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Using insights from animal behaviour and behavioural ecology to inform marine conservation initiatives

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Abstract

The impacts of human activities on the natural world are becoming increasingly apparent, with rapid development and exploitation occurring at the expense of habitat quality and biodiversity. Declines are especially concerning in the oceans, which hold intrinsic value due to their biological uniqueness as well as their substantial sociological and economic importance. Here, we review the literature and investigate whether incorporation of knowledge from the fields of animal behaviour and behavioural ecology may improve the effectiveness of conservation initiatives in marine systems. In particular, we consider (1) how knowledge of larval behaviour and ecology may be used to inform the design of marine protected areas, (2) how protecting species that hold specific ecological niches may be of particular importance for maximizing the preservation of biodiversity, (3) how current harvesting techniques may be inadvertently skewing the behavioural phenotypes of stock populations and whether changes to current practices may lessen this skew and reinforce population persistence, and (4) how understanding the behavioural and physiological responses of species to a changing environment may provide essential insights into areas of particular vulnerability for prioritized conservation attention. The complex nature of conservation programmes inherently results in interdisciplinary responses, and the incorporation of knowledge from the fields of animal behaviour and behavioural ecology may increase our ability to stem the loss of biodiversity in marine environments.

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The marine environment hosts some of the most biodiverse and biologically unique ecosystems on the planet, spanning shallow coastal coral reefs to deep-water seamounts. While their uniqueness confers intrinsic natural value, they also hold huge economic importance: as an asset, the world's oceans were recently valued at over \$24 trillion USD (£17 trillion GBP) per year (Hoegh-Guldberg, 2015) through their support of industries as diverse as fisheries, tourism and trade (Doney, Fabry, Feely, & Kleypas, 2009; Dixon, Munday, & Jones, 2010; Hoegh-Guldberg, 2015; Hughes, 1994; Hughes, Bellwood, & Connolly, 2002; Orr et al., 2005; Roberts et al., 2002). However, similar to their terrestrial counterparts, marine ecosystems have been subjected to sustained overexploitation and degradation, which in the most extreme cases has led to ecosystem collapse and environmental 'dead zones' (Botsford, Castilla, & Peterson, 1997; Diaz & Rosenberg, 2008; Frank, Petrie, Choi, & Leggett, 2005; Halpern et al., 2008; Hoegh-Guldberg, 2015; Waycott et al., 2009). However, while interdisciplinary conservation efforts have yielded some successes (e.g. Gaines, White, Carr, & Palumbi, 2010; Leslie, 2005; Worm et al., 2009), biodiversity continues to decline.

This review will provide an overview of some key areas where insights from the fields of animal behaviour and behavioural ecology may be able to improve the effectiveness of interdisciplinary conservation efforts in marine ecosystems, with a focus on the conservation of tropical fish assemblages and fisheries. In particular, we will focus on (1) how understanding larval behaviour can be used to maintain recruitment to healthy reefs and increase recruitment to degraded habitats, (2) how examining behavioural flexibility could help identify extinction risk in resource specialists and inform targeted conservation efforts, (3) how determining behavioural variability within populations could assist fisheries management and practices, and (4) how determining the relationship between physiology and behaviour can aid predictions of climate change effects. Promising avenues for future research will be discussed throughout.

Identifying Links Between Larval Behaviour, Habitat Selection and Connectivity

How species disperse and why they settle in particular places are questions of central importance to conservation biology (Klopfer, 1963; Mestre & Lubin, 2011; Morris, 2003; Radovic & Mikuska, 2009; Schulte & Koehler, 2010; Thorpe, 1945). For populations to persist, the immigration, emigration, birth rate and death rate must balance to a neutral or positive number, and behavioural ecology provides an established route to understanding the causes and consequences of these processes. While general similarities exist between the population dynamics of terrestrial and marine environments (e.g. Strathmann, 1990), they also possess intrinsic differences.

Behaviour is constrained by the surrounding environment, and the unique circumstances that face organisms in marine systems must be considered in order to develop effective conservation programmes. Terrestrial and marine habitats most notably differ in their biophysical properties, which have fundamental ramifications for the way that individuals live and move within their environment. As the density and viscosity of sea water is more than 800 times and ~60 times that of air, respectively, suspended particulate matter in the water column provides an easily accessible source of nutrients for small planktonic marine organisms. As a result, a variety of marine species have a planktonic dispersal life history stage that typically occurs just prior to, or following embryogenesis (Cowen & Sponaugle, 2009; Leis, 1991), and precedes metamorphosis into their adult form (Schrandt, Powers, & Mareska, 2015; Strathmann, 1990). Direct development, in which the organism does not exhibit a dispersal larval stage, also occurs in marine organisms but is much rarer than in their terrestrial counterparts (Christiansen & Fenchel, 1979). For example, while direct development is common in terrestrial vertebrates, only two of thousands of species of coral reef-associated fishes are known to display this developmental mode (Allen & Steene, 1995; Robertson, 1973). Given the period of time spent in the pelagic environment prior to settlement, planktonic larvae generally have the potential to disperse over far greater distances than species with direct development (Bernardi & Vangelli, 2004; Doherty, Mathers, & Planes, 1994). This has important conservation implications, as seemingly allopatric populations can be intimately connected through larval dispersal (Doherty, Planes, & Mathers, 1995; Palumbi, 1994). A major challenge in marine protected area design is ensuring that a sufficient total area is protected to safeguard the persistence of as many species as possible (Claudet et al., 2008; Pe'er et al., 2014). To meet this aim, identifying how populations are interconnected by drawing on source-sink/metapopulation theory (Pulliam, 1988), as well as incorporating knowledge of recruitment hotspots (e.g. Wen et al., 2013), and determining the behavioural underpinnings that influence larval recruitment patterns (e.g. Dixson, Abrego, & Hay, 2014) are essential.

