

**HABITAT USE, MOVEMENT, AND VULNERABILITY OF
SEDENTARY FISHES IN A DYNAMIC WORLD**

by

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ABSTRACT

In this thesis I quantify habitat use, movement, and vulnerability for seahorses and other sedentary fishes to understand how they may respond to habitat related threats. Surviving habitat change depends on either acclimatizing or escaping. Sedentary animals could be especially vulnerable if they require specific habitats or their ability to escape is reduced. However, dynamic coastal environments could promote greater flexibility in fish living there.

Populations of the sedentary seahorse *Hippocampus guttulatus* living in a dynamic estuary seem flexible in their habitat use, but individuals may be less so. I explored *H. guttulatus* habitat associations using underwater surveys and displacement experiments in the Ria Formosa lagoon. Seahorse populations declined substantially (73-94%) compared to previous surveys, but declines were unassociated with measured habitat changes. At low densities, *H. guttulatus* lived in a range of habitats but in warmer, deeper locations. When displaced, *H. guttulatus* moved to a variety of environments but individual seahorses moved towards locations with familiar depths and current speeds. Individual variability could help protect populations in degrading habitat but individuals may still need to move to survive.

Hippocampus guttulatus can move further than their small home ranges would suggest, which might help them escape habitat loss and degradation. In aquarium experiments I showed that small acoustic tags could be used on captive *H. guttulatus* with minimal effects on movement and behaviour. I displaced tagged *H. guttulatus* and found they moved ten times further than typical home range movements.

While *H. guttulatus* shows some capacity for acclimatizing and escaping, their sedentary nature could confer vulnerability to habitat loss and degradation. Models simulating fish movement across artificial seascapes predicted sedentary fish should be more sensitive to habitat loss and fragmentation than more mobile fish. Comparative analyses of movement and vulnerability among marine benthic fish species supported these results. Among fishes threatened by habitat degradation, those that rarely move beyond home ranges were more threatened than those that migrate or disperse.

My thesis identified general relationships between movement and vulnerability in marine fishes, which could help prioritize conservation, while raising further questions about the additional effects of habitat specialization and environmental variability.

PREFACE

This thesis represents my own work, some of which has been published elsewhere. Three of the chapters in this thesis have been published in peer-reviewed journals (Chapters 2, 3, and 4) and others are being prepared for submission (Chapters 5 and 6). I am (or will be) the lead author on all published papers. I was primarily responsible for conceptualization, experimental design, collecting information (with help from volunteers), data management, data analysis, and writing in each of the manuscripts. However, my co-authors have made significant contributions and improved manuscripts substantially. I list my co-authors and outline their contributions below.

A version of Chapter 2 has been published as: “Caldwell IR, Vincent ACJ (2012) Revisiting two sympatric European seahorse species: Apparent decline in the absence of exploitation. *Aquatic Conservation: Marine and Freshwater Ecosystems* doi: 10.1002/aqc.2238”. Dr. Amanda Vincent helped conceptualize the study, gave feedback on the design and implementation of surveys, and provided edits throughout the analysis and writing.

A version of Chapter 3 has been published as: “Caldwell IR, Correia M, Palma J, Vincent ACJ (2011) Advances in tagging syngnathids, with the effects of dummy tags on behavior of *H. guttulatus*. *Journal of Fish Biology* 78: 1769-1785”. Miguel Correia helped to design and implement aquarium experiments, collected much of the behavioural data while I was away from Portugal, and managed and manipulated the data for easier analysis. Dr. Jorge Palma assisted Miguel with some behavioral data collection and provided the seahorses, aquarium

space, and materials for the experiments. Dr. Vincent provided edits, feedback, and suggestions during analysis and writing.

A version of Chapter 4 has been published as: “Caldwell IR, Vincent ACJ (2012) A sedentary fish on the move: Effects of displacement on long-snouted seahorse (*H. guttulatus* Cuvier) movement and habitat use. *Environmental Biology of Fishes* doi: 10.1007/s10641-012-0023-4”. Dr. Vincent provided logistical support and gave feedback and suggestions during conceptualization, analysis, and writing.

I anticipate that a version of Chapter 5 will be sent to a peer-reviewed journal and will be co-authored by Dr. Sarah Gergel. Dr. Gergel helped me to develop the idea for the chapter as part of her Landscape Ecology course at The University of British Columbia (UBC). She continued to provide feedback and support as I built the model, analysed the results, and wrote the manuscript.

I anticipate that a version of Chapter 6 will be sent to a peer-reviewed journal with Dr. Philip Molloy and Dr. Amanda Vincent as co-authors. Dr. Molloy was particularly helpful in analysis and writing, providing suggestions for additional analyses that significantly strengthened the manuscript. Dr. Vincent helped formulate the original idea and provided feedback throughout the data collection, analyses, and writing phases.

All field work in this dissertation was approved by UBC’s animal care committee (A07-0077).

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“The most beautiful thing we can experience is the mysterious.

It is the source of all true art and science” – Albert Einstein

Chapter 1. Introduction

1.1 Rationale

In this thesis, I seek to quantify the links between habitat use, movement, and vulnerability in sedentary fishes, using seahorses as a model, to help understand how they may respond to increasing pressure from human activities. The research was partly prompted by a need to understand how limited movement in many seahorse species contributes to their vulnerability to extinction. Seahorses have some life history characteristics that could protect their populations from decline (e.g., rapid growth, early maturity, and short generation times), and others that could make them vulnerable to depletion (e.g., monogamous mating, elaborate parental care, and relatively few young) (Foster and Vincent 2004, Curtis and Vincent 2006). It has been hypothesized that their sedentary nature also makes seahorses vulnerable to exploitation and habitat loss/degradation (Curtis 2004), but this hypothesis has not been explored. It is particularly important to establish whether mobility is related to vulnerability for seahorses because they are of conservation concern, threatened by direct exploitation, accidental capture, and habitat loss/degradation (Vincent *et al.* 2011).

Beyond seahorses, I focused on sedentary fish because they represent one interesting end of the spectrum of animal movement and their strategies could have conservation implications. While they are capable of movement, sedentary animals have developed interesting strategies to acquire all their resources within a small area, even in relatively variable environments (e.g., seahorses in seagrasses; Curtis and Vincent 2006). Unfortunately, sedentary strategies, as with other behavioural tactics, may be less successful when humans disturb the environment unpredictably (Norris 2004). I seek to shed light on how well sedentary fishes

can cope in such a dynamic world by collecting biological information on their habitat use, movement and relative vulnerability.

In the remaining sections of this introduction I provide a context for the research and explain how the thesis is structured to address my overall goal. I begin by expanding upon my rationale with background information. I then provide a description of the model study species and location I used for my field-work based chapters. I end with an outline of my thesis chapters, explaining how each, in turn, addresses questions about habitat use, movement, and vulnerability in sedentary fish.

1.2 Background

1.2.1 Marine fish conservation

There is still much left to be learned about life in the ocean; an exciting prospect from the perspective of new discovery but a problematic one for conservation. In the last decade (2000-2010), a global effort to catalogue marine life led to the discovery of at least 1200 new species (Census of Marine Life Project; Costello *et al.* 2010). An even greater number of marine species (up to 91%) probably remain undiscovered (Mora *et al.* 2011). Even in fairly well-studied European waters, it is estimated that between 4000 and 12000 marine species have yet to be described (10-25% of those that have been described; Costello and Wilson 2011). Among those species that have been described, an even smaller proportion have been studied enough to judge their conservation status (Vié *et al.* 2009). With such a small subsample, it is difficult to estimate the total effect of human activities on the world's oceans. The need for more information on ocean life to support conservation decisions has been

recognized by the recent prioritization of 15,000 marine fish and reptiles for assessment on the International Union for Conservation of Nature's (IUCN) Red List of Threatened Species (Vié *et al.* 2009).

What is known about marine fishes suggests there is cause for concern. Marine fishes are threatened by (1) direct exploitation to support the needs of a growing human population, (2) habitat loss linked with exploitation and other human activities, (3) pollution along the world's coastlines, and (4) the introduction of invasive plants and animals (Jackson *et al.* 2001, Reynolds *et al.* 2005a, Costello *et al.* 2010). It was once thought that the world's fish were inexhaustible due to their high fecundity and large dispersal capabilities, but more recent evidence suggests that aquatic species exhibit the same (Dulvy *et al.* 2003) or greater (Jenkins 2003) extinction risk than terrestrial animals. Over-exploitation has led to the collapse of many of the world's fisheries (Worm *et al.* 2006). At the same time, key habitats used by fish (e.g., coral reefs, seagrasses, and mangroves) are suffering from habitat loss and fragmentation (Nyström *et al.* 2000, Alongi 2002, Bellwood *et al.* 2004, Waycott *et al.* 2009, Fraschetti *et al.* 2011). Increasing coastal populations will exacerbate these problems, leading to greater demands for fish and disturbing ocean environments even further; in 2001, 50% of the world's human population lived within 60 km of a coastline and by 2020 it is estimated that percentage will increase to 75% (Intergovernmental Panel on Climate Change, in DeMaster *et al.* 2001).

