

Detecting range shifts among Australian fishes in response to climate change

David J. Booth^{A,D}, Nick Bond^{B,C} and Peter Macreadie^A

^ASchool of the Environment, University of Technology Sydney, Broadway, NSW 2007, Australia.

^BSchool of Biological Sciences and eWater CRC, Monash University, Clayton, Vic. 3800, Australia.

^CPresent address: Australian Rivers Institute, Griffith University, Nathan, Qld 4111, Australia.

^DCorresponding author. Email: David.Booth@uts.edu.au

Abstract. One of the most obvious and expected impacts of climate change is a shift in the distributional range of organisms, which could have considerable ecological and economic consequences. Australian waters are hotspots for climate-induced environmental changes; here, we review these potential changes and their apparent and potential implications for freshwater, estuarine and marine fish. Our meta-analysis detected <300 papers globally on ‘fish’ and ‘range shifts’, with ~7% being from Australia. Of the Australian papers, only one study exhibited definitive evidence of climate-induced range shifts, with most studies focussing instead on future predictions. There was little consensus in the literature regarding the definition of ‘range’, largely because of populations having distributions that fluctuate regularly. For example, many marine populations have broad dispersal of offspring (causing vagrancy). Similarly, in freshwater and estuarine systems, regular environmental changes (e.g. seasonal, ENSO cycles – not related to climate change) cause expansion and contraction of populations, which confounds efforts to detect range ‘shifts’. We found that increases in water temperature, reduced freshwater flows and changes in ocean currents are likely to be the key drivers of climate-induced range shifts in Australian fishes. Although large-scale frequent and rigorous direct surveys of fishes across their entire distributional ranges, especially at range edges, will be essential to detect range shifts of fishes in response to climate change, we suggest careful co-opting of fisheries, museum and other regional databases as a potential, but imperfect alternative.

Additional keywords: catch databases, climate-change impacts, distributional patterns, distributional range, geographic limits, habitat loss, ocean acidification, range edge, sea-level rise.

Introduction

A central idea in the climate-change debate is that species distributions are generally shifted pole-ward as a result of climate change-induced temperature rises (e.g. Sorte *et al.* 2010). Across all aquatic systems – marine, estuarine and freshwater – a mix of high dispersal rates and potential vagrant populations, coupled with high levels of temporal environmental variability, present a challenging backdrop against which to clearly distinguish the effects of a changing climate. Climate-change drivers such as temperature and rainfall can operate directly to affect range or indirectly through effects on habitat or food resources of fishes (e.g. Morrongiello *et al.* 2011; Pratchett *et al.* 2011) or on their reproduction (Pankhurst and Munday 2011). Climate-change drivers can also interact with other factors such as overfishing, habitat removal, disease and pollution to reduce or spatially shift species. In the present review, we first develop definitions for fish ‘range’ and ‘range shift’, which have been poorly articulated.

Surprisingly few studies worldwide have attempted or successfully achieved tests of range shifts for fishes. Environmental drivers linked to climate change and fish distributions are briefly

reviewed in the paper, to complement more extensive reviews in this Special Issue of Marine and Freshwater Research. We review the available evidence for range shifts among fishes generally, as well as more specifically within an Australian context. We also summarise the various approaches that have, or could be, used in the future to detect or predict such shifts. Finally, for the purpose of managing and adapting Australian fisheries resources to a changing climate, we recommend key approaches to detecting range shifts and their causes.

What is ‘range’ for marine, estuarine and freshwater fishes?

Defining key ecological phenomena is never a trivial exercise (e.g. competition, Tilman 1987) and defining distributional range, and range edge, is problematic for organisms in most natural systems. Despite the fundamental importance of understanding distribution and range edges of fishes for both ecological understanding and species management, especially in the light of climate change, there is no satisfactory definition of range (or range edge) for fishes in the literature. Simply defining distributional range has a history of conflict in the

