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

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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.

The marine environment hosts some of the most biodiverse and biologically unique ecosystems on the planet, spanning shallow costal 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; Dixson, 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

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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 (Metcalfe, 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, & Wethey, 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