Biological questions need to be answered to understand how well marine fish can cope with human activities that threaten their populations. The survival of a species depends on its

adaptability to change. Most animals deal with change either by acclimatizing to the new conditions or escaping to a new location with better conditions. Questions of interest thus include the following:

1. How flexible are habitat associations in fish?
2. How capable are fish of escaping change?
3. How vulnerable are fish to specific threats given their adaptability to change?

1.2.2 Sedentary strategies and habitat use

Understanding how well animals can cope with different environmental conditions is important for any species, but for sedentary species it could be particularly crucial since their ability to avoid stress through movement is reduced. Sedentary animals have evolved strategies to acquire resources without needing to travel. Instead of fleeing predators, some animals use camouflage to hide in plain sight. Chameleons (e.g., *Chamaeleo chamaeleon*) primarily avoid predation by changing colour to blend in with surrounding vegetation (Cuadrado *et al.* 2001). Instead of chasing prey, some animals use an ambush (i.e., sit and wait) predation strategy. Orb web-building spiders (e.g., *Araneus diadematus*) may spend time and energy spinning their intricate webs but catch enough prey that it outweighs those costs (Peakall and Witt 1976). One drawback of a sedentary lifestyle would be finding reproductive mates, especially at low densities, but there are also strategies that minimize this problem. At low densities some terrestrial mammals and marine fish become monogamous (i.e., facultative monogamy), thereby limiting the need to find new mates repeatedly (Kleiman 1977, Whiteman and Côté 2004). Using sedentary strategies can minimize the time and energy spent on travel.

Ultimately, the amount and frequency of movement needed for survival, growth, and reproduction depends on the amount and distribution of resources required. For example, large animals tend to move further (i.e., have larger home ranges) than small animals, and carnivores move further than herbivores (Alexander 1982). Presumably this is because larger animals need more food to support their body size and prey animals are more highly dispersed than plants for consumption. Animals that disperse or migrate do so because either the needs of the animal or the distribution of their resources changes over time (McKeown 1984). The frequency of migration depends on the temporal scale of change. Regardless of the scale, for a strategy to be successful the benefits of moving must outweigh the costs.

In many cases, sedentary strategies are associated with habitat specialization. For example, among British butterflies there is a strong correlation between mobility and specialization: sedentary species tend to be specialists while mobile species are generalists (Warren *et al.* 2001). In some cases, anti-predator or feeding strategies are reliant on other species, which are, in turn, limited to certain environments. For example, clownfish (genera *Amphiprion* and *Premnas*) are protected from predators by stinging anemones (genus *Anemone*) (Fautin 1991). To take advantage of the symbiosis, clownfish must live in the subset of habitats (i.e., niche) where sessile anemones can settle. Other sedentary animals may have become specialized on an under-utilized food resource to avoid overlap with other species, thereby limiting the environments where they live. Koalas (e.g., *Phascolarctos cinereus*) remain within home ranges that contain specific Eucalyptus species (e.g., *Eucalyptus teresticornis*), on which they feed almost exclusively (Ellis *et al.* 2009). They have become specialized on

these nutrient-poor, toxic leaves presumably because few other animals can eat them, so inter-specific competition is minimal (Tyndale-Biscoe 2005).

Habitat specialization may work for sedentary animals in highly productive environments but is less effective in variable conditions. For a sedentary strategy to be successful, all necessary resources must be accessible within a single small area. Focusing on a small range of high-quality habitats can work if there are plenty of those habitats available. If the availability of habitats is uncertain, however, natural selection should favour a broadening of the niche (i.e., generalization) (Levins 1968). If niches are broad enough, an animal should be able to survive, grow, and reproduce in any small area. Generalist species can live in a wider range of habitats and are less susceptible to variation in habitat characteristics (Owens and Bennett 2000, Harcourt *et al.* 2002, Krauss *et al.* 2003).

1.2.3 Flexibility of sedentary fish strategies (habitat use and movement)

Coastal marine environments tend to be highly productive, with resources flowing over the seascape, making them conducive to both sedentary strategies and specialization. There tends to be greater import and export of nutrients in the ocean than in terrestrial environments because habitats are connected on broader scales (Carr *et al.* 2003). The high productivity and transfer of resources in coastal marine environments allows for animals to be sedentary as they are able to access needed resources in a smaller area. This is how coral reef fish are able to remain within smaller home ranges than freshwater fish, mammals, lizards, and birds (Turner *et al.* 1969, Harestad and Bunnell 1979, Kramer and Chapman 1999). Such high productivity should also favour specialization (Levins 1968).

While high productivity in the oceans favour specialization, the instability of some coastal marine habitats favours generalization (Levins 1968). In particular, seagrass habitats are prone to both natural and anthropogenic disturbance creating temporally variable habitat (Short and Wyllie-Echeverria 1996, Roy *et al.* 2001). In response to this environmental variability, fish populations living within seagrass also tend to shift their distributions over time (Livingston 1984, Jones and West 2005). Sedentary species may not be able to move to new areas when conditions change. It is possible that sedentary fish may instead rely on an ability to cope with change without moving.

When conditions are too unstable, the marine environment could aid in movement. Even the broadest niche does not fully encompass all possible environmental conditions. Beyond a physiological threshold, adaptation will no longer be possible. When that threshold is reached, the only other option is to move. The buoyancy of water and connectivity of the oceans make such movement easier for fish than terrestrial animals. The density of water is close enough to the density of living tissue that marine fish are virtually weightless (Wootton 1992). Without needing to fight against gravity, fish can use less energy than animals that run or fly (Alexander 1982). Fish can also use the high connectivity of the marine environment to their advantage (Carr *et al.* 2003), travelling passively along ocean currents. Further, there is evidence that the variability in the marine environment favours spatial learning in fish, allowing them to navigate beyond their home range when necessary (Odling-Smee and Braithwaite 2003). Marine fish could hedge their bets, remaining sedentary when resources are plentiful and relocating if resources disappear or become scarce.

1.2.4 Vulnerability of sedentary fish

If unable to either acclimatize or escape, sedentary fish could be at risk from habitat loss and degradation. Although coastal marine environments tend to be naturally variable, such changes are usually somewhat predictable. Habitat loss and fragmentation stemming from human activities are more extreme and less predictable (Nyström *et al.* 2000, Alongi 2002, Bellwood *et al.* 2004, Waycott *et al.* 2009, Fraschetti *et al.* 2011), with a greater possibility of surpassing physiological thresholds of sedentary fish. Habitat degradation is considered either the second (Jackson *et al.* 2001, Dulvy *et al.* 2003) or third (Halpern *et al.* 2008) greatest source of threat to marine life after direct exploitation. Furthermore, its effects are likely underestimated as most data available for fish species have been collected through their fisheries (Reynolds *et al.* 2005a).

If sedentary fish are particularly threatened by habitat loss or degradation, mobility (or lack thereof) could be used as a proxy to identify species of conservation concern. Unfortunately, there has only been enough data to assess extinction risk of a small proportion (11% in 2008) of described marine fish species (Vié *et al.* 2009). When direct vulnerability data is limited, shared traits that are associated with extinction risk could be used to infer vulnerability. In marine fishes, life history traits such as large size, late maturity, high trophic level, slow growth, demersal behaviour, and longevity are all related to extinction risk (Reynolds *et al.* 2005a). Individual movement (capability and frequency) has been linked to extinction risk in some terrestrial animals (Harcourt 1998, Warren *et al.* 2001, Jones *et al.* 2003), but such a link has not been examined in marine fishes.

1.3 Study species and system

As my model of a sedentary fish, I focused on seahorses (genus *Hippocampus*) which are notoriously sedentary. In most seahorse species, after juveniles settle and mature the adults tend to stay within small home ranges (Vincent *et al.* 2005, Foster and Vincent 2004), some no more than 1 m² (Perante *et al.* 2002). Seahorses avoid predation using camouflage, are ambush predators, and most are monogamous within a breeding season (Foster and Vincent 2004). These small fish have few reasons to travel extensively in search of resources and benefit from remaining still enough to remain unseen by predators or prey. Their unusual body morphology affords them maneuverability rather than speed. Seahorses swim by undulating their dorsal fin (i.e., amiiform swimming as in Lindsay (1978)), more appropriate for hovering than forward propulsion (Videler 1993). When not swimming they can wrap their prehensile tails around holdfasts to stay in one location.

Although adult seahorses are routinely sedentary, they are capable of voluntary movement and prone to involuntary displacement. Shallow areas of coral reefs, seagrass beds, mangroves, macroalgae and estuaries inhabited by seahorses are prone to both natural (e.g., storms, strong currents) and anthropogenic (e.g., fishing, coastal development) disturbances. These disturbances could lead to either involuntary displacement, or changes in the environment that motivate seahorses to move voluntarily. Adult seahorses have been found in the open ocean, hanging on to floating debris with their prehensile tails (Kuitert 2001, Dias *et al.* 2002), a possible vector for passive, long distance dispersal. Displacement and

environmental change are likely to result in changes in movement and habitat use, yet little is known about how seahorses respond to these changes.