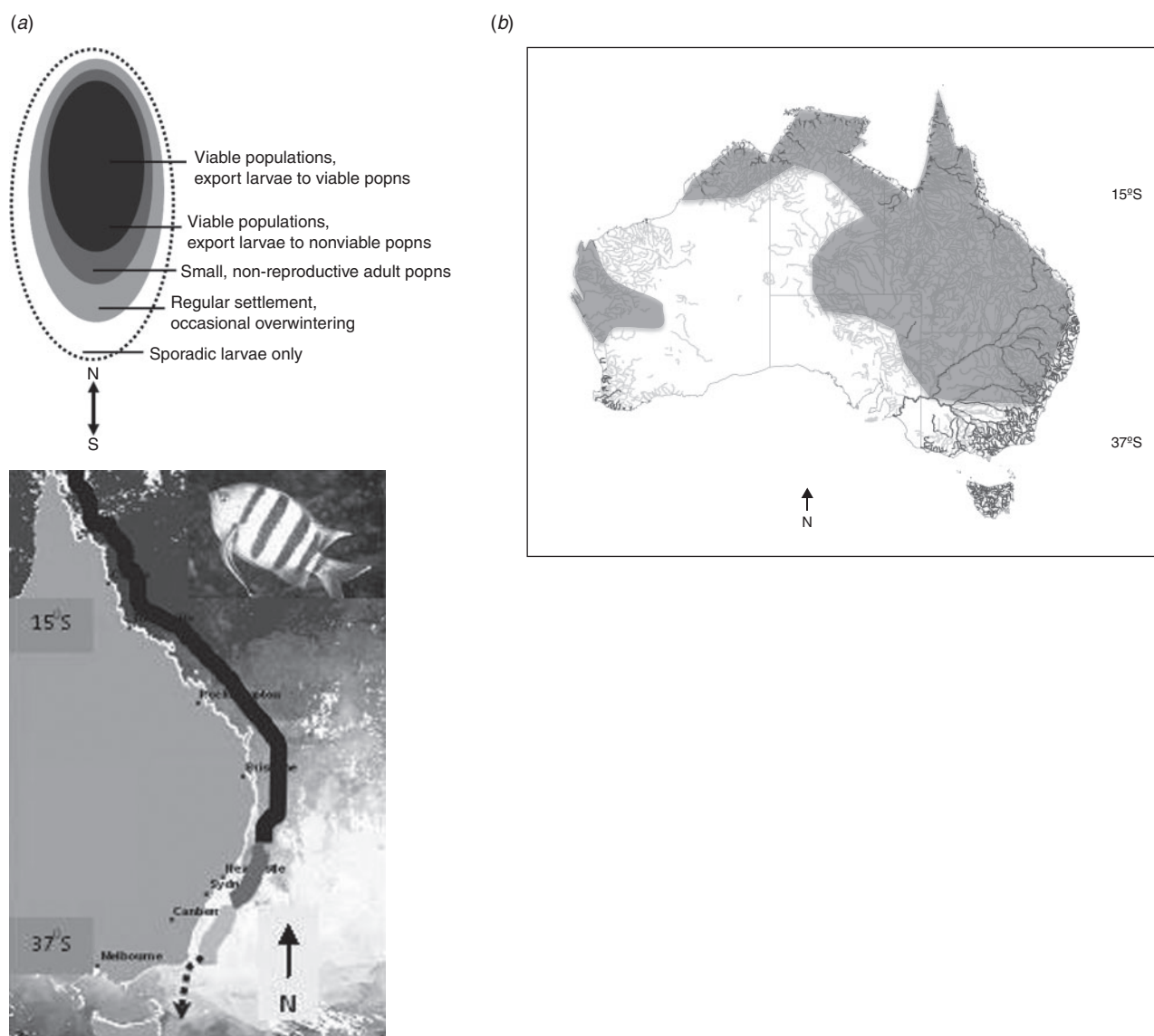


Fig. 1. Example ranges of Australian fish species. (a) Upper panel shows layers of distribution for general coastal marine reef fish. Lower panel shows distribution in SE Australia of the sergeant-major damselfish (*Abudefduf vaigiensis*) with shading representing distribution layers following upper panel (D. Booth, unpubl. data). See text for further explanation. (b) Distribution of spangled perch (*Leiopotherapon unicolor*) which occur through large parts of inland Australia where most rivers are intermittent (light grey drainage lines) rather than perennial (dark grey drainage lines). Populations within the core adult range are patchily distributed, with prevalence linked to wet–dry cycles. Adapted from data from Native Fish Australia and Stein (2006).

ecological literature. From early definitions such as from Elton (1924), which stated that range encompasses broad geographic limits inside which a species may be found more or less permanently distributed, it has been unclear how species can be captured in such a definition if their ranges fluctuate widely on a seasonal basis, or if their offspring disperse well beyond the core adult range (Andrewartha and Birch 1954). This poses a significant challenge in examining range shifts in fish across marine, estuarine and freshwater environments.

Marine reef fish species are characterised by a bipartite life cycle (Leis 2006), with larvae as the dispersive phase, sometimes moving thousands of kilometres after hatching. Some

inland species will also move large distances during flood periods in particular (Unmack 2000). This makes range measurement especially difficult. Parmesan *et al.* (2005) and Sorte *et al.* (2010) defined 'range shift' as a change in the distribution of species boundaries from their previously recorded boundaries, which may include range contractions, range relocations and range extensions. In freshwater systems, range shifts can be heavily constrained by catchment boundaries. For many species that have highly dispersive larvae, distribution patterns are most appropriately described by using metapopulation models (Kritzer and Sale 2004), with adult populations connected by larval propagules. Therefore, the vagaries of larval dispersal as

well as persistence in adult habitat are key ingredients to successful establishment. We here propose a layered model of species distribution that can be applied in marine, estuarine and freshwater systems (see Fig. 1), including the following:

Core adult range: distributional area over which breeding populations produce offspring that settle within the core area;

Non-viable breeding adult range: breeding populations within the core adult area that produce offspring that settle outside the core area;

Non-breeding adult range: non-breeding adult populations;

Recruitment periphery: consistent settlement of recruits that only occasionally mature into adults – storage effects not sufficient to form adult populations; and

Sporadic recruitment periphery: occasional settlement only.

An example of marine reef fish distribution (Fig. 1a) highlights the concept of core breeding range and layers extending to peripheral recruitment habitat. Which part of this constitutes range must be defined. For example, breeding range may be most important for species conservation, whereas full range, including recruitment periphery, may be required for disease- or parasite-transmission studies. Depth distributions may differ across latitudinal ranges (Kingsford and Carlson 2010; Malcolm *et al.* 2010) so surveying must incorporate this, and although usually quite sedentary and persistent, recruit densities may fluctuate widely within and among years (Booth *et al.* 2007).

In contrast, many estuarine and freshwater fish populations are not at spatial equilibrium; that is, their ranges and occupancy of suitable habitat expand and contract. These expansion and contraction events reflect the dynamic nature of each of these environments. Estuaries occupy relatively small, transitional zones between rivers and the sea, and are subjected to marine influences (e.g. waves, tides and saltwater incursion) and freshwater influences (e.g. freshwater runoff, which brings influxes of nutrients and sediments), all of which create physical barriers that influence dispersal, feeding, reproduction and other life-history parameters of estuarine fish. Further, these influences change over short (e.g. seasonal) and long (e.g. ENSO cycles) time scales, and at local (within estuaries) and regional (between estuaries) spatial scales. A key challenge for defining range in estuarine fish then becomes separating temporary vagrancy, which relates to tolerance, from actual range shifts, which requires long-term persistence (Davis and Shaw 2001). For this review, we define a fish as having an 'estuarine-range' if it spends the majority of its life cycle in a semi-enclosed body of water where freshwater and saltwater meet, although we note that there are other 'estuarine-dependent' fish species (e.g. diadromous fish species) that may show range shifts in response to climate change.

In freshwater systems, and arid-zone rivers in particular, inter-annual variation in rainfall and runoff generate highly dynamic patterns of habitat persistence, with periodic contractions to isolated refugia (Fig. 1b), resulting in highly variable patterns of occurrence through time (Unmack 2001; Arthington *et al.* 2005; Bunn *et al.* 2006). In such systems, detection of range shifts becomes difficult because vagrant and previously unsurveyed populations are likely to be encountered relatively often. Thus, even where, for example, a more southerly occurrence is recorded in a particular survey, without very extensive

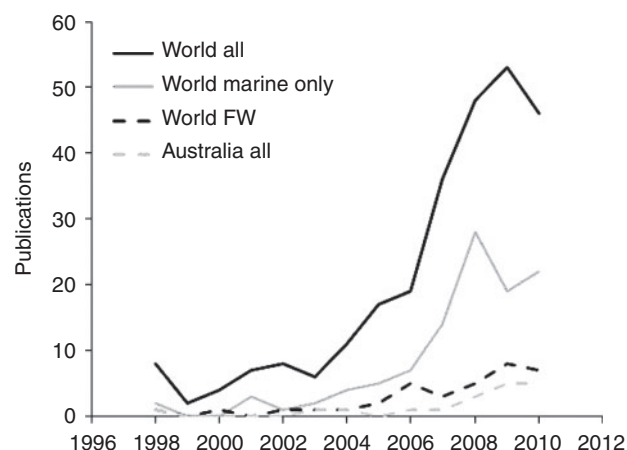


Fig. 2. ISI database range-shift publications 1996–2010 (publications per year), using keywords fish* and climate change and (range* or distribution) and (shift or edge or change).

records it becomes difficult to demonstrate that a range 'shift' has occurred as distinct from the existing range being poorly defined.

Meta-analysis of worldwide climate-change range-shift studies in fishes

Surprisingly, very few fish studies worldwide adequately show range shifts, and fewer demonstrate indisputable links to climate change. Meta-analysis of papers drawn from the ISI database Web of Science (Fig. 2) showed several trends by using appropriate keywords. Worldwide, there are fewer than 300 studies on fish range linked to climate change. Most are marine, few are estuarine or freshwater, although numbers have increased rapidly in the past decade, partly fuelled by the climate-change debate. About 7% of these studies have been Australian. Only one-quarter of the studies involve extensive field sampling of ranges, and a further one-quarter incorporate some field data into predictive or descriptive models. Given the importance of evaluating range shifts to understanding the impacts of climate change on the environment and its economic value, this paucity of empirical data is worrying.