On the surface, a parallel between marine larval dispersal and dispersal in terrestrial organisms, such as flowering plants, may be drawn. However, there are a variety of processes that affect marine dispersal and connectivity that do not affect terrestrial organisms (Strathmann, 1990). Notably, the larvae of marine animals often possess well-developed behavioural and sensory abilities that allow them to actively seek out and settle in habitats that would not be available to them if their dispersal patterns were solely a function of the ocean's currents (Leis, Siebeck, & Dixson, 2011; Queiroga & Blanton, 2005; Young, 1995). These abilities are present in the larvae of both vertebrate (Buston, Jones, Planes, & Thorrold, 2012; Cowen, Hare, & Fahay, 1993; Cowen & Sponaugle, 2009; Kingsford et al., 2002; Leis, 1982; Leis et al., 2011; North et al., 2008; Paris, Chérubin, & Cowen, 2007; Swearer et al., 2002) and invertebrate species (Butman, 1987; Carriker, 1951; Dixson et al., 2014; Hadfield & Koehl, 2004; Vermeij, Marhaver, Huijbers, Nagelkerken, & Simpson, 2010; Wood & Hargis, 1971), and can operate on a surprising variety of geographical scales (Kingsford et al., 2002). For example, olfactory stimuli are key for determining the availability of potential settlement sites (Atema, Kingsford, & Gerlach, 2002) as well as the suitability of particular settlement microhabitats in a variety of marine organisms (von der Medan, Cole, & McQuaid, 2015; Vail & McCormick, 2011). Other sources of information

that could be used as orientation cues by larval organisms (Queiroga & Blanton, 2005; Young, 1995) include tidal currents (Cowen, Lwiza, Sponaugle, Paris, & Olson et al., 2000; Forward & Tankersley, 2001; Shanks, 1995), magnetic and celestial positioning (Boles & Lohmann, 2003; Smith & Smith, 1998), visual and polarized light (Kobayashi, 1989; Leis & Carlson-Ewart, 1999), chemical gradients (Atema, 1995, 1996; Dixson et al., 2008, 2011; Kingsford et al., 2002; Leis et al., 2011; Munday, Dixson, et al., 2009), electrical fields (Metcalf, Holford, & Arnold, 1993) and underwater sounds (Montgomery, Jeffs, Simpson, Meekan, & Tindle, 2006; Stanley, Radford, & Jeffs, 2012). Of these, a variety of species' larvae are known to have well-developed chemosensory and auditory systems, which has resulted in research emphases being placed on understanding their importance for larvae ecology.

The larvae of coral reef-associated species are particularly well-studied in this regard (Hay, 2009; Kingsford et al., 2002; Leis et al., 2011). For example, both vertebrate and invertebrate larvae can distinguish between preferred and nonpreferred habitats based on chemical or auditory cues alone (e.g. Dixson et al., 2014; Stanley et al., 2012), offering exciting opportunities to promote ecosystem resilience and recovery through use of cues that promote settlement behaviours. Studies are starting to identify chemical compounds that influence larval behaviours (DeBose, Lema, & Nevitt, 2008; De Nys et al., 1995; Dixson et al., 2014; Dreanno et al., 2006; Ganapiriya, Maharajan, & Kumarasamy, 2012; Rittschof, 2000), and larvae appear able to obtain detailed information, such as the likely direction of origin, concentration and degree of degradation from an olfactory cue (Atema, 1995, 1996; Chivers, Dixson, White, McCormick, & Ferrari, 2013; Finelli, Pentcheff, Zimmer, & Wetthey, 2000; Weissburg & Zimmer-Faust, 1993, 1994). Together these studies raise the possibility of artificially synthesizing these cues to promote recruitment to degraded habitats. However, for this to be possible we must not only identify the specific sources of cues used by larvae but also establish the scales over which these cues are behaviourally relevant. Similarly, several studies have estimated that vertebrate larvae may be influenced by auditory stimuli at distances spanning 1 km (Egner & Mann, 2005; Mann, Casper, Boyle, & Tricas, 2007) to 5–6 km (Wright, Higgs, Belanger, & Leis, 2005, 2008, Wright et al., 2010) from the source (also see Wright, Higgs, & Leis, 2011), and that healthy reefs produce stronger auditory signals than their degraded counterparts (Piercy, Codling, Hill, Smith, & Simpson, 2014). Again, this suggests that broadcasting favourable auditory cues may be an effective and relatively low-cost tool for manipulating recruitment patterns of marine larvae. The incorporation of auditory cues into light traps increases their catch rates (Leis, Carson-Ewart, Hay, & Cato, 2003; Simpson, Meekan, McCauley, & Jeffs, 2004; Tolimieri, Haine, Jeffs, McCauley, & Montgomery, 2004), providing encouraging small-scale evidence for this concept.