It is not clear how their sedentary nature contributes to their vulnerability, but most seahorse species assessed by the IUCN are either Data Deficient (29 species) or of significant conservation concern: seven are Vulnerable and one is Endangered (IUCN 2012). Only one is not of concern. Seahorse populations are threatened both by exploitation (mainly through by-catch but also targeted for the marine ornamental, traditional medicine, and curio trades) and habitat loss/degradation (Vincent *et al.* 2011).

The European long-snouted seahorse (*H. guttulatus*) is a Data Deficient species but what is known about its movement and habitat use suggests it would be a good model of a sedentary fish in a dynamic world. After approximately eight weeks in the plankton (Boisseau 1967), *H. guttulatus* settle into small ($19.9 \pm 12.4 \text{ m}^2$), overlapping home ranges (Curtis and Vincent 2006). *H. guttulatus* are generally found in seaweed or algal-dominated shallow, inshore waters of the Mediterranean Sea, the Black Sea, and the eastern Atlantic Ocean from the north coast of Africa to the Netherlands (Lourie *et al.* 2004). The seagrasses they inhabit are prone to both natural and anthropogenic disturbance, creating temporally variable habitat (Cunha *et al.* 2011). Unlike some seahorse species whose camouflage is only effective when attached to certain species (e.g., the pygmy seahorse *Hippocampus bargibanti*; Baine *et al.* 2008), *H. guttulatus* use a variety of plants and sessile animals for cover (Curtis and Vincent 2005).

I focused my study on *H. guttulatus* in the Ria Formosa lagoon, located in southern Portugal (36°59'N, 7°51'W), where some population and habitat use data have been collected in the past. The shallow, estuarine lagoon is 55 km long and 6 km at its widest point, with water temperatures varying seasonally between 12 °C and 27 °C (Newton and Mudge 2003). The substrate tends to be mostly bare (fine sand, coarse sand, and shell fragments), with living substrate dominated by seagrass (mainly *Cymodocea nodosa*), macroalgae, and benthic invertebrates (Curtis and Vincent 2005). In 2001/2002, *H. guttulatus* was found in unusually high densities (0.073/m²) in the lagoon (Curtis and Vincent 2005), an order of magnitude greater than in other species (Foster and Vincent 2004). During that time, *H. guttulatus* was found primarily on holdfasts within complex seagrass habitat but did not specialize on any particular type of micro-habitat (Curtis and Vincent 2005).

An advantage of working in the Ria Formosa lagoon is that I could focus on environmental effects in the absence of direct fishing pressure. The Ria Formosa is a semi-protected lagoon where towed demersal fishing gear is prohibited (Erzini *et al.* 2002), so accidental capture should be minimal. Most seahorse species around the world are caught as trawl bycatch of other fisheries (Vincent *et al.* 2011), and working in the Ria Formosa allowed me to study these species in the absence of such a threat.

1.4 Thesis outline

This thesis is divided into five data-based research chapters, each of which examines an aspect of sedentary fish that could affect their ability to survive threats from human activities (habitat use, movement, or vulnerability), followed by a general synthesis. Chapters 2, 3, and

4 are field-based data chapters using the long-snouted seahorse (*H. guttulatus*) as a model of a sedentary fish. Chapters 5 and 6 test whether what I learn from *H. guttulatus* in the previous chapters can be applied more generally to sedentary fish species. Each chapter addresses (directly or indirectly) at least one of the three research questions of interest I outlined earlier.

1. How flexible are habitat associations in a sedentary fish? (Chapters 2 and 4)

The dynamic environment found in the Ria Formosa lagoon could be conducive to habitat generalization in *H. guttulatus* (Levins 1968), which could in turn protect them from unpredictable change from human activities (Owens and Bennett 2000, Harcourt *et al.* 2002, Krauss *et al.* 2003). To assess whether these sedentary fish living in a dynamic world tended towards habitat generalization or specialization, I attempted to identify habitat associations first through underwater visual census (UVC) surveys (Chapter 2) and then through displacement experiments (Chapter 4). In my UVC surveys, I compared habitat associations of *H. guttulatus* (and the smaller, sympatric congener species *Hippocampus hippocampus*) with those found in earlier surveys (Curtis and Vincent 2005). In my displacement experiments I captured, released, and repeatedly located displaced fish, quantifying their habitat at each location. If these fish are habitat generalists I would expect that habitat associations would be inconsistent over time and displaced seahorses would either stay in the location they were released or move randomly with respect to habitat characteristics.

2. How capable are sedentary fish of moving to new locations? (Chapters 3 and 4)

The connectivity and instability of the marine environment could assist in long distance movement (Carr *et al.* 2003, Odling-Smee and Braithwaite 2003), helping sedentary fish move beyond home ranges when necessary. In order to find out about movement of *H. guttulatus*, I needed a technique to follow these small fish with minimal effect on their behaviour. In Chapter 3, I tested the effects of the smallest available acoustic tags on the movement and general behaviour of captive *H. guttulatus*. In Chapter 4, I used those tags to track the movement of displaced seahorses. I compared those movements to known home ranges (Curtis and Vincent 2006) to determine whether *H. guttulatus* move further than normal when displaced.

3. Do human activities (habitat degradation or fishing) affect sedentary fish differently than more mobile ones? (Chapters 5 and 6)

If unable to cope with change or escape it, sedentary fish may be more vulnerable than mobile fish. In Chapter 5, I assessed how differing amounts of habitat loss and fragmentation might affect the movement of sedentary and mobile fishes. I adapted a landscape ecology modeling framework to create artificial seascapes with different current strengths, habitat abundance, and habitat fragmentation. I simulated the movement of three model fish of different mobility across each seascape to predict the relative effects of habitat structure on connectivity. In Chapter 6, I tested whether sedentary marine fishes are at greater extinction risk from either exploitation or habitat degradation than more mobile counterparts. In a comparative analysis I tested whether individual movement (capability, extent or frequency) is related to extinction risk (as categorized on the IUCN Red List) among marine benthic fish

species. I further subdivided species by threat type to determine whether relationships differed among fishes threatened by habitat degradation and those threatened by exploitation.

Although much of my research focused on a sedentary seahorse species, the results of my research should have implications beyond seahorses and even other sedentary fishes. In the concluding chapter of my thesis (Chapter 7), I discuss these implications after bringing together the results of my five data chapters to address the overall goal of my thesis: to relate movement, habitat use, and conservation in sedentary fishes.

Chapter 2. Revisiting two sympatric European seahorse species: Apparent decline in the absence of exploitation

2.1 Summary

Seahorses are marine fish with several life history characteristics hypothesized to make them resilient, but they are of conservation concern because of their international trade and habitat loss. Surveys of two unexploited European seahorse species (*H. guttulatus* and *H. hippocampus*) in Ria Formosa lagoon, Portugal, were repeated 7 years after their populations in the lagoon were found to be among the densest in the world. Population densities of both species declined significantly between 2001/2002 and 2008/2009 surveys (94% and 73% for *H. guttulatus* and *H. hippocampus* respectively). *H. guttulatus* declines were not associated with any environmental changes measured (i.e., percentage live benthic habitat cover, depth, temperature, water current speed, horizontal visibility). *H. hippocampus* declined more where current speed had decreased. At the low densities found in 2008/2009, occurrence for both species was best predicted by depth: seahorses were found in deeper locations throughout the lagoon. Other important predictors were temperature for *H. guttulatus* (found at sites warmer than average) and current speed for *H. hippocampus* (found in locations with faster currents). The large declines in seahorse densities made it difficult to compare habitat use results over time. Presence–absence and abundance modelling at multiple scales can help to ensure that data are comparable even when populations fluctuate drastically.

2.2 Introduction

It has been argued that marine species have low vulnerability of extinction because of their high fecundity and wide dispersal capabilities (Musick 1999, Powles *et al.* 2000), yet at least

133 local, regional and global extinctions of marine populations have been reported (Dulvy *et al.* 2003). While no marine fish species is known to have gone extinct in recent times, many populations have collapsed, with a median decline of 83% for 232 fish populations monitored for 10 years or more (Hutchings and Reynolds 2004). Such drastic declines cannot be explained by the natural variation in most marine fish populations (Hutchings 2001).

Populations decline and disappear if deaths exceed births and/or emigration exceeds immigration. The main threats to marine populations are exploitation and habitat loss (Dulvy *et al.* 2003). Exploitation directly removes individuals from a population and, depending on the gear used, can cause disturbance that leads to emigration or death even of non-target organisms. In turn, habitat loss usually acts indirectly to generate emigration or death. Other potential causes of fluctuation that could lead to decline include species interactions (e.g., predator–prey dynamics, disease), or non-linearity in single species dynamics (e.g., recruitment pulses) (Shelton and Mangel 2011).

Seahorses are examples of marine fish with life history characteristics that might make them either very resilient or highly vulnerable to decline. In general, seahorses grow rapidly, mature at young ages, and have short generation times (Foster and Vincent 2004), suggesting that they could recover rapidly from a decline (Curtis and Vincent 2006). However, many seahorses also have monogamous mating patterns, elaborate parental care and relatively few young (Foster and Vincent 2004), suggesting vulnerability.