The best available evidence of climate-related range-shifts has made opportunistic use of rigorous historical data on fish catches, which are then compared with contemporary fish catches and linked with changing water temperatures. For example, Perry *et al.* (2005) used a commercial fishery dataset from the North Sea to show that two-thirds of exploited and non-exploited species have shifted in mean latitude or depth during 1977–2001. Similarly, Nye *et al.* (2009) analysed temporal trends in fish stocks in the north-eastern USA continental shelf during 1968–2007 and identified pole-ward shifts of many stocks in relation large-scale temperature increases and changes in ocean circulation.

Such examples from estuarine systems are rare; however, Fodrie *et al.* (2010) quantified changes in fish assemblages within seagrass meadows of estuaries (albeit a rather loose definition of estuary; Able 2005) within the Gulf of Mexico between the 1970s and 2006–2007, and identified a suite of

tropical and subtropical species that were present in the latter sampling period, but not in the former, which they attributed to regional increases in air and sea-surface temperatures ($>3^{\circ}\text{C}$) during the 30-year period.

In freshwater systems, there are several long-term studies linking patterns of climate variability to periodic shifts in demographic processes. For example, in a 30-year study of brown trout (*Salmo trutta*) populations in north-western England, Elliott *et al.* (1997) showed a clear impact of drought years on survivorship and recruitment, and many more studies demonstrated the influence of climatic variables in explaining historic distributional patterns (e.g. Minns and Moore 1995). Depending on the way in which a species range is characterised, there is also evidence that periodic droughts will extirpate local populations, particularly at the margins of a species' distribution (e.g. Closs and Lake 1996). Fragmentation of populations during protracted droughts or wet-dry cycles may also last sufficiently long to promote genetic divergence (Douglas *et al.* 2003; Faulks *et al.* 2010a). Evidence for recent range shifts, however, is limited, although several studies implicated climate shifts in causing changes in species distributions. For example, Daufresne and Boët (2007) analysed trends in the distribution of fish in the Rhone River in France, and observed longitudinal changes in the distribution of thermophilic fish, namely chub (*Leuciscus cephalus*) and barbell (*Barbus barbus*), which began to replace dace (*Leuciscus leuciscus*) in more northerly upstream habitats. These shifts were correlated with changes in water and atmospheric temperatures over the same period, and appeared independent of changes linked to more localised aspects of river hydrology and thermal pollution. Similarly, Boughton *et al.* (2005) implicated climatic factors in the northward range shift of rainbow trout (*Oncorhynchus mykiss*) in California, although anthropogenic barriers to migration are seen as the primary driver of population declines.

Key climate-change impacts that can affect life history and range

Many of the environmental drivers that would be expected to be correlated with shifts in range or large-scale abundance of fish species are climate-change related, and each of these may impinge differently depending on life-history stage or habitat. These drivers, and their links to life-history events that shape range, are summarised in Table 1 and briefly described below. We note, however, that this discussion is by no means exhaustive and we direct readers to other papers in this Special Issue for a more detailed discussion of the direct and indirect pathways of climate-change impacts (e.g. Lough *et al.* 2011).

Water temperature

For ectotherms such as fishes, water temperature and its links to metabolism and swimming ability is a key environmental variable. For marine fish larvae, swimming speed and consequent dispersal are positively affected by temperature (Munday *et al.* 2009) but opposing this is the inverse relationship between water temperature and days to metamorphosis (e.g. O'Connor *et al.* 2007), by which time larval reef fish must have located suitable adult habitat. The sum of these temperature influences, along

with ocean current speed, will determine the dispersal envelope. Pearce and Hutchins (2009) presented a 25-year dataset on recruitment of the tropical damselfish (*Abudefduf vaigiensis*) to Rottneest Island, south-eastern Western Australia, which correlates well with temporal patterns of sea-surface temperature (SST), implying a net dispersal increase with rise in SST.

For fishes advected well outside their adult ranges, an 'overwintering bottleneck' may occur where low winter water temperatures appear to have a severe modifying effect on densities (e.g. Figueira and Booth 2010). Projections of an average 2°C rise in winter water temperatures off the south-eastern Australian coast by 2080 suggest that overwintering may be a regular occurrence for a suite of coral reef fishes by then, with consequent range shifts likely. Differences in general temperature tolerances among fish species may also indicate shifts in range and assemblage structures under future climate change (Nilsson *et al.* 2009). In contrast, a suite of reef fishes restricted to the southern Great Barrier Reef has little scope for southern range shift because of unsuitable habitat, and may drastically contract in range (Munday *et al.* 2007). Species with shifting distributions in relation to changes in water temperature can have faster life cycles and smaller body sizes than non-shifting species (Perry *et al.* 2005).

For estuarine fish, temperature (along with salinity) is one of the key determinants influencing both their distribution (e.g. Harrison and Whitfield 2006) and abundance (e.g. Power and Attrill 2003), especially for those that live in shallow estuaries with irregular riverine flow or exchange with the sea (e.g. coastal lagoons). Temperature affects physiological processes in estuarine fish, including maturation, feeding and growth (Gill *et al.* 1996; Power and Attrill 2002; Power and Attrill 2007). There is also evidence that temperature indirectly determines the distribution of fish within estuaries through its influence on resource distribution (Attrill and Power 2002; Attrill and Power 2004), although links of temperature-driven range shifts in estuarine fish are lacking.

Thermal constraints are equally important in freshwater environments, and the range of most species is probably limited to some extent by either upper or lower temperature tolerances, although these can be extreme. For example, the upper and lower LD₅₀ temperatures for spangled perch (*Leiopotherapon unicolor*), one of Australia's most widespread fish species, span a range from 5°C to 39°C , and it is only in the very south that the lower temperature bounds have an impact on the species range (Llewellyn 1973). Together with species such as golden perch (*Macquaria ambigua*), rainbowfish (*Melanotaenia fluviatilis*) and some gudgeon species (e.g. *Hypseleotris* and *Philypnodon*), spangled perch may therefore expand southward under a warming climate, although such trends may be constrained by reduced streamflows, particularly in smaller rivers (Bond *et al.* 2011). In contrast, several cool-water native species, including river blackfish (*Gadopsis marmoratus*) and two-spined blackfish (*G. bispinosus*), will likely contract in range towards more southerly or higher altitude streams (e.g. Bond *et al.* 2011).