Modifying current human practices may also be used to positively reinforce or promote the recovery of larval settlement. For example, chemical cues derived from terrestrial vegetation can act as indicators of suitable fringing reef settlement habitats for larval reef fishes (Dixson et al., 2008, 2011). Many terrestrial coastal areas are rapidly being developed and converted to agricultural farmlands, increasing the risk that human activities will inadvertently have a negative effect on larval recruitment to nearby aquatic coastal ecosystems. While little is known about the required concentrations of either positive or

negative terrestrial derived compounds in marine systems, techniques such as land sharing, where agricultural intensity is interdispersed with native terrestrial coastal vegetation in order to minimize the net negative effect on local biodiversity (e.g. Phalan, Onial, Balmford, & Green, 2011), may prove useful for reducing the impacts of terrestrial human practices on recruitment of nearby marine populations. This, in particular, is an interesting area for future research. Similarly, while larval organisms can use auditory cues to locate suitable settlement habitats, artificial noises, such as those produced by boat activity, can deter recruitment behaviours (Holles, Simpson, Radford, Berten, & Lecchini, 2013) and increase mortality rates (Nedelec et al., 2014). Minimizing the amount of boat traffic in areas of particular conservation concern during recruitment periods may help mitigate the negative effects of human activities on marine biodiversity in these areas. Other sensory modes are also likely to influence larval settlement behaviours, but in the meantime, developing techniques and modifying current practices according to already accumulated knowledge may provide cost-effective ways to assist conservation efforts.

Overall, a greater understanding of how larval marine organisms behave and, specifically, how environmental cue-modified behaviour affects population dynamics and transport pathways, is needed. This information should then be thoroughly incorporated into aspects of classic connectivity theory, such as source-sink and self-recruitment dynamics, as well as metapopulation theory. By doing so, realistic predictions of how connectivity will be affected by habitat loss, and how habitat alterations affect sensory cue generation and propagation could be generated. This information is also necessary for the establishment of effective marine protected areas that take into account minimum viable habitat size requirements.

Behavioural Flexibility, Vulnerability to Habitat Degradation and Minimizing Biodiversity Loss

While an animal's habitat provides all the resources that are required for survival, it is likely to contain a wider range of resources than are normally used. As with habitat selection, the use of resources for food, shelter and other essential requirements is often the result of active behavioural decisions by the individual, with the species average existing somewhere along an axis from specialist, only selecting a limited range of items from those available, to generalist, exhibiting greater selective flexibility (MacNally, 1995). Resource specialists evolve when organisms have stable access to preferred resources and often have physical or behavioural adaptations that allow them to maximize the efficiency with which they can exploit these resources (Forister, Dyer, Singer, Stireman, & Lill, 2011; Futuyma & Moreno, 1988). When access to preferred resources is not limited, specialists can be expected to hold a competitive advantage over more generalist species occupying the same habitat (Caley & Munday, 2003); however, these adaptations may be a disadvantage if the preferred resources become scarce. Under nonideal conditions, specialists that can successfully switch to nonpreferred resources may suffer sublethal effects, such as declines in condition that reduce their relative competitiveness (Berumen, Pratchett, & McCormick, 2005). Following this, if an individual, population or species is so specialized that it is unable to adequately modify its behaviour to compensate for changing external circumstances, the overly specialized

individuals may suffer lethal consequences and the species may face extinction (Biesmeijer et al., 2006; Gaston & Blackburn, 2000; Pintor, McGhee, Roche, & Bell, 2014). Given that the preservation of biodiversity is a key aim of conservation biology, identifying drivers of specialization, how resource specialists interact with their environment and how declines in resource availability will alter the behaviour of these species are key considerations for conservation management strategies.

