken on the amphidromous Hawaiian gobies. Sorensen & Hobson (2005) found that, based on SIA, the larvae of many amphidromous gobies used regions near the mouths of rivers as their nursery habitat. Similar research on several Australian amphidromous species may prove useful in understanding their habitat use, as many could well have similar lifecycles to the Hawaiian gobies. This suggestion is supported by some recent otolith chemistry studies which found that some Australian goby species enter marine environments but do not appear to utilise open ocean waters (Miles *et al.* 2009).

Other studies have also used SIA to better understand fish habitat use in marine environments. For example, in Zanzibar (East Africa) isotopic signatures were used to determine habitat use of juvenile fish (<5 cm) in estuarine habitats (Lugendo *et al.* 2006). SIA has also been used to understand the settlement processes of many estuarine and marine species (Herzka *et al.* 2001; Cocheret de la Moriniere *et al.* 2003). In the Australian context, SIA should prove valuable for determining larval and juvenile movement, in understanding habitat use and for identifying important food resources. This information could be especially useful in providing data to support conservation of fish species, for example when assessing the potential benefits of marine parks, which are now present in many regions of Australia.

SIA studies on fish typically require destructive sampling. Most studies rely on either otoliths, which have the advantage of providing information across large temporal scales (Dalerum and Angerbjörn 2005) or white muscle tissue, because it accurately reflects the isotopic composition of the diet over periods of several months (Pinnegar and Polunin 1999; Jardine *et al.* 2011). As an alternative to destructive sampling of fish, which can potentially have severe negative impacts on threatened and/or endangered species, Jardine *et al.* (2011) investigated the use of fin tissue collected from several species in the northern tropics of Australia. This research involved examining the relationship of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in white muscle tissue and fin-clips of 27 species including several diadromous species. They found that fin-tissue was a useful replacement for muscle tissue when examining food webs. However, the suitability of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in fin clips for examining movement between marine and freshwater remains largely unknown. The use of fin clips for SIA is also supported by research that has used the method, in conjunction with telemetry, to understand the movement and foraging of Atlantic salmon *Salmo salar* L. 1758 (Cunjak *et al.* 2005). The development of such non-destructive methods will be essential when carrying out research on species such as *P. maraena*, which is considered threatened but about which there is little information available on the marine larval and juvenile stages.

A major consideration when adopting the SIA methodologies is that the isotopic signatures are influenced by changing dietary intake, which may reflect either a change in the surrounding environment or a migration between two separate habitats (Cunjak *et al.* 2005). Also many catadromous and other diadromous species do not actually feed during their adult migrations, which further limits the effectiveness of the SIA technique. As a result, a great deal of further research is required to validate the use of this technique for the study of Australian diadromous fishes.

Olfaction and emerging physiological techniques (fMRI)

The importance of odours and environmental cues for migration, homing and spawning in diadromous fishes has been highlighted in several studies (e.g. Moore and Scott 1991; Shoji *et al.* 1994; Shoji *et al.* 2000). Several of these studies have used electrophysiological recordings using electroolfactogram (EOG) from the olfactory nerve or receptor and electroencephalogram (EEG) from the olfactory bulb, to determine odours that are important for behaviours such as migration, homing and spawning. No research on odorants or stimulants for migratory movements has been undertaken for Australian diadromous fish. However, information is available on closely related species in New Zealand, where EOG has also been used to investigate the response of banded kokopu *Galaxias fasciatus* (Gray, 1842) to various odours (Baker *et al.* 2006). It was found that bile acids present in the gallbladder, which are important attractants for other species such as salmonids and lampreys, were unlikely to be a major component of the species specific attractants for upstream migration in juvenile *Galaxias fasciatus* (Baker *et al.* 2006). Furthermore, behavioural experiments conducted on juvenile *Galaxias maculatus* (Jenyns, 1842) and *Galaxias brevipinnis* Günther, 1866 in New Zealand indicated that they were attracted to adult galaxiid odours (e.g. pheromones) but variation was detected between species, possibly due to differences in their lifecycles (i.e. type of diadromy/migratory patterns, longevity and habitat selectivity) (Baker and Hicks 2003). This suggests that the role of odours or stimulants in migration (as a trigger or for navigation) for some southern hemisphere fish groups (e.g. galaxiids) may differ markedly from that reported for other well studied northern hemisphere fish groups (e.g. salmonids). This further supports the urgent need for olfactory research on Australian diadromous species.

Increased understanding of olfaction in Australian diadromous fishes is essential for the long-term conservation of some species. Studies on fish olfaction have shown that it provides critical environmental information to fishes, enabling activities such as mating, locating food, discriminating kin, avoiding predators and homing (Tierney *et al.* 2010). Therefore any activities or pollutants that interfere with olfaction can disrupt the life history processes causing a decline in fish stocks. Previous research has focused primarily on metals and its impairment to olfactory ability in species such as chum salmon *Oncorhynchus keta* (Walbaum, 1792) (Sandahl *et al.* 2006). However, agricultural run-off such as pesticides can also impact on the olfactory discriminating abilities of fish (Sandahl *et al.* 2004; Tierney *et al.* 2010). For example, Sandahl *et al.* (2004) used electrophysiological recordings from the olfactory epithelium and the olfactory bulb in coho salmon *Oncorhynchus*

kisutch (Walbaum, 1792) to measure the response to odours after exposure to copper, chlorpyrifos and esfenvalerate (pesticides) for a 7 day period. The results suggested that periodic, non-point source contamination with current-use pesticides could interfere with olfactory function and with behaviours that are important for the survival and migration of salmonids. Therefore, studies on olfaction in Australian diadromous fishes should attempt to not only look at factors which may be important for triggering migrations or for navigation during migration, but also factors which may inhibit the olfactory ability of fishes and thereby reduce the likelihood of successfully completing important lifecycle events such as migration and spawning.