In fact, most seahorse species are either understudied or of conservation concern. Seahorse populations tend to be patchily distributed and at low densities (Foster and Vincent 2004), potentially because of bycatch, direct exploitation (for marine ornamental, traditional medicine, and curio trades), or habitat loss (Vincent *et al.* 2011). Of the 38 seahorse species included in the IUCN Red List, only one is considered Least Concern while the remainder are Data Deficient (29), Vulnerable (7), or Endangered (1) (IUCN 2012).

Populations of two sympatric European seahorses (*H. guttulatus* and *H. hippocampus*), both assessed by the IUCN as Data Deficient, were found in unusually high densities in the Ria Formosa lagoon, Portugal in 2001/2002 (Curtis and Vincent 2005) compared with most other seahorse densities (Foster and Vincent 2004). Although there is some evidence of directed and incidental capture of these species in Portugal as curios (Project Seahorse 2003a, Project Seahorse 2003b), the Ria Formosa is a semi-protected lagoon with regulations against the use of nets and other fishing gear that could lead to by-catch (Erzini *et al.* 2002). These protections could be responsible for densities an order of magnitude greater than seahorse populations that are directly exploited (Foster and Vincent 2004).

The Ria Formosa lagoon was resampled in 2008/2009 to identify any population changes in *H. guttulatus* and *H. hippocampus*, and to explore whether there were associated changes in the environment or in habitat use relationships. The first objective was to compare relative densities of the two species at sites throughout the lagoon with previous densities. The second was to identify environmental variables that correlate with (a) changes in species densities, (b) species occurrence (at two spatial scales), and (c) species density. Since these

populations are largely free from direct exploitation, the hypothesis tested was that changes in density would be associated with changes in habitat. Since there is habitat niche partitioning between the two species (Curtis and Vincent 2005, Curtis *et al.* 2007), a further hypothesis was that relative changes in density would be associated with differences in habitat use between the species.

2.3 Methods

2.3.1 Study species

H. guttulatus and *H. hippocampus* both inhabit shallow, coastal waters of the north-eastern Atlantic Ocean and Mediterranean Sea (Lourie *et al.* 2004). The species are best distinguished by the differing number of trunk rings and angle of the coronet, with *H. hippocampus* having a higher and more pointed coronet (Lourie *et al.* 2004). Although the two species use similar habitats, there appears to be some habitat niche partitioning. At the high densities in 2001/2002, *H. guttulatus* was found within more complex, seagrass habitat while *H. hippocampus* was found in bare, sandy habitats (Curtis and Vincent 2005). This preference was confirmed by experimental seining that showed decreases of *H. guttulatus* and increases of *H. hippocampus* when habitat cover was reduced through seining (Curtis *et al.* 2007). Both species preferred to use holdfasts (i.e., habitat they can hold onto with their prehensile tails) over barren surfaces but differed in the types of holdfasts they preferred: *H. guttulatus* had no preference while *H. hippocampus* preferred solitary holdfasts (Curtis and Vincent 2005).

2.3.2 Underwater visual census

Thirty-three locations (i.e., sites) within the Ria Formosa lagoon, Portugal were surveyed in 2008/2009 using the same underwater visual census methods and 32 of the sites used in 2001/2002 by Curtis and Vincent (2005). Seventeen sites were surveyed between 15 July and 20 November 2008 and 16 sites between 27 August and 28 November 2009. At each site, scuba was used to count seahorses along three randomly placed 30 m long transects, with each transect placed at least 5 m apart. Due to high currents and turbidity, surveying was limited to high slack tides (i.e., 1 h before to 1 h after high tides). Because of low visibility at most sites, it was only possible to count fish within 2 m of the transect line (i.e., 4 m wide transects), although better visibility at two sites meant it was possible to survey an area 6 m wide. The total surveyed area was 12240 m². Whenever a seahorse was encountered, its species was recorded and it was categorized as either a juvenile or adult. The sex of adults was also recorded using the presence or absence of a brood pouch to differentiate (Lourie *et al.* 2004).

2.3.3 Habitat characteristics

Habitat was assessed wherever a seahorse was found and at three control plots per transect (0 m, 15 m and 30 m). A 1 m² quadrat was centred around seahorses and at control sites. The quadrat was further subdivided into 0.1 m² sections to visually estimate percentage live benthic habitat cover more accurately within the square. Water depth (m), water temperature at depth (°C) and water current speed (m s⁻²) were also measured within the quadrat. Horizontal visibility was estimated as the furthest visible measure along a transect tape.

2.3.4 Changes in species distributions and densities

Using the GPS coordinates of each survey site, abundances of both species were mapped in GIS software (ESRI ArcMap 10.0). For each of the 32 sites surveyed by Curtis and Vincent (2005), changes in density (number of individuals per m²) were compared with a Wilcoxon matched pairs test (as the density data were non-normal and transformations were unsuccessful). Density rather than abundance was compared to account for sampling differences (i.e., belt transect width) between the 2008/2009 surveys (4 m wide belts) and the 2001/2002 surveys of Curtis and Vincent (2005; 2 m wide belts). To test whether there was a difference in the proportion of juveniles vs. adults and whether there was a sex bias in either species, chi-square tests were used in GraphPad PRISM software (Version 5.02).

2.3.5 Environmental correlates of density changes

Changes in the environment of the Ria Formosa lagoon were examined by comparing environmental variables measured in 2008/2009 (i.e., percentage live cover, depth, temperature, current, visibility), with those measured in 2001/2002 by Curtis and Vincent (2005). Most variables were directly comparable. However, since horizontal visibility was estimated in both surveys and water current speed was a qualitative measure in the earlier surveys, visibility and current needed to be normalized before comparison (i.e., transformed to have the same range and mean). Changes in environmental characteristics at each of the 32 shared sites were analysed using Wilcoxon matched pairs tests (as data were non-normal and transformations were unsuccessful), in PRISM software.

To identify any changes in the environmental characteristics measured associated with the changes in population densities, generalized linear models (GLMs) were used. Changes in environmental variables and species densities were calculated for each of the 32 shared sites by subtracting 2001/2002 survey data from 2008/2009 data. Before model selection, a Spearman rank correlation matrix was created using PRISM software to compare changes in each environmental variable with changes in densities of each species and to identify any collinearity between variables (Curtis and Vincent 2005). A non-parametric test was used because environmental data were non-normal and transformations were unsuccessful. Change in density data was mostly negative with a left skew so was transformed by taking the square root of the sum of the negative of the data plus the maximum of the data to approximate a Gaussian distribution for GLMs.

Results of univariate Spearman rank correlations were used to inform model selection (West *et al.* 2006). Starting with the variable with the highest significance (i.e., lowest P-value), and adding variables in a forward stepwise process, GLMs were created assuming a Gaussian distribution and a log link function. Models were compared using ANOVA to test for differences in deviance (Zuur *et al.* 2009). Variables and/or their interactions were only retained if their addition significantly reduced model deviance according to an F test ($P < 0.05$).

2.3.6 Habitat use

To identify environmental variables of potential importance to each of the two seahorse species, the relationship between the five environmental characteristics measured and two

dependent variables (i.e., seahorse occurrence and density) was analysed for each species. The relationship between environmental characteristics and occurrence (presence/absence) was analysed at two spatial scales (site and quadrat). However, the relationship between environmental characteristics and density (m^{-2}) could be analysed only at the site scale because there was only one seahorse per quadrat. At both the site and quadrat scales, occurrence relationships were analysed using the data from all 33 sites. At the quadrat scale, occurrence relationships were further analysed using data only from those sites where a species was found (removing zeros). The latter analysis was to determine whether the seahorse location (i.e., quadrat) within a site is related to different variables than among sites.

It was necessary to use three different types of models for the different scales and dependent variables: (1) mixed effects models for the occurrence analysis at the quadrat scale; (2) binomial generalized linear models for the occurrence analysis at the site scale; and (3) generalized linear models assuming a Gaussian distribution for the density analysis (site scale). Mixed effects models were needed at the quadrat scale to include site as a random factor. This controlled for the fact that quadrats within sites are probably more similar than quadrats among sites. The software package lmer within the statistical program R (R Development Core Team 2011) was used for mixed effects analyses. Average values per site were used for the site scale analyses. All 33 sites were used for the occurrence analysis at the site scale. However, for each species, only the sites where that species was present ($n = 8$ in each case) were used for the density analysis. For both of the site scale analyses the software package glm within the statistical program R was used.

For each of the model types, the same forward stepwise process was used to select the best model. Models were first run using only the dependent variable and each of the environmental variables alone. The results of these univariate analyses were used to guide forward stepwise development of multivariate models (West *et al.* 2006, Jewell *et al.* 2007). As in the analysis of correlates of change, models were created starting with the environmental variable with the lowest univariate significance value (P-value), and sequentially adding variables with successively higher significance. Successive models were selected only if model deviance was reduced significantly with the addition of a variable according to an F test ($P < 0.05$). To test whether the survey year had an effect on the model (i.e., 2008 vs. 2009), year was added as a variable to each model and retained if it significantly reduced model deviance.