Resource specialists from a diverse range of taxa are found across the marine environment, from the polar oceans to shallow tropical seas (e.g. Pitman & Durban, 2012; Stella, Pratchett, Hutchings, & Jones, 2011), where they often fulfil important ecological or socioeconomic roles (Bellwood, Hoey, & Choat, 2003; Graham & Nash, 2013; Grutter, Murphy, & Choat, 2003; Pratchett, 2001). However, as the condition of marine habitats steadily declines, specialist species are expected to face the greatest risk of extinction following changes in resource availability, while generalist species are expected to increase in abundance (Clavel, Julliard, & Devictor, 2010). Despite this prediction, accurate assessment of species' vulnerability is often hindered by a limited understanding of (1) the exact types of resources used and (2) the degree of behavioural flexibility exhibited at the individual, population and species level (Bastiaans & Swanger, 2015). For example, many of the organisms found on coral reefs have a critical dependence on reef-building scleractinian corals, for food, shelter, or during settlement processes (Bonin, 2012; Cole, Pratchett, & Jones, 2008; Stella et al., 2011), with declines in coral cover leading to declines in the abundance of many reef-associated species (Jones, McCormick, Srinivasan, & Eagle, 2004; Pratchett, Wilson, & Baird, 2006). While the importance of corals for the health, diversity and socio-economic viability of reef communities is well documented (Graham, 2014; Graham et al., 2011; Pratchett et al., 2008), an increasing body of research into the behaviour of coral-associated animals is revealing that many are far more specialized than previously thought (Brooker, Jones, & Munday, 2013a, 2013b; Gardiner & Jones, 2010; Munday, 2004; Pratchett, 2007; Rotjan & Lewis, 2009; Stella et al., 2011). The degree of specialization displayed by these species appears to correlate with extinction risk. For example, Munday (2004) found that declines in the abundance in a guild of coral-dwelling gobies following coral loss was directly correlated with the breadth of corals that each species used as habitat. Likewise, while dramatic declines in the abundance of highly specialized coral-feeding fishes have been observed following catastrophic reductions in coral abundance (Brooker, Munday, Brandl, & Jones, 2014; Kokita & Nakazono, 2001), other more generalist corallivores appear to be somewhat resilient to these changes (Pratchett, Wilson, Berumen, & McCormick, 2004). Thus the magnitude of decline appears to not only reflect specialization but also the degree of behavioural flexibility that species exhibit, with documented local extinctions correlating with declines of certain corals despite an abundance of taxonomically similar alternatives (Brooker et al., 2014; Hoverman, Cothran, & Relyea, 2014). While coral reef health is often assessed using measures such as total coral cover, the high degree of coral specialization inherent within these systems may make these broad metrics of limited use when attempting to assess the vulnerability of resident organisms. Although currently difficult in practice, including factors such as species-level coral community composition in benthic surveys as well as categorizing the differential susceptibility of coral species to disturbance (e.g. Marshall & Baird, 2000) may

be necessary when identifying potential risks to reef-associated biodiversity as a primary research objective.

Much like corals on coral reefs, living organisms are often the primary ecosystem engineers within marine environments, creating habitat structure and diversity (Gutiérrez, Jones, Strayer, & Iribarne, 2003; Jones, Lawton, & Shachak, 1996, 1997). Examples of biotically formed habitats can be found throughout the marine realm, such as macroalgae within temperate reef ecosystems (Steneck et al., 2002) or sessile invertebrate communities in many deep-water habitats (Rowden et al., 2010). Engineer species are themselves often specialized with regards to resource requirements or abiotic tolerance (e.g. Smale & Wernberg, 2013) and are also vulnerable to environmental degradation, with interspecific differences in vulnerability likely to shift benthic composition towards low-diversity communities dominated by tolerant generalist species (Pratchett, Trapon, Berumen, & Chong-Seng, 2011). As such, declines in total biodiversity may not only follow declines in total resource abundance, but also occur as a result of subtle compositional changes to benthic communities that reduce niche diversity. Management strategies that aim to preserve benthic habitat composition (e.g. by limiting practices such as dredging or those that contribute to ocean acidification) or facilitate its creation (e.g. adding hard substratum to otherwise barren areas: Baine, 2001) may play a critical role in preserving and facilitating the recovery of associated biodiversity. The rapid development of coastal and offshore infrastructure such as seawalls or offshore wind farms and turbines (Chapman & Blockley, 2009; Inger et al., 2009) provides a prime opportunity to consider these possibilities and maintain or increase local biodiversity (Inger et al., 2009; Petersen & Malm, 2006; Wilhelmsson, Malm, & Öhman, 2006). Numerous success stories exist in which increases to local biodiversity occur following the incorporation of factors such as slope angle or complexity into marine structure design (reviewed in Dafforn et al., 2015). However, while these opportunities may facilitate some species, they could also have deleterious effects on others through the creation of deterring noise (Simpson, Purser, & Radford, 2015) or facilitating the proliferation of invasive species (Glasby, Connell, Holloway, & Hewitt, 2007), so care must be taken when considering these options.

Many species exhibit unrecognized variation with regards to the type or breadth of resources targeted, either at the population or interindividual level (Lawton, Cole, Berumen, & Pratchett, 2012), and ascertaining this information is important for potential conservation initiatives. Within populations, variable resource selection may inadvertently aid conservation initiatives by providing a potential buffer against the sudden decline of specific resources. While species can often appear highly specialized when populations are viewed in isolation, examining variation in resource use across gradients in resource availability can help to identify potential behavioural flexibility. For example, while several studies have concluded that the chevron butterflyfish, *Chaetodon trifacialis*, is extremely vulnerable to habitat loss due to a species-specific coral diet (Pratchett, 2007), comparisons of resource use over its geographical range suggest that its dietary scope is much broader than assumed (Lawton & Pratchett, 2012). Given limited resources for targeted conservation, having solid estimates of species vulnerability will prove invaluable to resource managers when determining conservation priorities.