Although electrophysiological techniques such as EOG and EEG have proven useful in understanding migratory mechanisms in the past, the spatial limitations and potential animal ethics issues mean that these techniques may not be suitable in many circumstances. A new technology termed functional magnetic resonance imaging (fMRI) appears to overcome many of these issues. fMRI is a non-invasive method that can measure the neuronal activity via changes in cerebral blood flow and metabolism, as well as offering a more comprehensive measurement of responses of fishes to odorants or stimulants than EOG or EEG (van den Burg *et al.* 2005; Bandoh *et al.* 2011). Most fMRI studies have examined cognitive and psychological fields in humans, or investigated brain functions in small animals, such as mice, songbirds and fish (Van der Linden *et al.* 2007; Bandoh *et al.* 2011). In common carp *Cyprinus carpio* L. 1758, fMRI studies based on blood oxygenation level-dependent (BOLD) contrast and changes in cerebral blood volume have reported brain responses to fluctuations in ambient water temperature (van den Burg *et al.* 2005). Bandoh *et al.* (2011) used BOLD fMRI to successfully map the olfactory bulb and telencephalon and they also identified strong responses in salmon to natal stream water and L-serine. In addition to migratory response and triggers, fMRI has also been suggested as a useful tool for investigating the stress of various factors on fish (Van der Linden *et al.* 2007; Donaldson *et al.* 2008).

Although fMRI is a relatively new technique, it appears to provide useful data on important migratory cues (e.g. odours), as well as information which helps us to understand the threats to fish survival, such as river regulation and associated cold water releases (Miles and West 2011). The key problems with the use of fMRI is that it has only been adopted in a very small number of studies and, as the technique is relatively new, access to equipment and expertise may be difficult for many researchers. Nevertheless, understanding the stimulants for migration, odours used for navigation and any factors which may hinder these migrations is crucial for many Australian diadromous species. Identifying these stimulants and odours will provide a better understanding of the full extent of the impacts of climate change, pollution, river regulation and the potential mechanisms behind the effectiveness of environmental flows.

Summary and future research

In this review, we have provided a summary of the status and knowledge gaps in the lifecycles of Australian diadromous species. Overall, Australia has a diverse assemblage of diadromous fishes that display a wide variety of lifecycle strategies.

Due to the distinctive but poorly studied lifecycles of many species, there is a great opportunity to use new and improved technologies to gain a better understanding of their lifecycle and potential or current threats. The key areas for research on Australian diadromous fishes include: (1) determining the level of facultative diadromy and variation in the diadromous movements across all populations for each species; (2) gaining a greater understanding of the larval and juvenile marine life stages of catadromous and amphidromous species; and, (3) determining the role of olfaction in important life history events (such as migration and spawning) and how anthropogenic factors such as impoundments and agricultural run-off are likely to affect these events.

Further information is required on migratory movements and occurrence of facultative diadromy for many species. Telemetry and otolith chemistry will be important tools for providing this information. In regards to telemetry, the use of existing networked arrays and regional collaborations between researchers will be critical for providing this data. However, further research on the impact on fishes of the tagging process and further quantification of the relationship between water and otolith chemistry is required before a deeper understanding of the lifecycle of many species can be gained. The use of tags fitted with temperature, depth, salinity and other sensors will also be important for understanding the migrations, habitat use and impacts of anthropogenic factors on the lifecycle of many species.

There is also a need to better understand the role of marine environments in the lifecycle of many Australian diadromous species, with a particular emphasis being placed on the use of marine habitats by larvae and juveniles. Given previous research, it appears that a combination of SIA and otolith chemistry will be essential in providing this information. Initially, validation studies will be needed for both otolith chemistry and SIA to determine fine scale habitat use and to locate key sites in the marine environment. These techniques would be highly suitable for providing data on the lifecycle of amphidromous species that are found in northern Australia. Many of these species also occur throughout the tropic regions of Indonesia, New Guinea and some Pacific Islands, but have received little research attention. As a result, any new data and life cycle information would be hugely beneficial for management across the whole region.

Information is also needed on potential cues or mechanisms determining the migration of Australian diadromous species, as well as the factors which may inhibit the olfactory ability of these species. Of particular importance is an understanding of anthropogenic impacts on water quality, such as agricultural or industrial run-off, which may interfere with fish olfaction, and in turn, interfere with major life history events critical for survival of these species. Although EMG and EEG have been the most commonly used tools for identifying this information in the past, newer less destructive techniques such as fMRI might provide a better alternative in the future, especially for threatened species.

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