2.4 Results

Both seahorse species were absent from 66% of the sites surveyed in the Ria Formosa lagoon in 2008/2009 (i.e., 22 of 33 sites). The sites where seahorses were found tended to be either in the central lagoon near a major shipping channel between Faro and an entrance to the lagoon or near one of the other entrances to the lagoon (Fig. 2.1). *H. guttulatus* was the more common species with an overall density of 0.004 m^{-2} (± 0.002 S.E.) whereas *H. hippocampus* density was 0.001 m^{-2} (± 0.0006 S.E.) (Table 2.1). Densities per site, though, ranged almost an order of magnitude larger, as high as 0.035 m^{-2} for *H. guttulatus* and 0.019 m^{-2} for *H. hippocampus*.

More *H. guttulatus* were found at sites surveyed in 2009 than those surveyed in 2008 and juveniles of both species were found only during 2009 surveys (Table 2.1). However, these data represent different sites so could not be compared over time. Similar numbers of juveniles were found for both species (Table 2.1), but since there were far fewer *H. hippocampus* overall, juveniles represented a higher proportion of the population of *H. hippocampus* than *H. guttulatus* (28% and 10% respectively; chi-square test, $P = 0.0012$). Neither species was significantly biased towards either sex (*H. guttulatus*: 22 male, 30 female, chi-square test, $P=0.267$; *H. hippocampus*: 8 male, 5 female, chi-square test, $P=0.405$).

Both species had declined since 2001/2002, although the decline was more severe for *H. guttulatus* (Fig. 2.2). In 2001/2002 *H. guttulatus* was found in 29 of 32 sites but they had disappeared from 21 sites of those sites by 2008/2009. Overall densities of *H. guttulatus* decreased significantly from 0.0691 m^{-2} to 0.00434 m^{-2} (Wilcoxon matched pairs test, $P<0.0001$). At most of the sites ($n=18$), *H. hippocampus* was absent in both 2001/2002 and 2008/2009. *H. hippocampus* did appear at four new sites, where they had not been found in 2001/2002. However, there was a decline in density at the remaining ten sites and an overall significant decline from 0.00469 m^{-2} to 0.00127 m^{-2} between 2001/2002 and 2008/2009 (Wilcoxon matched pairs test, $P=0.0129$).

The only environmental change detected throughout the lagoon was in water depth. Sites were significantly deeper in 2008/2009, with median depth changing from 2.41 to 3.60 m

(Wilcoxon matched pairs test, $P = 0.001$). There were no significant changes in percentage live cover or temperature (Wilcoxon matched pairs tests, $P > 0.519$ in both cases). No significant changes in relative visibility or water current speed per site were detected (Wilcoxon matched pairs tests, $P > 0.325$ in both cases), but the power to detect a change in these variables was diminished by the need to normalize the data sets for comparison.

The only environmental change correlated with the declines was a change in the water current speed. *H. hippocampus* declines were greater at sites where the relative water current speed had decreased between 2001/2002 and 2008/2009 (Spearman rank correlation, $P = 0.047$). However, the relationship was weak ($\rho = 0.400$), and was based on normalized comparisons since current speed was measured qualitatively in the earlier (2001 and 2002) surveys so the relationship is questionable. None of the other environmental changes were correlated with changes in *H. hippocampus* densities (Spearman rank correlations, $P > 0.194$ in all cases). *H. guttulatus* declines were not correlated with any of the environmental changes measured (Spearman rank correlations, $P > 0.0596$ in all cases).

The multi-scale habitat use analysis identified two environmental variables related to *H. guttulatus* occurrence and two related to *H. hippocampus* occurrence (Tables 2.2 and 2.3). Depth was positively correlated with occurrence in both species, indicating that both species avoided shallow waters (less than 3 m depths). Besides depth, the other variables related to occurrence of *H. guttulatus* (temperature) and *H. hippocampus* (water current speed) were only identified at one spatial scale in each case (site and quadrat, respectively). Temperature was not a significant predictor of *H. guttulatus* occurrence when analysed alone ($P > 0.05$), but

positively associated with occurrence when combined with depth at the site scale ($P < 0.05$): *H. guttulatus* were found in sites that were warmer than average when depth was taken into account. Water current speed was positively associated with *H. hippocampus* occurrence within sites where the species was present, but only when combined with depth: *H. hippocampus* were found in locations with stronger currents.

None of the environmental variables measured were correlated with densities of *H. guttulatus* or *H. hippocampus* in 2008/2009. However, the low densities found in 2008/2009 make it difficult to analyze any relationship with density: even though 32 sites were surveyed, this analysis was based on only eight sites for each species since each had disappeared from the remaining sites. None of the environmental relationships identified differed between 2008 and 2009 (i.e., year was not significant in any model).

2.5 Discussion

Populations of both European seahorse species experienced marked declines (94% for *H. guttulatus* and 73% for *H. hippocampus*) in the absence of direct fishing pressure. Although both species are sometimes caught in Portugal and sold as curiosities (Project Seahorse 2003a, Project Seahorse 2003b), they comprise, at most, a tiny part of the international trade in seahorses for traditional Chinese medicine or ornamental display (Vincent 1996). Most seahorses around the world are caught as trawl bycatch of other fisheries (Vincent *et al.* 2011), but the Ria Formosa lagoon is a semi-protected lagoon where the use of towed demersal fishing gear is prohibited (Erzini *et al.* 2002), so accidental capture should be minimal.

The population declines do not seem to be explained by any one obvious environmental change in the lagoon. *H. hippocampus* densities did decline more at sites where the water current speed decreased over time. As ambush predators, seahorses rely partly on water currents to bring their small prey (Foster and Vincent 2004). The weak relationship between *H. hippocampus* decline and change in water current speed could be due to an associated relationship with prey availability. The lagoon did become deeper but the habitat-use results from 2008/2009 suggest that should promote seahorse presence rather than lead to a decline; in 2008/2009 seahorses were present at deeper sites close to the main channel and near lagoon inlets.

Other environmental variables that were not measured might explain some decline.

Clustering of the remaining populations of seahorses around the main channels and inlets could be explained by a difference in water quality throughout the lagoon (Wayland *et al.* 2008), or an apparent shift in the dominant seagrass species (Curtis and Vincent 2005, Cunha *et al.* 2011). Although the lagoon has a large tidal exchange, the water in the smaller channels does not circulate as much as in the main channels (Newton and Mudge 2003), and increased coastal development in the Ria Formosa has led to higher amounts of ammonium and phosphate at greatest concentrations within the inner channels (Wayland *et al.* 2008).

Poor water quality in the inner channels could explain why seahorses have largely disappeared from those areas while they are still found in the main channels and inlets. A shift in dominant seagrass species from *Cymodocea nodosa* in 2001/2002 (Curtis and Vincent 2005) to *Zostera noltii* in 2007 (Cunha *et al.* 2011) may or may not be important.

Cymodocea nodosa does grow in deeper habitats of the lagoon (Cunha *et al.* 2011), where seahorses remained in 2008/2009, but only one seahorse was actually found in seagrass in the 2008/2009 surveys.

Difficulties encountered in comparing the 2008/2009 habitat use data with earlier research on these species (Curtis and Vincent 2005) reflect the problem that changes in population density over time were not anticipated in the earlier research. In fact, the high densities in 2001/2002 (Curtis and Vincent 2005) made it impossible to compare sites with and without seahorses. Subsequently, very low densities in the 2008/2009 surveys reduced the power to detect any significant relationship between density and environment even at the broadest scale (site). More thinking needs to be done about how to anticipate population changes and their potential ties to habitat use, perhaps by collecting data on scales fine enough for presence–absence modelling and broad enough for abundance modelling.

It may be that the declines in seahorse densities were a manifestation of population fluctuations, perhaps linked to species interactions (e.g., predator–prey dynamics, disease; Shelton and Mangel 2011) rather than environmental causes. Unexploited populations of the Australian seahorse *Hippocampus abdominalis* declined 79 to 98% over 3.5 years without any obvious environmental cause (Martin-Smith and Vincent 2005), but appear subsequently to be increasing (K. Martin-Smith, personal communication). There are only two documented predators of European seahorse species, the common octopus (*Octopus vulgaris*) and the loggerhead sea turtle, but the cuttlefish *Sepia officinalis* eats closely related European pipefish species (Kleiber *et al.* 2010). Octopus and cuttlefish were commonly seen in

2008/2009 surveys (personal observation), but seahorse predators tend to be opportunistic feeders (Kleiber *et al.* 2010). There were no obvious signs of disease or parasites on any of the seahorses found in 2008/2009 (personal observation), but any outbreak may have already passed. If the cause of declines has disappeared then one might expect to see a size structure skewed to young animals as the population rebuilds. The greater number of juveniles, and indeed adults, in 2009 (compared with 2008) may hint at such a possibility but with such a small sample this explanation is hardly compelling, especially as the two years represent different areas of the lagoon.