By understanding the interspecific dependencies of specialist species, habitat conservation efforts can focus on habitat-forming species that have the greatest number of reliant specialist species (e.g. *Acropora* corals or *Macrocystis* kelps). Some specialized animals also play keystone roles within ecosystems, having a disproportionate effect on surrounding biodiversity. For this reason, focusing conservation effort towards identifying and ensuring the persistence of these specific species may be necessary. For example, macroalgae is a pressing threat to coral reef biodiversity as it can rapidly outcompete corals, reducing complex habitats into low-diversity systems (Hughes et al., 2007). While many coral reef fishes are herbivorous, only a limited number will selectively feed on the species that pose the greatest threat (Bellwood, Hughes, & Hoey, 2006). Protection of functionally important species or genera (such as *Scarus* and *Sparisoma* spp. on the Great Barrier Reef) is therefore paramount, and could be achieved through the reduction of targeted fishing pressure via community education or the creation or expansion of marine protected area networks. Likewise, the cleaner wrasses (*Labroides* spp.) have a highly specialized diet consisting of parasites consumed during cleaning interactions (Grutter, 1996). However, the removal of cleaner wrasse from reefs can result in massive declines in the diversity, abundance, recruitment and health of local fish communities (Clague et al., 2011; Grutter et al., 2003; Sun et al., 2015). As with many coral reef fishes, wild stocks of cleaner wrasse are often heavily exploited for the commercial aquarium trade. Reducing pressure on wild stock by shifting reliance onto the growing ornamental aquaculture industry may be an achievable method of limiting declines in fish diversity.

Incorporating Behavioural Variation into Resource Conservation and Management

The ability of an individual, or a population of individuals, to adapt to changing circumstances is key to persisting in a changing world. As is the case with the specificity of an ecological niche, the degree of behavioural flexibility of an individual or a population can be essential for survival if circumstances change (Sih, 2013). Interindividual consistency in behavioural tendencies are almost ubiquitously recognized across taxa (reviewed in Gosling, 2001; Réale, Reader, Sol, McDougall, & Dingemanse, 2007), with individuals differing in a variety of behavioural traits (reviewed in: Carter, Feeney, Marshall, Cowlshaw, & Heinsohn, 2013; Dall, Houston, & McNamara, 2004; Réale et al., 2007). If an individual displays consistency in a single behaviour over time or in different contexts, it is termed a 'personality' trait, whereas consistency in the relationship between two or more functionally different behaviours is termed a 'behavioural syndrome' (Garamszegi & Herczeg, 2012). The presence of personality traits and behavioural syndromes implies that an individual is constrained to a limited number of behavioural responses, creating cost-benefit trade-offs (Kelley, Phillips, & Evans, 2013) that can influence survival (Dingemanse, Both, Drent, & Tinbergen, 2004; Downes, 2002; Smith & Blumstein, 2008), reproductive success (Both, Dingemanse, Drent, & Tinbergen, 2005; Pruitt & Ferrari, 2011; Sih & Watters, 2005) resource acquisition (Webster, Ward, & Hart, 2009) and growth (Meekan, von Kuerthy, McCormick, & Radford, 2010). Determining how variable and flexible behavioural traits are, both within and between individuals, is critical for understanding the ecology and evolution of species, as well as how they will respond to ecological change (Dall et al.,

2004; Sih, Bell, Johnson, & Ziemba, 2004; Wilson, Clark, Coleman, & Dearstyne, 1994). For example, the level of behavioural consistency within populations will directly influence distribution and abundance, interspecies interactions, population dynamics (Mittelbach, Ballew, & Kjelvik, 2014; Pruitt, Grinstead, & Settepani, 2013; Sih, Cote, Evans, Fogarty, & Pruitt, 2012), ecological invasions (Conrad, Weinersmith, Brodin, Saltz, & Sih, 2011; Sih et al., 2012) and responses to environmental and ecological shifts (Réale et al., 2007; Sih et al., 2012). If individuals within a population display a range of behavioural responses to ecological change, this may increase that populations overall adaptability and ability to persist under novel conditions. It is therefore beneficial to have a spectrum of behavioural phenotypes within a population in order to cope with future selective pressures (Powell & Gartner, 2011). Therefore, as with resource selectivity, determining variability within populations, and taking measures to preserve it, may be an important conservation tool (Berger-Tal et al., 2011; Biro & Dingemanse, 2009; McDougall, Réale, Sol, & Reader, 2006; Powell & Gartner, 2011; Smith & Blumstein, 2008).