Effects of increasing temperature will also be exacerbated by reduced flow volumes, and in some lower-altitude catchments, a lack of suitable upstream refuges may lead to local extinctions. Thus, increasing temperatures may extirpate some introduced species such as brown trout (*Salmo trutta*) from some streams,

Table 1. Climate-change drivers and their interactions with fish faunas in Australia

Yes, driver likely to affect fish ranges; expand, overall increase in species ranges; contract, overall reduction in species ranges; shift, movement of range boundary; unknown: not enough data to predict. The last row lists key human impacts, not necessarily climate-related, that affect fish ranges and may interact with climate change

Climate-change driver	Predictions for 2070 (see Hobday and Lough 2011 and Pratchett <i>et al.</i> 2011)	Coastal marine fishes	Estuarine fishes	Diadromous fishes	Freshwater fishes
Water temperature	Sea-surface temperature (SST): 1.5–3°C rise, highest in south-east. Freshwater: expected increase	Yes (expands tropical species and shifts, contracts temperate species and shifts), especially in south-eastern and south-western Australia. Affects larval swimming (+), pelagic larval duration (–), overwinter survival of tropical vagrant species (+): (Pearce and Hutchins 2009; Figueira and Booth 2010)	Yes (contracts the range of estuarine fishes, shifts boundaries southward). Estuaries show more extreme temporal temperature fluctuations than do adjacent oceans, which has implications for species tolerances	Yes (contracts and/or shifts). Extreme variation in temperature could exceed the tolerance of some species, which will affect their ability to travel among the systems (Sarre 1999)	Yes (contracts species with small ranges and tolerances). Physiological tolerances are likely to be exceeded during summer for some species
Freshwater flow and rainfall	Annual rainfall is projected to decline by 5–10% for south-eastern Australia and by 10–20% for south-western Australia. Low flow leads to higher river salinity in Murray–Darling basin (Pratchett <i>et al.</i> 2011)	No, except in extreme storm events	Yes (sporadic, possibly removes species for systems that flood). Altered productivity and survival as result of changes in salinity and sediment and nutrient transport	Yes (possibly contracts or makes distribution patchy). Spawning and recruitment are salinity-dependent in diadromous Australian Bass/galaxiids (Harris 1986; Hicks <i>et al.</i> 2010)	Yes (range contractions). Decreased flows in southern Australia will reduce habitat size, quality and permanence
Habitat loss	Habitat-dependent, e.g. kelp habitat contracts south, urchin barrens habitat expands south	Yes (expansions, contractions and shifts) (e.g. urchin barrens). Expansion of urchin barrens south; major changes in fish assemblages (Ling and Johnson 2009). Urchin damage (kelps). Coral bleaching	Yes (contractions). Severe loss of habitat, especially as a result of human sea-level rise mitigation works, which causes physical damage to shorelines and can reduce habitat availability and complexity	Yes (contractions), including artificial impediments to migration (e.g. dams) and removal of refugia	Yes (contractions). Linked to river flows

(Continued)

Table 1. (Continued)

Climate-change driver	Predictions for 2070 (see Hobday and Lough 2011 and Pratchett <i>et al.</i> 2011)	Coastal marine fishes	Estuarine fishes	Diadromous fishes	Freshwater fishes
Sea-level rise	20-cm to 1-m rise	No	Yes (unknown). Increasing water depths indirectly cause loss of habitat (e.g. saltmarshes, mangroves and seagrasses), unless shoreward migration is possible	Yes (unknown), through the same mechanisms that affect coastal, estuarine and freshwater fishes	n.a.
Extreme events	Storms: increased severity in temperate regions. Cyclones: lower frequency of cyclones, but projected increases in cyclone intensity/storm surge from a return period of 100 years, to a 55-year by 2050 and a 40-year event when sea-level rise is included	Yes (unknown). Storms more severe, can disrupt settlement and remove habitat, e.g. kelp	Yes (unknown). Wave disturbance at estuary mouths. Increased water turbidity can affect organisms	Unknown	Yes (contractions). Increased storm activity and associated rainfall lead to increased intensity of extreme flooding
Water chemistry (e.g. ocean acidification, etc.)	Ocean pH: decrease by 0.2–0.3 units by 2100. Freshwater: increased effects of acid sulfate soil	Yes (contraction). Ocean acidification. Loss of predator discrimination (Munday <i>et al.</i> 2010)	No. Estuarine organisms are generally resilient to water-chemistry fluctuations	No. Diadromous fishes are generally resilient to water-chemistry fluctuations	Yes (reduction). Effects of acid sulfate soils
Ocean currents (e.g. EAC)	EAC: 20% increase in flow	Yes (expansion and shift of tropical species). Increased fish larval supply (O'Connor Bruno <i>et al.</i> 2007). Changes in upwelling; expanding anoxic dead zones southward. Changes in carbon flux from surface-impact deep-sea community composition; overfishing	Yes (expansion of East-Australian-Current-dispersed species). For species that rely on larval advection from the adjacent ocean	Yes (expansion where ocean dispersal phase exists). Swimming ability will be affected by current direction and strength, which will ultimately influence migration ability	No
Other key drivers (that may interact with the above)		Seagrass removal. Sewage and stormwater pollution. Dredging, overfishing		Dams and diversions	Invasive species. Removal of riparian vegetation. Dams and diversions

potentially reducing their competitive and predatory impacts on small native fish such as *Galaxias olidus*, which (in some populations) has a higher thermal tolerance than do salmonids (e.g. see Closs and Lake 1996). The effects of temperature on growth rates may also have indirect impacts by altering reproductive output and competitive interactions (e.g. Morrongiello *et al.* 2011).

Freshwater flow

Estuarine fishes

Estuarine fish abundances are linked to annual fluctuations in freshwater discharge (Cyrus and Blaber 1992). Levels of freshwater runoff are determined by climate (e.g. rainfall), hydrological characteristics in a given area (e.g. dynamics of drainage channels) and anthropogenic activities (water consumption and runoff generation). Salinity is the main physical parameter that influences demographic processes in fish and is linked with freshwater input; however, freshwater flow also influences turbidity, pH and temperature. In contrast to northern hemisphere estuaries, Australian estuaries are characterised by irregular freshwater flow regimes (Roy *et al.* 2001). This has become particularly noticeable in south-eastern Australia, with recent drought conditions (which have been linked to climate change) causing declining abundances of estuarine fish (Gillson *et al.* 2009).

Freshwater input affects a range of life-history parameters of estuarine fish, including the timing of spawning (e.g. Newton 1996), the buoyancy of eggs and early stages (e.g. Mackenzie *et al.* 2007), shifts in the amount and location of suitable spawning grounds (Nicholson *et al.* 2008) and the movement patterns of fish (e.g. Childs *et al.* 2008). Freshwater inputs can also affect survival, particularly during major pulse events or low-rainfall periods, which can cause mass mortality of fish (Chuwen *et al.* 2007). There is good empirical data to support a link between freshwater inflows and estuarine fish production (e.g. Meynecke *et al.* 2006; Balston 2009), and thus long-term changes in inflows associated with climate change may increase production of some species. Most research on the effects of freshwater inputs has come from descriptive and small-scale experiments (Gillanders and Kingsford 2002); however, increasing use of acoustic tracking technology is allowing better coupling of patterns of fish movements with freshwater flow into estuaries (e.g. Hindell 2007; Hindell Jenkins *et al.* 2008).