With so few snapshots it is difficult to distinguish whether decline might be due to changes in survival (i.e., increased deaths), reproduction (i.e., decreased births), movement (i.e., increased emigration and/ or decreased immigration), or some combination of all three. *H. guttulatus* live, on average, 3–5 years (Curtis and Vincent 2006), so it is unlikely that any of the seahorses found in 2001/2002 were still alive in 2008/2009. If there truly was no change in the lagoon, it should have been equally suitable for survival and reproduction from 2001–2009, suggesting they either suffered recruitment failure or moved away from the sampled sites. Adult *H. guttulatus* are capable of longer distance movement when disturbed (Chapter 4), but tend to stay within small, overlapping home ranges (Curtis and Vincent 2006). Their young, however, spend the first eight weeks of their lives in the plankton (Boisseau 1967), and changes outside the lagoon could affect movement of that planktonic stage. Shifts in lagoon inlets over time (Cunha *et al.* 2011) could affect water currents that facilitate movement of planktonic juveniles into and throughout the lagoon. Limited penetration of

planktonic juveniles into the lagoon could explain why seahorses were found mostly around the main channels and inlets in 2008/2009.

Whatever the cause, the two sympatric species appear to have responded differently in the face of population declines. Despite the fact that populations of *H. guttulatus* declined proportionally more than *H. hippocampus*, it was still the more common species. In an experiment testing the effect of fishing effort, the two species responded differently to increases in live habitat cover: *H. guttulatus* abundances increased while *H. hippocampus* decreased (Curtis *et al.* 2007). It was expected that this differential response would lead to increased densities of *H. guttulatus* and decreased densities of *H. hippocampus* at sites where the amount of live cover had increased in 2008/2009 and the opposite responses at sites where live cover had decreased. However, there was no relationship for either species with percentage live cover. Instead, water current was positively related to changes in densities and occurrence of *H. hippocampus* but not *H. guttulatus*, while temperature was positively related to occurrence of *H. guttulatus* but not *H. hippocampus*. The only common response in both species was their occurrence in deeper water in 2008/2009.

Regardless of whether population declines are part of fluctuations or not, populations at low densities become vulnerable to any additional stressors, including demographic or environmental stochasticity (Fagan *et al.* 2001). For many seahorse species, their monogamous mating pattern, their slowness to re-mate when widowed, and their reduced brood sizes with new partners (Foster and Vincent 2004) could all generate Allee effects in

populations. Much still needs to be learned about compensatory responses in seahorses and other fishes that have similar life history characteristics.

The seahorse declines in the Ria Formosa, should they persist for a few more years, would qualify local populations of *H. guttulatus* as Critically Endangered and *H. hippocampus* as Endangered under IUCN population decline criterion A (population declines of >80% and >50% respectively over ten years or three generations, whichever is longer; IUCN 2012).

Such an assessment would not hold for the entire species over their wide ranges (Lourie *et al.* 2004). Indeed, there is evidence that in other locations European seahorse populations are reappearing where they had once disappeared (Pinnegar *et al.* 2008, BBC News 2011). Even if seahorses were to disappear from the Ria Formosa lagoon, nearby populations might well be able to reseed the area. In contrast, the Endangered Knysna seahorse (*Hippocampus capensis*) is only found in a few estuaries (Bell *et al.* 2003), and might not recover from equivalent declines.

2.6 Acknowledgements

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Figure 2.1 Map of the Ria Formosa lagoon, Portugal showing the relative number of *H. guttulatus* (white) and *H. hippocampus* (black) during underwater visual census surveys at 33 locations. The total number of seahorses encountered per site is given. © John Wiley and Sons, Ltd. 2012, by permission.

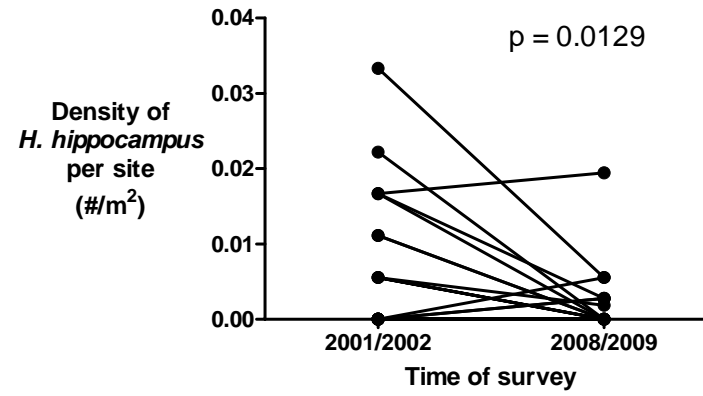
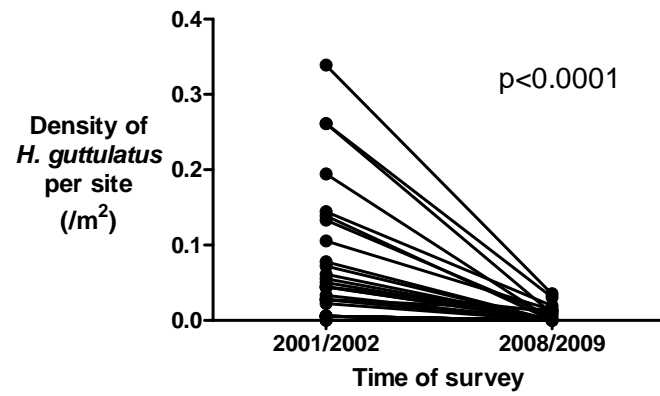


Figure 2.2 Comparison of densities of *H. guttulatus* and *H. hippocampus* during underwater visual census surveys in 2001/2002 (Curtis and Vincent 2005) and 2008/2009 (this study) in the Ria Formosa lagoon.

Table 2.1 Indices of abundance for *H. guttulatus* and *H. hippocampus* in the Ria Formosa lagoon, Portugal. Occupancy refers to the percentage of sites where a species was found and n refers to the number of individuals of the species found during underwater visual census surveys.

	<i>H. guttulatus</i>				<i>H. hippocampus</i>			
	2001/2002 Combined*	2008	2009	2008/2009 Combined	2001/2002 Combined*	2008	2009	2008/2009 Combined
Total n	384	11	47	58	41	8	10	18
juveniles n	48	0	6	6	1	0	5	5
# Sites surveyed	32	17	16	33	32	17	16	33
% Occupancy	90.6	17.6	31.3	24.2	37.5	11.8	37.5	24.2
Maximum density (m ⁻²)	0.51	0.014	0.035	0.035	0.072	0.019	0.008	0.019
Mean density (m ⁻²)	0.073	0.002	0.007	0.004	0.007	0.001	0.002	0.001
Lower 95% CI	0.039			0.001	0.003			0.0001
Upper 95% CI	0.110			0.007	0.014			0.003

*From Curtis and Vincent (2005)

Table 2.2 Results of univariate analyses (p-values) testing the relationship between single environmental variables and occurrence (at two spatial scales: quadrat and site) or density (at site scale) of two seahorse species in the Ria Formosa lagoon, Portugal (ns = not significant). Significant values (p < 0.05) are in bold. Direction of relationship is given for all variables with p < 0.1 at either scale.

Variables	<i>H. guttulatus</i>					<i>H. hippocampus</i>				
	Quadrat		Site		Direction	Quadrat		Site		Direction
	All sites	Sites with	Occurrence	Density		All sites	Sites with	Occurrence	Density	
Depth	0.046	0.190	0.014	0.886	Deeper	0.002	0.072	0.014	0.479	Deeper
Temperature	0.480	0.921	0.067	0.853	Warmer	0.886	0.546	0.916	0.804	ns
% live cover	0.707	0.394	0.881	0.160	ns	0.946	0.954	0.929	0.958	ns
Visibility	0.713	0.620	0.301	0.043	<visibility	0.754	0.456	0.394	0.891	ns
Current speed	0.902	0.176	0.203	0.616	ns	0.907	0.635	0.498	0.685	ns

Table 2.3 Significant variables retained in multivariate models for *H. guttulatus* and *H. hippocampus* occurrence and density with test statistics and significance values for regression results (β and p_β) and chi square (quadrat) or F tests (site) comparing models with and without variable (Chi square/F and p_f).

Species	Scale	N	Variables	β	p_β	Chi square/ F	p_f
<i>H. guttulatus</i>	Quadrat (all sites)	362	Depth	2.00	0.046	4.62	0.031
	Quadrat (sites with)	131	None				
	Site (occurrence)	33	Temperature	2.14	0.033	5.83	0.016
			Depth	2.19	0.029	9.29	0.002
Site (density)	8	None					
<i>H. hippocampus</i>	Quadrat (all sites)	362	Depth	3.11	0.002	14.3	<0.001
	Quadrat (sites with)	124	Depth	2.33	0.020	6.38*	0.041
			Current	2.11	0.035	48.5*	<0.001
			Depth*Current	-2.14	0.033	4.94	0.026
	Site (occurrence)	33	Depth	2.44	0.014	12.6	<0.001
Site (density)	8	None					

*without interaction and other main effect

Chapter 3. Advances in tagging syngnathids, with the effects of dummy tags on behaviour of *H. guttulatus*

3.1 Summary

Artificial marking and tagging techniques have been used to study movement, population dynamics, behaviour, ecology, survival and growth of at least 25 syngnathid species.