As evolutionary change is thought to happen faster in populations with larger variation in behavioural phenotypes, reducing a population's variation may make it vulnerable to environmental change (Wolf & Weissing, 2012), which could limit its recovery potential (Hutchings & Reynolds, 2004). In marine ecosystems, individual fish and fish populations vary consistently in their behaviour and display differences in their behavioural heterogeneity (Biro, Beckmann, & Stamps, 2010; Carter & Feeney, 2012). Selective pressures that limit variation in behavioural types may reduce the viability of these populations to respond or adapt to their environment, and this may already be occurring in some exploited populations (Mittelbach et al., 2014). For example, commercial fisheries for both fishes and marine invertebrates typically target the largest individuals, indirectly biasing populations towards phenotypes with slow growth and early maturation (Biro & Post, 2008; Fenberg & Roy, 2008). As individuals with fast growth phenotypes are on average more active, bold and aggressive, this makes them more vulnerable to fishing methods that use passive gear (such as hook-and-line or traps) compared to their more slow-growing conspecifics (Biro & Dingemanse, 2009; Biro & Post, 2008; Wilson, Binder, McGrath, Cooke, & Godin, 2011). While at a smaller scale than commercial operations, recreational angling methods can also selectively target particular behavioural phenotypes, which may have similar effects on fished populations. For example, vulnerability to angling in largemouth bass, *Micropterus salmoides*, correlates with aggression, parental care and reproductive fitness (Cooke, Suski, Ostrand, Wahl, & Philipp, 2007; Sutter et al., 2012). Trophy fishing also actively targets the largest and most fecund individuals within a population (Shiffman et al., 2014). Fisheries policy decisions that take catch size and behavioural diversity into account are therefore necessary to ensure population persistence and the ongoing viability of fisheries. Imposing maximum as well as minimum size catch restrictions, removing incentives for catching large individuals of threatened species, as well as selectively targeting species with naturally short life spans, might allow for a greater range of personality types to persist in wild populations and allow for a less biased removal of personality types.

As the global exploitation of marine fisheries continues to rise, reintroduction and stock enhancement programmes are likely to become increasingly important. While captive-bred

reintroduction programmes are commonly used, and despite increased release rates of hatchery-reared fishes, many populations have continued to see declines in spawning biomass (Blaxter, 2000; Svåsand et al., 2000). This may be because fish raised in hatcheries for release are often reared using commercial production techniques that do not emphasize preparation for the wild (Petersson, Camargo Valencia, & Järvi, 2014). Consequently, released fish can tend to exhibit reduced rates of growth, survival and impaired habitat use (Brown & Day, 2002; Tatara, Riley, & Scheurer, 2010), tend to be bolder, more aggressive and less experienced with predators than their uncultivated counterparts (Jackson & Brown, 2011; Sundström, Petersson, Höjesjö, Johnsson, & Järvi, 2004), and often have a limited ability to recognize, capture and handle wild prey (Brown & Day, 2002). This is similar to results from terrestrial reintroduction programmes, which suggest that captive-reared individuals tend to forage less efficiently (Ellis & Nash, 1998; Sol, Timmermans, & Lefebvre, 2002), demonstrate poorer antipredator behaviours (Alvarez & Nicieza, 2003; Armstrong & Seddon, 2007; Fischer & Lindenmayer, 2000; Koolhaas et al., 1999) and are less adept at finding quality territories (Deverill, Adams, & Bean, 1999; Mathews, Orros, McLaren, Gelling, & Foster, 2005) than their wild counterparts. Numerous studies have examined the possibility of reducing mortality rates of hatchery-reared fishes through the behavioural training of juveniles (e.g. Brown & Day, 2002; Brown & Laland, 2001) and have delivered some successes. For example, juvenile Atlantic salmon (*Salmo salar*) reared in environmentally enriched conditions take less risks compared to controls (Roberts, Taylor, & Garcia de Leaniz, 2011), have improved learning abilities (Salvanes et al., 2013) and exhibit greater foraging rates towards novel prey (Rodewald, Hyvaärinen, & Hirvonen, 2011). However, Petersson et al. (2014) demonstrated that, while prerelease exposure to predators improved antipredator responses in hatchery-reared brown trout, *Salmo trutta*, they still lagged behind their wild conspecifics, suggesting that further refinement of these techniques is needed.

Improved training success could also be accomplished via exposure to conspecifics that exhibit a desired behavioural trait. A number of social animals, including various species of fishes, have demonstrated an ability to rapidly acquire the ability to complete novel tasks or important antipredator skills through social learning (Griffin & Evans, 2003; Kelley, Evans, Ramnarine, & Magurran, 2003; Manassa & McCormick, 2013; Manassa, McCormick, & Chivers, 2013), and individual variation in the retention of learned information can also influence postrelease survival (Brown, Ferrari, & Chivers, 2013). In their recent paper, Brown et al. (2013) suggested methodological approaches such as increasing the strength and frequency of conditioning, reducing time between conditioning and release, reducing food supply prior to release, conditioning with multiple predator cues and conditioning in an appropriate habitat could improve rates of critical information retention in reared fish stocks. Furthermore, when dealing with group-living species, terrestrial studies suggest that established social networks should be maintained for species that depend on social interactions (Shier, 2006; Whitehead, 2010). For example, black-tailed prairie dogs, *Cynomys ludovicianus*, translocated in family groups have been shown to be five times more likely to survive and reproduce when compared to animals released individually, factors that may also prove important for some marine species.