Freshwater species

Spatial patterns of runoff are a major determinant of fish distributions in rivers and streams, especially river size (mean discharge), patterns of flow variability (from daily to interannual time-scales) and the presence or absence of particular flow events such as overbank floods and periods of cessation of flow (Poff and Allan 1995; Bunn and Arthington 2002). These various components of the flow regime strongly influence habitat availability and water quality, and can influence a range of life-history processes (Balcombe *et al.* 2011). Floods in particular are an important trigger for spawning in some species and deliver a pulse of energy to rivers that drives productivity in the channel. Several studies have demonstrated the importance of cease-to-flow events in excluding certain species from

some rivers (e.g. Dodds *et al.* 2004; Bond *et al.* 2010, 2011). Such patterns are likely to arise from both direct habitat loss (drying) and the rapid changes in water quality (increasing temperatures and decreased dissolved oxygen) when flows cease (Boulton and Lake 1990). Researchers are now beginning to consider the impacts of climate change on ecologically important aspects of flow regimes, as well as runoff *per se* (Sanborn and Bledsoe 2006; Gibson *et al.* 2005), and incorporation of this information into species-distribution models highlights the importance of hydrology in predicting range shifts (e.g. Lyons *et al.* 2010; Bond *et al.* 2011).

Habitat loss

In coastal reefs, despite some climatic buffering, large-scale habitat changes have occurred and are expected to occur under climate change, largely as a result of water-temperature rises. For example, coral bleaching is now widespread, and can result in dramatic loss in reef fishes (Booth and Beretta 2002; Pratchett *et al.* 2008). So far, this has led to drastic local reductions in the range of some species, but not yet in a biogeographically significant way (i.e. widespread range shifts; see discussion in Munday *et al.* (2007) for coral reef fishes). Key temperate marine habitats are shifting in response to climate change-related SST shifts. Ling *et al.* (2009) demonstrated that urchin (mainly *Centrostephanus rodgersii*) barrens, a key coastal reef habitat in south-eastern Australia, are expanding pole-ward into south-eastern Tasmania, at the expense of kelp (e.g. *Ecklonia* sp., *Phyllospora* sp., Wernberg *et al.* 2011). Reef fish assemblages differ greatly among these habitats. In New South Wales (NSW), Gillanders and Kingsford (1998) found small blue groper (*Achoerodus viridis*) in greater numbers in kelp beds than in adjacent urchin barrens, although the species appeared to be flexible in its use of habitats on reefs, suggesting that populations would persist if urchin barrens expanded in an area. In north-eastern New Zealand, some species of reef fish have shown similar patterns, whereas others were more closely linked to kelp or urchin barrens (Anderson and Millar 2004). *Parma microlipsis* in NSW has been shown to depend on barrens habitat (Holbrook *et al.* 1994). Therefore, range shifts of habitat-specific species of fish can be expected (see Last *et al.* 2011).

Urbanisation of estuarine shorelines has caused widespread habitat loss worldwide, including Australia (Edgar *et al.* 2000). Climate change will exacerbate further losses through a variety of environmental drivers (e.g. increases in water temperature, sea level rise) discussed herein (Kennish 2002). Physical impacts associated with coastal development (e.g. installation and construction of docks, piers and boat ramps), and dredging, pollution and destructive fishing all negatively affect aquatic habitat. Loss of estuarine habitats has far-reaching ecological ramifications. For estuarine fish, the most obvious outcome is a loss of available habitat. This is especially consequential for fish that use estuarine habitats as a nursery ground during their juvenile stages of development – of which there are many Australian species (Gillanders *et al.* 2003; Meynecke *et al.* 2008). Estuarine fish may also be indirectly affected through changes in trophic cascades. For example, Edgar and Barrett (2000) showed that urbanisation of Tasmanian estuaries caused

changes in sediment composition from sandy to muddy beds, and a concomitant shift in benthic community assemblages (which are an important food source for estuarine fish).

In many parts of Australia, existing hydrologic stress due to human water use is already high, and these impacts are likely to intensify under expected climate scenarios (CSIRO 2008; Pratchett *et al.* 2011). Together with land-use change and other anthropogenic impacts, hydrologic alteration has already led to substantial range contractions for many freshwater fish in Australia (Mallen-Cooper 1992). Modelling suggests that in areas with significant agricultural development, the pre-existing impacts of human water use on stream flows far exceed the magnitude of changes resulting from climate change alone (CSIRO 2008; Pratchett *et al.* 2011). Nonetheless, impacts from climate change will increase periods of cease to flow in low-rainfall areas, further decreasing habitat availability in many rivers during dry periods (Bond *et al.* 2010). Such shifts and associated impacts on fish populations have been well documented during recent drought in south-eastern Australia (Bond and Lake 2005). Other potential changes to habitat include, at a very fine scale, the loss of aquatic plants, which provide important structural habitat in rivers and wetlands (Balcombe *et al.* 2011), and at much larger scales, levels of connection among habitat patches containing local populations (Labbe and Fausch 2000). Thus, at larger spatial scales, changes in connectivity among local populations may increase overall extinction risk of local and regional populations, as has been previously predicted and documented for fragmented fish populations in desert streams (see Fagan 2002; Fagan *et al.* 2002).

Sea-level rise

Sea-level rise is likely to have strong indirect effects on fish production through its effects on key estuarine fish habitats, namely mangroves, seagrass and saltmarsh (Kennish 2002; Bond and Lake 2005). Theoretically, these habitats have the potential to respond to sea-level rise by slowly migrating up the shore (Haslett *et al.* 2001); however, their ability to do this depends on land being available for a landward progression, i.e. sediment accretion rates need to keep up with rising sea levels (Kennish 2001). In addition, there should not be physical barriers (e.g. bulkheads, rock walls) to block habitat migration up the shoreline.

In Australia, mangrove stands are increasing in area at the expense of saltmarsh in the south-east, and key saltmarsh habitats are shrinking (Saintilan and Williams 1999; Ellison 2005). Saltmarsh is a nursery for crab zoea (larvae) production that, in turn, acts as a key food source for estuarine fishes (Mazumder *et al.* 2006). Sea-level rise in Australia may also directly affect estuarine and marine fish during their pre- and post-settlement phases. For example, Jenkins *et al.* (1997) showed that spatial and temporal variability in recruitment of a temperate, seagrass-associated fish, King George whiting (*Sillaginodes punctata*), was largely determined by physical processes, including the residual sea level (caused by changes in barometric pressure). Other Australian commercial species that might be similarly affected include pink snapper (*Pagurus auratus*), southern sea garfish (*Hyporhamphus melanochir*),

Australian herring (*Arripis georgianus*), whiting and mullet (Fletcher and Head 2006).