External necklace-style tags and injection of visible implant elastomer have been the most used techniques, uniquely identifying hundreds of individual syngnathids to study population dynamics, mortality, behaviour, ecology and growth in at least 13 and 12 species, respectively. Only two studies, both on larger syngnathid species, have tested the use of internal or electronic tags. This new case study reveals that dummy tags, weighing up to 6% of individual body mass, have minimal effect on normal *ex-situ* behaviour of the long-snouted seahorse *H. guttulatus*, a smaller syngnathid. In paired aquarium trials, tags did not affect movement, holdfast use or general behavioural state, and only had a short-term effect (1 day) on vertical orientation. Tagged *H. guttulatus* gained more mass during the 5 day trials, a result which warrants further exploration but indicates that tags did not reduce feeding. This study shows promise for using electronic tagging to study *H. guttulatus* and similarly sized syngnathids in the wild.

3.2 Introduction

Studying individual fish provides insight into the biology and management of fish species, insight that would not be gained otherwise. An improved understanding of population structure, movement, mortality or abundance requires re-sampling individual fish, and repeated measures of the same individual can provide growth estimates used in fisheries and

population models (Parker *et al.* 1990, Nielsen 1992, Pine *et al.* 2003). Incorporating individual behaviour into population or stock models has helped explain past fisheries collapses and can guide future management and conservation solutions (Jennings 2001, Rowe and Hutchings 2003, Palumbi 2004, Fromentin and Powers 2005, Botsford *et al.* 2009).

Studying an individual fish in the wild relies on differentiating that fish from others. When natural markings are unreliable, artificial marking and tagging techniques can be used to identify individuals (Parker *et al.* 1990, Nielsen 1992, Nielsen *et al.* 2009). These techniques can be separated into four broad categories: external tags, external (artificial) marks, internal tags and biotelemetric (or electronic) tags (Nielsen 1992). The most useful techniques should be durable without maintenance (for long-term monitoring and estimation of life-history variables) and should allow for many different combinations (for large sample sizes and population-level estimation), but should also have minimal effects on welfare and behaviour (so that results are representative of unmarked or untagged fishes) (Nielsen 1992, Jepsen *et al.* 2002, Bridger and Booth 2003, Cooke 2003, Murchie *et al.* 2004).

Syngnathids are of such biological, evolutionary, ecological, economical and conservation interest that appropriate marking or tagging methods are important. Species within the family Syngnathidae share unusual biological characteristics such as male pregnancy, suction feeding and a distinctive morphology and swimming mode (Kuitert 2000). While these unusual characteristics have been well documented, more basic knowledge is needed for improved biological and ecological understanding and to assess the conservation status of

most syngnathid species: only 82 of the 337 syngnathids in the Catalogue of Fishes have been assessed in the IUCN Red List and of those 44 are listed as data deficient (Eschmeyer and Fong 2010, IUCN 2012). The limited data on syngnathids is troubling as many syngnathids are exploited by humans for use in traditional medicines, as curios and as ornamental aquarium fishes (Foster and Vincent 2004). Of the syngnathids for which there is sufficient information, all but three are listed in categories that indicate conservation concern (Critically Endangered, Endangered, Vulnerable or Near Threatened). As in other fishes, marking and tagging studies could help to assess the conservation status of Data Deficient syngnathids and guide conservation and management for syngnathids at risk.

The dual aims of this chapter were to: (1) review past use of marking and tagging techniques for studying syngnathids and (2) advance knowledge of the effects of tag size on small syngnathids with empirical work. The latter objective was achieved using *H. guttulatus* and dummy tags of the same size and mass as the smallest available acoustic tags to test whether similarly sized electronic tags can be used to study small syngnathids without affecting their welfare and behaviour.

3.3 Syngnathid marking and tagging

Identifying individuals using natural markings is ideal as it does not require interference with the animal. There has been enough variation in body morphology to allow for identification and study of individuals of at least five syngnathid species without the need for artificial tagging or marking (Table 3.1). While three of these species were studied using either small sample sizes (nine to 20 individuals) or short time periods (<1 year), the diverse facial

markings of worm pipefish *Nerophis lumbriciformis* (Jenyns 1835) and abdominal markings of weedy seadragons *Phyllopteryx taeniolatus* (Lacépède 1804) allowed for reliable identification of 133 and 43 individuals over 18 and 19 month periods, respectively (Monteiro *et al.* 2005, Martin-Smith 2011). While other morphological characters such as appendages have been used to confirm identifications (Martin-Smith 2011), they are less reliable than facial or abdominal patterns and can change over time making them unsuitable for long-term studies or even for identifying among species (Connolly *et al.* 2002a, Curtis 2006a). Unfortunately, many syngnathid individuals are too similar for reliable identification using natural markings. Estimating population-level characteristics or life-history variables in these species will require artificial marking and tagging techniques.

Artificial marking and tagging (both external and internal) have contributed to understanding the biology of at least 25 syngnathid species (Table 3.1), but the syngnathids' small body size [pipefishes average maximum standard length (L_S) = 246 mm, seahorses average maximum L_S = 143 mm: Wilson 2009] and distinctive morphology pose challenges (Vincent and Sadler 1995, Le Cheminant 2000, Woods 2005a). There has been a general, albeit disputed, guideline that tags should be less than 2% of body mass to minimize negative effects on welfare and behaviour of fin fishes (Jepsen *et al.* 2005). Maximum masses of syngnathid species marked or tagged in the past range from 0.05 to 57.00 g (Table 3.1; Masonjones *et al.* 2010). Under the 2% guideline, tags weighing <0.001 to 1.100 g would be needed for those species. The rigid body and reduced fins of syngnathids make it difficult to inject or attach tags that are normally either placed in the body cavity or on the dorsal fins of larger fishes (Nielsen 1992). The upright swimming posture of seahorses can make tagging particularly

difficult as placement on the dorsal fin could alter balance and make swimming difficult (Moreau and Vincent 2004).

External tagging methods (i.e., attaching externally visible foreign material for means of identification) have been used to study reproductive ecology, behaviour, movement, activity patterns, growth and social structure in at least 15 syngnathid species (Table 3.1). For many fish species, external tags need to be secured through a fin or other part of the body (Nielsen 1992). The presence of bony scutes in syngnathids, and the horse-like shape of *Hippocampus* species in particular, has meant that tags could instead be tied around the neck or tail without slipping off the body, a less invasive method of attachment. Coloured and patterned thread has been tied around the bodies of syngnathids to identify groups (i.e., those which have been measured or from a given location) (Felicio *et al.* 2006, Rosa *et al.* 2007). The addition of small, individually numbered discs to such necklaces has made it possible to follow hundreds of syngnathids in the wild. Lipton and Thangaraj (2007) used numbered necklace-style tags to identify and study the growth of 452 spotted seahorses *Hippocampus kuda* Bleeker 1852 with minimal effect on short-term behaviour. Although tied necklaces have minimal short-term effect on behaviour, they must eventually be loosened, replaced or removed to prevent injury as the fish grow (Vincent and Sadler 1995, Perante *et al.* 2002, Bell *et al.* 2003). This technique is therefore suitable only for closely monitored populations and is less suitable for the measurement of life-history variables such as mortality that require long-term data.

Vincent *et al.* (1994) used shrinking plastic to secure ends of the necklace, which may allow the loop to expand and eventually fall off if broad-nosed pipefish *Syngnathus typhle* L. 1758 were not recaptured. External tags could be attached to bony appendages (Connolly *et al.*

2002b), but such appendages are not found in all syngnathid species or even on all individuals within a species (Curtis 2006a). Alternative methods for attaching external tags to syngnathids, such as gluing tags to the body, have proven unsuccessful (Le Cheminant 2000).

Externally visible marks, created by injecting visible implant fluorescent elastomer (VIFE) beneath the skin, have been used to identify hundreds of syngnathids uniquely (up to 637 *H. guttulatus* in one study), have minimal effect on behaviour or mortality and remain visible for years (Woods and Martin-Smith 2004, Curtis 2006b, Curtis and Vincent 2006). VIFE has been used to study reproductive behaviour, population dynamics, growth, habitat use, movement, home range, and survival of at least 12 syngnathid species (Table 3.1). VIFE had minimal effect on behaviour, growth and mortality in all syngnathids studied and marks remained visible for up to 2.5 years in the wild (Le Cheminant 2000, Matsumoto and Yanagisawa 2001, Woods and Martin-Smith 2004, Sogabe *et al.* 2007). Batch marking and assessment of population abundance have been achieved with single colours of elastomer while multiple colours and injection sites have allowed the unique marking of hundreds of individuals. Other external marking techniques such as uprooting dorsal spines and injecting acrylic paint caused severe skin irritation and should not be used (Matsumoto and Yanagisawa 2001). A disadvantage of both external marking and external tagging is that they require recapture or re-observation of marked fishes. With such techniques, many individuals must be marked to obtain sufficiently high recapture rates.