Physiological Drivers of Animal Behaviour Across Biomes and Climate Threats

In addition to considering the life histories, ecological niches and behavioural flexibility of species in an area of concern, effective conservation efforts should also consider the external and internal stressors that can influence their behaviour (Cooke et al., 2014; Wikelski & Cooke, 2006). While it is well known that habitat degradation or exploitation can affect critical behavioural patterns, subtle changes in the external environment (e.g. water biochemistry and temperature) can cause dramatic physiological and behavioural changes in individuals and populations, ultimately leading to reductions in fitness and abundance in habitats that would otherwise appear healthy (see Buckley, Waaser, MacLean, & Fox, 2011; Cheung et al., 2013; see also Møller, Rubolini, & Lehikoinen, 2008, for terrestrial examples). Understanding the connection between physiology and behaviour, particularly the behavioural strategies that aquatic and terrestrial organisms typically use to alleviate physiological stressors provides a strong theoretical and practical foundation for effective conservation strategies (Cooke et al., 2014).

The majority of marine and freshwater organisms are ecto-thermic, making their capacity for physical and physiological performance directly related to the ambient water temperature (e.g. Pörtner & Farrell, 2008; Pörtner, Schulte, Wood, & Schiemer, 2010). Rising temperatures increase the rate of biochemical and cellular processes, which increases the energetic cost of activity, growth and reproduction (Baumann, Talmage, & Gobler, 2012; Hein & Keirsted, 2012; Pörtner et al., 2010). In fishes, for example, energetic requirements generally rise two- to three-fold for every 10 °C increase in temperature (Evans & Claiborne, 2006), suggesting that the energetic cost of hunting prey can rise significantly during warmer summer months, particularly in temperate regions with large seasonal temperature fluctuations. If global warming causes the predicted 0.3–4.8 °C increase in mean surface temperature by 2100, the basal metabolic maintenance cost of fishes could increase by 30–40% (Evans & Claiborne, 2006; IPCC, 2015). To preserve energy, individuals can decrease their swimming speeds or activity rates. However, species that travel vast distances to spawn, or that require large home ranges or that expend relatively high amounts of energy may be particularly vulnerable in a warming ocean (Baumann et al., 2012; Johansen, Messmer, Coker, Hoey, & Pratchett, 2014). Importantly, it is unlikely that all trophic levels will adapt equally to their rapidly changing environment, which may lead to increased top-down competition (Graham, 2014; Johansen et al., 2015; Jones et al., 2004; Pratchett et al., 2008) and potentially lead to cascading changes in species compositions and abundance across ecosystems.

While most predictions for changes to species performance or abundance are based on sound theoretical expectations (e.g. the thermal physiology of ectotherms), many hypotheses can be relatively easily tested prior to inclusion in predictive conservation strategies. For example, shelter selection and within-habitat settlement patterns are often tightly linked to thermal physiological metrics such as aerobic scope. Aerobic scope is the difference between standard metabolic rate and maximum metabolic rate, indicating the physiological capacity for critical activities at a given temperature. In fishes, aerobic scope has been

related directly to hypoxia tolerance (Nilsson, Östlund-Nilsson, & Munday, 2010), swimming performance (Johansen & Jones, 2011), competitive dominance (Killen et al., 2014) and reproductive output (Donelson, McCormick, Booth, & Munday, 2014). Of these, hypoxia tolerance is particularly important in tropical coral reef fishes as many species seek shelter among coral branches where oxygen levels become depleted at night (Nilsson et al., 2010). As hypoxia tolerance in fishes is generally dictated by metabolic oxygen demand, elevated temperatures, which increase this demand, can force species to vacate established night-time shelters and relocate into open habitats with a greater risk of predation (Nilsson et al., 2010). Diminished aerobic scope may also compromise maximum oxygen delivery and consumption by tissues and muscles, diminishing the ability to swim. Indeed, prolonged exposure to elevated temperatures may even have the capacity to reduce maximum swimming speeds to such an extent that some fishes may no longer be able to occupy high-current habitats (Johansen & Jones, 2011). As a result, conservation strategies aimed at safeguarding habitat structure or population composition may benefit from an understanding of the physiological parameters that can cause temporal changes in habitat shelter selection or distribution patterns within habitats.

Most current efforts to conserve heavily fished species consist of bans on fishing during the spawning season, an approach that is not always effective (Grüss, Robinson, Heppell, Heppell, & Semmens, 2014). Gonadal development and reproduction of many species is regulated by photoperiod and temperature, with a long photoperiod often required for reproductive stability (e.g. Bapary, Fainuulelei, & Takemura, 2009). As a result, species that have a broad latitudinal distribution can exhibit differential onset of courtship, spawning and migratory behaviours and may benefit from a corresponding staggering of fishing closures. Additionally, global warming is expected to change the onset and conclusion of the breeding season of numerous species by limiting reproduction to acceptable thermal windows and photoperiods during early spring and late summer (see Pankhurst & Munday, 2011). Similar trends are also prevalent in the terrestrial biome, where the timing of bird migrations and breeding have advanced significantly in recent decades due to warmer springs (Charmantier & Gienapp, 2013; Gill et al., 2014). This change may particularly affect the biodiversity of specialist species such as those that are dependent on other species for their reproductive efforts (Saino et al., 2009). The tight link between reproductive physiology and ambient biophysical conditions suggests that changes in reproductive behaviours, such as the timing of migratory movements to spawning and breeding grounds, can potentially be anticipated in conservation strategies and form a behaviourally driven basis for management.