Ocean currents and wind patterns

Western (EAC) and Eastern (LC: Leeuwin) Boundary currents bracket Australia and are expected to alter under climate-change scenarios. The strength of the LC is influenced by ENSO-related thermocline anomalies, and may be weakening, whereas the EAC is projected to strengthen and drive further pole-ward into Tasmanian waters by late this century (Ridgway 2007). The LC and its interannual variability have profound impacts on marine ecosystems off the western and southern coasts of Australia. For example, high recruitment of the western rock lobster (*Panulirus cygnus*) fishery of Western Australia is influenced by a stronger LC and the associated warmer water temperatures (Caputi *et al.* 2009). The strengthening EAC will lead to higher SSTs in south-eastern Australian waters, but also advect tropical and subtropical fauna pole-ward. Especially for the EAC, strengthening and increasing southward extent is likely and have already occurred as a result of climate change. This, of course, interacts with water temperature (see above) and also increases potential for warmer-water species to move south through advantages to larval dispersal. Conversely, southern species may find it difficult to disperse north or even maintain range, possibly precipitating a shift south.

Changes in wind strength and direction are predicted under climate-change scenarios, which can affect mixing and circulation of water. In Port Phillip Bay (Victoria, Australia), post-larval abundances of King George whiting (*Sillaginodes punctata*) at seagrass sites are strongly correlated with zonal westerly winds, the main westerly wind belt over Tasmania, and are likely to be influenced by climate change (Jenkins *et al.* 1997; Jenkins 2005).

Acidification

Reductions in ocean pH, and the linked increase in CO₂ concentration, have been shown to affect homing in coral reef fishes (Munday *et al.* 2010); however, the generalisation of these results to marine fishes and the implications for range shifts are unknown at present. Relative to ocean and freshwater systems, the effects of acidification on estuarine fishes have been largely ignored. However, recent data from the Puget Sound, a large estuary complex in the USA Pacific North-west, suggest that ocean acidification accounts for 24–49% of the pH decrease relative to pre-industrial values, and up to 49–82% of atmospheric CO₂ increase (Feely *et al.* 2010). It is difficult to know whether estuarine fishes will respond in similar ways to freshwater and marine fishes, given that most of the literature has focussed on responses (e.g. reproduction, early development, growth and behaviour) of marine and freshwater fishes to prolonged CO₂ exposure (Ishimatsu *et al.* 2008), whereas estuarine fishes are more likely to be exposed to pulses in CO₂ exposure because of the highly dynamic nature of estuarine environments. Acidification of rivers in Australia will most likely arise only in localised areas as a result of decreasing river flows exposing acid sulfate soils (ASS) rather than from increased CO₂ absorption. The extent and magnitude of such impacts are demonstrated by impacts from drought in parts of

the Lower Murray River in Victoria and South Australia (Fitzpatrick *et al.* 2009), where reinundation of ASS led to rapid oxidation, resulting in low oxygen concentrations and low pH, thus causing severe fish kills (Lamontagne *et al.* 2004). Fish species such as the already threatened Murray hardyhead (*Craterocephalus fluviatilis*) that inhabit shallow floodplain wetlands along the lower Murray River, and other areas with ASS, are particularly at risk.

Approaches to range-shift detection in Australian fishes

Our review has uncovered little in the way of direct evidence for climate-induced range shifts in Australian fish species, but has considered a range of likely climate-induced changes in aquatic ecosystems that may affect species distributions in the future. Much anecdotal evidence of climate-driven local-species extinctions exists; however, the lack of scientifically rigorous monitoring is apparent. Nonetheless, there are numerous clearly identified mechanisms by which climate change is expected to induce range shifts across marine, estuarine and freshwater environments. The challenge will be in determining whether these do occur in the future. Here, we review the few reliable studies linking non-stationary climate drivers to range shifts, before discussing a range of indirect approaches to inferring range shifts or predicting likely range shifts in response to future climate change.

Direct field census v. recorded change in environmental variables

One of the rare examples of direct evidence of a relationship between faunal changes and climate-change drivers in Australia is that of Stuart-Smith *et al.* (2010) who used over 100 underwater surveys to compare assemblages on Tasmanian rocky reefs between the early 1990s and 2005. Long-term SST monitoring at Maria Island showed SST rises of up to 1°C over the course of the study, however, the authors concluded that reef communities had remained relatively stable over that time. Significantly, however, ranges of several key eastern marine fishes had shifted south. For instance, the southern-range edges of the weed whiting (*Siphonognathus attenuatus*) and luderick (*Girella tricuspidate*) shifted over two degrees of latitude off eastern Tasmania, and two previously absent eastern species, the crimson-band wrasse (*Notolabrus gymnogenis*) and the marbledfish (*Aplodactylus lophodon*) were observed in 2005.

Probably the most compelling and comprehensive example of demonstrated climate-induced range shifts of fishes in Australia was recently reported in Last *et al.* (2011). This study monitored Tasmanian coastal fish distributions and included data since the late 1800s using multiple methods (e.g. spearfisher records, commercial-fisheries data, scientific surveys, REDMAP data) to quantify perceived changes in ichthyofauna. In total, 61 of 300 fish species off the coast of Tasmania appeared to have undergone significant shifts in range and/or abundance.

Some losses (e.g. 5 predatory fish species) were attributed to exploitation; however, 45 species (in 27 families) showed poleward range shifts, possibly likely to be related to climate change (SST increases, strengthening East Australian Current).

Existing databases

Commercial-catch databases

Given the generational nature of fishing fleets, it is likely that commercial fishers can provide anecdotal accounts of climate-related range shifts that may serve to trigger further investigation of changes in fish ranges. Of course, comparisons of past and present fish catches are susceptible to sampling artefacts, especially in commercial-fishing records, whereby fishing gears change through time, or where earlier records failed to report fish lacking commercial value (Byrkjedal *et al.* 2004). An example of the use and limitations of such datasets comes from the NSW commercial catch database housed and maintained at Industry and Investment NSW. This database is divided by fishery, such as estuarine haul, ocean line and trap, and by latitude. From 1940 to 1960, no effort data were recorded, whereas from 1961 to 1997, effort data were not reliable in most cases. For the whole database, catch was not only related to availability but also to market preferences, circumstances of fishers and changes in legislation. Also, privacy requirements prevent reporting of datasets from groups of under five fishers, which can in some cases severely restrict the spatial resolution (e.g. latitudinal precision) of the data.

Despite these issues, Gillson *et al.* (2009) were able to use the estuary database to explore how catches of key commercial fish species caught by gill-net varied with river flow. D. Booth (unpubl. data) has used the database, in consultation with Industry and Investment NSW specialists, to follow catch and CPUE changes across time in key species that may be expected to alter distribution with climate change along the NSW coast, a key global hotspot for climate-change increases in SST and ocean currents (Ridgway 2007). For example, Fig. 3a shows a systematic increase in overall CPUE of the northern mudcrab (*Scylla serrata*), which may be interpreted as a response to climate-change SST increases over that period, although other explanations such as change in capture efficiency are plausible.