Incorporating behavioural mitigation patterns, such as the tendency of populations to relocate to more favourable habitats, into conservation strategies is expected to become increasingly important as global climatic conditions change in aquatic and terrestrial biomes (Booth, Bond, & Macreadie, 2011; Burrows et al., 2011, 2014; Cheung et al., 2009; Dulvy et al., 2008; IPCC, 2015; Madin et al., 2012; Molinos et al., 2015; Pinsky, Worm, Fogarty, Sarmiento, & Levin, 2013). The environmental conditions found in some marine ecosystems may change to become physiologically incompatible with the biology of local species, forcing these species to either relocate or face local extinction. For example, most coral reef fishes found in the Red Sea and Arabian peninsula are absent from reefs in the Arabian gulf where temperatures can reach $>35^{\circ}\text{C}$ during summer months (Al-Rashidi, El-Gamily, Amos,

& Rakha, 2009; Burt et al., 2011). The absence of species in the gulf despite suitable habitat and food suggests that these species have an upper limit for thermal adaptation (Al-Rashidi et al., 2009; Burt et al., 2011). Similarly, recent work on equatorial fish populations has revealed reduced capacities to tolerate the 3 °C temperature increase expected by 2100 (Rummer et al., 2014), while populations at higher latitudes appear better able to tolerate comparable temperature rises (Gardiner, Munday, & Nilsson, 2010; McLeod et al., 2015; Takahashi, McCormick, Munday, & Jones, 2012). Work by Schurmann, Steffensen, and Lomholt (1991) and Killen (2014) has shown that some marine teleosts will actively search for habitats with ambient water temperatures that facilitate optimal physiological performance and avoid habitats that promote metabolic depression. Therefore, efforts to conserve specific habitats should consider both how current conditions benefit the inhabiting species and how these conditions may change over time.

While species with short generation times and those species that are not living close to their physiological limits may be able to adapt to ocean warming (e.g. Donelson et al., 2014), others may not (Munday, Crawley, & Nilsson, 2009; Rummer et al., 2014). There is increasing evidence that rising sea temperatures are changing the distributions of thermally sensitive marine species, a trend that is expected to increase over time. The species most likely to relocate are those with larger body sizes, longer generation times and greater mobility (Feary et al., 2014), with low levels of parental care (e.g. broadcast spawners), and those with relatively wide latitudinal ranges. To date, more than 360 species of tropical fishes spanning 55 different families have been recorded settling in cooler higher-latitude regions (Feary et al., 2014), with no species demonstrating the opposite trend of moving to lower latitudes following range shrinkage (Feary et al., 2014). However, while some species appear able to relocate to compensate for changing environmental conditions, evidence suggests that changing climatic conditions will have detrimental effects on the majority of affected populations. For example, specialized species should have a limited capacity for geographical shifts in habitat use compared to generalist species. Major changes in habitat structure and species distribution patterns are therefore expected to create novel ecosystems with completely different fish assemblages, dominated by habitat generalists (Graham, 2014). Such changes will have unpredictable consequences for many species and ecosystems, with new stabilization points and species interactions potentially leading to the evolution of novel specialists and generalists alike. From a conservation standpoint, localized extinctions are inevitable. However, given adequate insight into the physiological resilience and physiologically driven behavioural changes of ecologically and economically important species, we may be able to formulate effective mitigation strategies and prepare industries for expected changes to species distribution and abundance. For example, prior to investing heavily in processing plants and infrastructure, it may be valuable for fisheries to know whether an important stock is likely to relocate hundreds or thousands of kilometres poleward over the next 30–50 years. Informed management and industry investment may allow us to reduce the severity of ongoing changes either through increased protection of sensitive habitats or catch-regulations that reduce impacts on vulnerable species.

Conclusions

Incorporating knowledge from the fields of animal behaviour and behavioural ecology into conservation initiatives offers a potential avenue for increasing their effectiveness at stemming the loss and increasing the recovery of biodiversity. In this review, we have discussed this in the context of tropical marine ecosystems, with a particular focus on how understanding the ecology and evolution of larval ecology can inform the creation of effective protected areas, how behaviours associated with habitat selection and particular ecological niches may affect species' vulnerability to population decline and potential for recovery, how knowledge of behavioural variation within- and between-populations can be affected by external pressures and how it may affect rates of population recovery, and how changes to the external environment can affect the physiology and behaviour of marine organisms. We suggest how changes to industry practices, such as current commercial fishing methods, may stem biodiversity loss and have positive effects on recruitment patterns and how conservation efforts that focus on particular ecologically important species (e.g. habitat-building corals or cleaner wrasses) may prove particularly important for conservation initiatives by promoting natural facilitators of biodiversity. Conservation behaviour and animal behaviour/behavioural ecology are intuitively complementary fields of research, and the continued intertwining of these fields will continue to provide parallel benefits for both.

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