Recreational catch and 'citizen-science' databases

Where scientific databases are lacking, and provided data can be cross-referenced and calibrated, various recreational-fishing databases can be useful to determine species range shifts, which can then be related to climate drivers. First, records from fishing competitions, where catches are carefully recorded, including weights and identifications, can be valuable despite obvious biases (e.g. fish samples are biased towards larger individuals or desirable species). Such competitions are held regularly and in the same place, including spearfisher, game fishing and other marine competitions. Provided the researcher is allowed access and understands limitations, these can be useful (Steffe *et al.* 2005).

New online public websites (e.g. REDMAP, available at www.REDMAP.org.au, accessed 15 June 2010) coordinate widespread fish observations across a range of amateur fishing, diving and scientific observers, and have the potential to capture new appearances and range shifts of fishes in coastal marine habitats. 'Reeflife' surveys (Edgar *et al.* 2009) have combined rigorous experimental design and data manipulation and storage with amateur diver training to survey habitat and key fish and invertebrate species around southern (and more recently

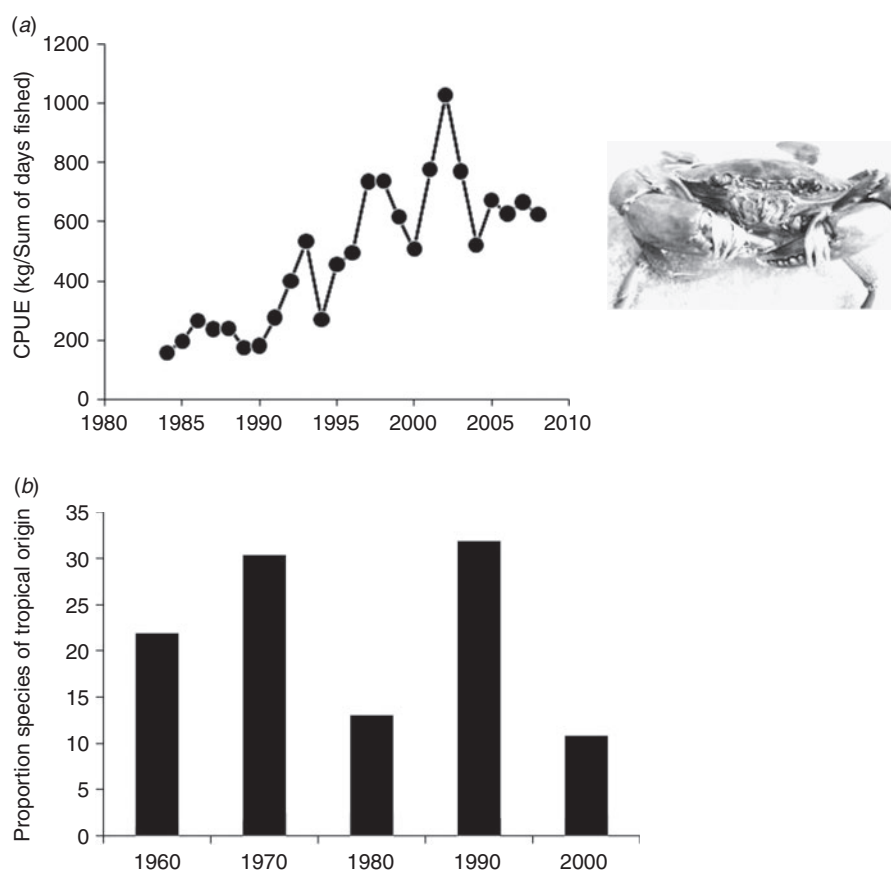


Fig. 3. (a) Change in northern mudcrab (*Scylla serrata*) catch per unit effort in estuarine and ocean-haul fisheries in New South Wales waters since 1985 (source: Industry and Investment NSW Fisheries database). (b) Decadal changes in species collected of tropical origins from Australian museum rotenone collection stations in south-eastern Australia 1960–2009.

northern) Australia. The consistent methodology and frequent surveys will make it an excellent vehicle to detect range shifts over the coming years.

Museum and government collection databases

Museums sponsor collecting trips around the Australian coast and in freshwater habitats, and the archived specimens and data collected could be of value in mapping ranges and range shifts of fishes. On the plus side, the collections are often quantitative (e.g. rotenone stations), specimens are usually accurately identified, locations are often revisited over decades, and specimens are usually stored in collections that can be accessed for measurement later. Similarly, most government agencies maintain databases of fish survey records from government and university research programs. Historically, these have been an underutilised resource; however, increasingly they are being used as a source of data for examining species distribution patterns via more quantitative modelling approaches, incorporating GIS to link species records to spatial information layers on climate, runoff and other environmental variables (e.g. Grown 2008; Bond *et al.* 2011). Shortcomings in relying on these sources of data include the range of sampling approaches used, varied sampling objectives and variable

collection intensity, all of which may render them inadequate for detection of subtle or early beginnings of range shifting. However, range shifts are largely going to be reflected in changes in the presence or absence of species, and government databases are mostly quite reliable in the way they capture this type of binary data. Nonetheless, in some cases even cursory examinations of these sorts of databases can reveal interesting trends. For example, latitudinal changes in the proportion of tropical species over decadal time scales, on the basis of data from Australian Museum rotenone collections stations from coastal NSW sites from the 1960s to the present (Fig. 3b), do not show expected steady increase in species of tropical origin.

Physiological models

Another indirect approach to monitoring range shifts is to overlay known physiological limits of the taxon in question on current and/or historical distribution maps and to extrapolate distribution changes on the basis of projections of how the environmental variable in question is predicted to change (e.g. cane-toad invasions; Shine 2010). Elith *et al.* (2010) and Cheung *et al.* (2009) used a dynamic bioclimate envelope model to project range shifts of over 1000 exploited fishes and invertebrates, using past data and future models of values for key ocean

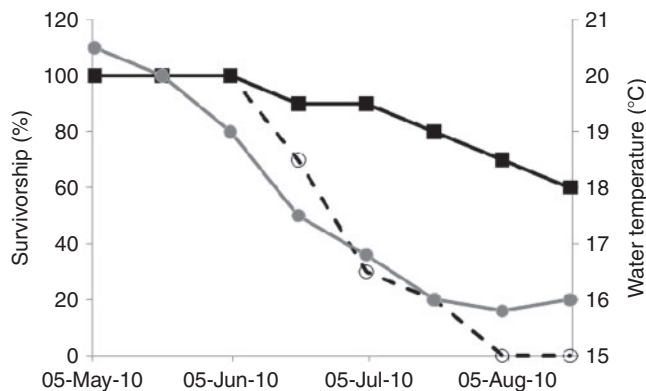


Fig. 4. Example of different laboratory v. field physiological responses for coastal fishes. For the vagrant tropical damselfish (*Abudefduf vaigiensis*) in temperate south-eastern Australia, survivorship under laboratory conditions (solid black line) is 60% at water temperatures down to 15°C, whereas fish from the same cohort in the field (dashed line) disappear below 17°C (adapted from Figueira *et al.* (2009) and D. Booth, unpubl. data). Field water temperatures are shown by grey line.

environment variables such as SST, sea ice cover, salinity and upwelling. That is, they coupled past distribution change with these environmental variables to project future changes.

Laboratory data on physiological tolerances to key environmental drivers can supplement and refine these models. For example, Hofmann (2005) used biochemical and molecular techniques to gain insight into the role of temperature in setting species distribution patterns in the marine environment, and Barnes *et al.* (2009) inferred range limits based on physiological tolerances in benthic Arctic marine invertebrates. However, these laboratory-based approaches should be used with care. For instance, vagrant damselfishes (*Abudefduf vaigiensis*) can survive under laboratory conditions down to at least 15°C (Figueira *et al.* 2009), whereas the same species disappears in the field below 17°C (D. Booth, unpubl. data; see Fig. 4). Predation pressure appears to account for losses of this species off Sydney below 17°C, at which temperature they have slowed escape responses (D. Booth, pers. comm.). The overall problem with this approach is that information on physiological tolerances and other relevant traits is lacking for many Australian species (e.g. see Crook *et al.* 2010 in relation to uncertainty around tolerances for freshwater fish).

Limitations of physiological approaches to predicting range shifts include no recognition of the capabilities or constraints of larval dispersal and the effects of key resource requirements (habitat and food). For example, pole-ward shifts in distribution of fishes may partly depend on changes in local environmental conditions as a result of climate change (e.g. Lough 2008).

Other indirect approaches

Demographic models

Although correlative approaches have been widely used to infer potential range shifts in fish, changes in physiological costs and demographic processes such as survivorship or reproductive output may also lead to eventual population losses and hence range contractions (e.g. Van Winkle *et al.* 1997). Relatively data-intensive, demographic models may be more likely to

reveal ecological surprises than are simple bioclimatic modelling approaches, because of their potential to capture dynamic feedbacks, which can give rise to strong non-linearities and identify thresholds of collapse in local populations (Perry and Bond 2009).

Paleoecology

Interrogating palaeoecological data to understand contemporary and future biotic responses to climate change offers an increasingly promising approach, especially when data records are extracted from lake and marine sediments because of their ability to log climate change and concomitant biological responses (Willis *et al.* 2010). The obvious advantage of paleoecological datasets is that they have the capacity to record ecological and evolutionary processes over time scales that far exceed most observational records. For example, Newbrey *et al.* (2009) used fossil fish material from the Cretaceous Dinosaur Park Formation of Alberta (Canada) to document the presence of members of the Characiformes (relatives of the piranha and neon tetras) in North America in the Late Cretaceous, a time of significantly warmer global temperatures than the present time. Fish otoliths, which can act as records of growth, chemical environment and life-history events are well preserved in sediments, aboriginal middens and other archival sources, and show great promise as paleogeological tools to detect climate change and range shifts. In addition to help understand the geographical range of fish, paleoecological data can be used to make inferences about range shifts over time (e.g. Read *et al.* 2006; Murray and Wilson 2009). This approach has not been successfully used for Australian fishes as yet (B. Gillanders, pers. comm.).

Genetics

The genetic structure of populations can provide information on the potential biogeographic history of organisms. In aquatic environments, range expansion and contraction events can be inferred by matching information on the phylogenetic separation of taxa with information on oceanic circulation and physical barriers that might limit dispersal (e.g. Barber *et al.* 2000; Dawson 2001; Ayre *et al.* 2009; Faulks *et al.* 2010b). Such approaches are now widespread; however, there is also an increasing move towards relying not only on the use of neutral markers to assess historical patterns of gene flow, but towards the detection of genes that are actively being selected for along environmental gradients. This is an area that offers considerable promise in terms of understanding variation in the adaptation potential of not only different taxa but also different populations distributed in different geographic areas (Hoffmann and Willi 2008).

Conclusions and recommendations

Whereas the resolution and availability of past and predicted data on climate-change environmental variables are rapidly increasing with advances in technology, (e.g. satellite SST and ocean-colour data), biological data such as fish distributions are much sparser and more field labour-intensive and have not kept pace. Matching the temporal and spatial resolution of the 'independent' (physical) and 'response' (biological) variables is problematic. We conclude that the present knowledge of the

actual fish ranges in all three ecosystems, especially that of the non-commercial species, is poor. Key guidebooks (e.g. Gomon *et al.* 1994) and distribution websites (e.g. FishBase (www.fishbase.org) and Biomaps (www.biomaps.net.au)) provide information on regional distributions and range edges of marine species; however, it is unclear how accurate and recent all of these sources are in their field monitoring of range edge.

We recommend the following:

- (1) *Targeting key regions and habitats for intensive monitoring.* Climate-change hotspots, such as coastal waters off south-eastern and south-western Australia would be areas of most change for marine and estuarine species and should be the focus for studies. In freshwater systems, less-heavily regulated river basins may provide independent measures of climate-change impacts, although in many cases, climate impacts will be greatest in modified river systems (Palmer *et al.* 2008). Threatened habitats such as urbanised estuaries vulnerable to sea-level rise and vanishing kelp habitats (eastern and western coast) could also be targeted. Locations, such as the south-eastern Tasmanian coast (Last *et al.* 2011), should be targeted because they represent places that are most likely to show actual loss of species and where range shifts may be most obvious.
- (2) *Targeting key species.* Key commercial fish species may be prone to shifting away from the economic zones of the states or even national waters, so research on predicting these changes could be targeted. Range-shifters have some of the attributes of invasive species and stronger collaboration with biosecurity researchers would be useful.
- (3) *Improving value and cross-referencing of databases.* Although many non-specific databases have problems with data accuracy and geo-referencing, they clearly have much to offer in terms of examining large-scale and long-term trends in fish-occurrence patterns. It is important that such databases are adequately maintained and we recommend a national approach to calibrating and/or cross-referencing databases in the future. The newly formed National Climate Change Adaptation Research Facility (NCCARF) would be an excellent vehicle to investigate such dataset consolidation.
- (4) *Supporting field monitoring of fish distributions and key climate drivers.* Undisputedly, the best evidence for change in fish distributions would come from intensive spatially structured and frequent fish censuses. These are rarely carried out at temporal or spatial scales sufficient to resolve range shifts. The development of the Integrated Marine Observing System (IMOS) and linked inshore ocean-climate measurements will assist in monitoring of climate-change drivers at appropriate scales in marine systems. It is possible that some of the auditing programs in freshwater systems will have similar value in the long term. These potential benefits should be considered in evaluating the wider usefulness of such programs.
- (5) *Linking understanding of climate-induced range shifts in fishes to management responses.* For instance, in NSW, the State Government's Monitoring, Evaluation and Reporting Program seeks to support ongoing range monitoring of key terrestrial, freshwater and marine habitats and to interface them with appropriate practical responses.

Given Australia's position as a world 'hotspot' for climate change and our relatively advanced knowledge of key species, we have an exciting opportunity to lead worldwide in understanding climate change-induced range shifts of marine and freshwater fishes.

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