Internal VI-alpha tags are numbered to allow for even more fish to be uniquely identified than VIFE but they have only been tested on one syngnathid species. As with VIFE, these

small numbered tags are injected just beneath the skin so their numbers can still be seen through the skin. VI-alpha tags did not affect the growth or mortality of the big-bellied seahorse *Hippocampus abdominalis* Lesson 1827 (Woods 2005a). VI-alpha tags, however, need to be larger (1 mm × 2.5 mm) than VIFE marks for the numbers to remain visible. Although they did not affect the welfare of *H. abdominalis*, they may be less suitable for smaller syngnathid species (Table 3.1; Woods 2005a). As with VIFE, reading VI-alpha tags requires repeated capture or observation.

Electronic tags can be used to remotely track individual fish and collect environmental data but have hitherto seldom been used with syngnathids, partly because of these tags' larger size. The newest of these tags can store and remotely transmit information about water temperature, depth, time and location of multiple fishes without a need to recapture or observe the fishes after tagging (Nielsen 1992, Nielsen *et al.* 2009). Ultrasonic (acoustic) tags have been used successfully to study the movement and habitat use of the leafy seadragon *Phycodurus eques* Günther 1865 (Connolly *et al.* 2002b), and passive integrated transponder (PIT) tags had only minimal effects on the growth of *H. abdominalis* (Woods 2005a). These are two of the larger syngnathid species (Table 3.1), however, making larger tags less of a burden. Their suitability for smaller syngnathids has not been tested but the emergence of smaller electronic tags may make this technique more generally applicable (Nielsen *et al.* 2009). Acoustic tags can be attached to smaller syngnathids using necklaces or around the appendages of *P. eques* and should be attached so that they will fall off after their battery life has expired (Connolly *et al.* 2002b). The battery life of acoustic tags has traditionally limited their usefulness to short-term studies, although battery life can be extended by programming

tags to shut down and start up periodically. This emerging technology provides an opportunity to learn more about the movement and environment of these fish on much finer time scales than was previously possible. However, before these tags enter broad usage more must be known about their effects on fish welfare and behaviour.

3.4 Methods

3.4.1 Species description

H. guttulatus is a small-bodied fish living in shallow, macrophyte-dominated environments of the north-eastern Atlantic Ocean, Mediterranean Sea and Black Sea (Lourie *et al.* 2004). In a wild population in southern Portugal, this species ranged in size from 65 to 215 mm L_S and 0.57 to 22.5 g wet mass (M_w) (Curtis and Vincent 2006). After settling, *H. guttulatus* maintain relatively small home ranges of 1.4 to 400 m² (Curtis and Vincent 2006, Garrick-Maidment *et al.* 2010). Further information is needed to assess the global conservation status of *H. guttulatus* but it is protected regionally in the U.K. under the 1981 Wildlife and Countryside Acts and in Slovenia under the 1993 Protection of Threatened Animals Act and is listed in the Red Books of France and Portugal (Project Seahorse 2003a). The fish used in this study were originally collected from Portugal's Ria Formosa lagoon with permission from national authorities at the Parque Natural da Ria Formosa.

3.4.2 Aquarium trials

Individual fish were marked with dummy tags modelled after the smallest commercially available transmitters at the time of the experiments (October to December 2008), those produced by Lotek Wireless Inc. (www.lotek.com) and VEMCO (www.vemco.com). Lotek

produces a cylindrical acoustic transmitter measuring 6.2 mm in diameter and 13 mm in length, weighing 0.9 g in air and 0.6 g in water (model MAP6_1). Dummy tags (i.e., tags without the electronics of acoustic tags meant only for testing) were built with the same dimensions and mass as Lotek's MAP6_1 transmitter.

Aquarium trials were used to assess how dummy tags affect individual *H. guttulatus* behaviour and mass. Recorded behaviours included movement, orientation, holdfast use and behavioural state. Holdfast use was recorded because *H. guttulatus* curl their prehensile tails around marine plants and animals to remain sedentary and upright (Curtis and Vincent 2005); differences in how often a holdfast is used might suggest distress. Differences in the general behavioural state may also indicate stress induced by tagging. Finally, food intake has been used to assess welfare in a variety of fish species (Huntingford *et al.* 2006, Faleiro *et al.* 2008), and mass change was used as a proxy for food intake.

Trials were conducted in four 80 l cubic tanks housed at the Ramalhete field station of the University of Algarve in Faro, Portugal. Filtered sea water was fed into the tanks using a flow-through system. Temperature of the tanks was maintained at 18°C, range $\pm 0.1^\circ\text{C}$. An air hose and stone provided moderate aeration. Tanks were illuminated from above using two 36 W fluorescent tubes at a photoperiod of 12L: 12D (0800–2000 hours) controlled by a timer. Before and during experiments food (frozen shrimp, mysids and adult *Artemia* sp.) was provided daily ad libitum. A plastic mesh grid was placed on the bottom of the tank to allow for measurement of movement. The mesh was separated into a 5 × 5 cell grid, each cell measuring 100 mm × 100 mm. Two different materials were attached vertically to the grid to

mimic the variety of holdfasts available in the wild: (1) a 150 mm length of wire coated with plastic to simulate rigid holdfasts (e.g., tube worms and sea squirts) and (2) a 150 mm length of balloon ribbon to simulate less rigid holdfasts (e.g., seagrass and algae). Holdfasts were attached in the centre of each grid cell, with each type alternating between cells.

Paired aquarium trials were conducted with one tagged and one untagged *H. guttulatus* per tank. Fish were originally collected from the Ria Formosa lagoon in 2007 for use in a feeding study (Palma *et al.* 2008). Except for the 12 weeks of those feeding experiments, the individuals used in the tagging trials had been housed in two 500 l circular tanks for 2 years. Thirty-two *H. guttulatus* (16 males and 16 females) were measured, weighed and sexed, then each was marked with a unique colour combination using VIFE. The fish were paired with matching size and sex, resulting in eight female and eight male pairs. One of the individuals in a pair was randomly assigned to have the tag and each pair was randomly assigned to one of the four tanks and one of the four trials. Individual VIFE marks were used to ensure fish were used in the tank and trial to which they were assigned and each fish was used for only one trial. The dummy tags were tied around each fish's neck using cotton thread. Each untagged fish was handled similarly, but without actually attaching a necklace or tag. After each 5 day trial, tags were removed and fish were re-weighed before releasing them back into a 500 l tank with the remaining fish.

Each pair of *H. guttulatus* was observed for 30 min each day over the 5 day trial period. The following were recorded once per minute during the focal period for each fish: grid location within the tank, orientation (vertical or not), holdfast and behavioural state. If a fish changed

locations from 1 min to the next, the straight-line distance between grid locations was calculated for movement. As a holdfast, fish could choose one of the types provided (wire or balloon ribbon), other materials in the tank (e.g., air hose, mesh base and water outflow), the other fish or none. Behavioural states were categorized sensu Faleiro *et al.* (2008) as stationary (St), head movement (Mh), slow body movement (Ms), fast body movement (Mf) and swimming (Sw), with the addition of tail movement (Mt) and clicking (Cl). Only the initial behavioural state was recorded each minute (i.e., behaviours were treated as mutually exclusive). Tail movement was assigned when the fish was curling or uncurling its tail while keeping the rest of its body stationary. Clicking was assigned when the fish moved its jaw, creating a sound, but otherwise remained stationary. Clicking has been associated with feeding as well as negative responses to environmental stimuli and aggressive interactions (Fish 1953, Colson *et al.* 1998).

The effects of tagging were analysed using paired comparisons (paired *H. guttulatus*), while the effect of time (i.e., day since first tagged) was analysed using repeated measures of individual fish and comparisons between sexes were unpaired. Before each comparison, the data were first tested for normality and constant variance. Parametric comparisons were used unless the assumptions of normality and constant variance were violated. Initial M_w of *H. guttulatus* was compared between treatment groups (i.e., tagged and untagged) to determine whether pairs were matched appropriately and between sexes. The effect of tagging on M_w before and after trials was compared using a two-way repeated measures ANOVA with treatment (tagged and untagged) and time (before and after) as the two factors. Bonferroni post-tests were used to identify whether there were differences in mass within each treatment

group. A one-sample t-test, comparing M_w change (final – initial mass) against a mean of zero, was used to test whether there was significant mass gain or loss in either treatment group. Mass change was further compared between tagged and untagged fish (paired comparisons) and between sexes (unpaired comparisons). To identify any tagging effects on behaviour (i.e., distance moved, frequency of vertical orientation, frequency of using a holdfast and frequency of observing each behavioural state), each day was treated as a replicate (i.e., the sum of the behaviours over the 30 min of observation per day). Before analyzing the effects of tagging, each behaviour was first compared between days using repeated measures to determine whether there were changes in *H. guttulatus* behaviour over the trial period. If there were no differences between days, the total for each fish over the trial period was calculated and this total was used in the paired analysis of tagging effects. If there were differences between days, paired analysis of tagging was done for each day. In addition to comparing the distance moved between the two sexes (unpaired comparisons), the relationship between movement and *H. guttulatus* size (M_w) was analysed using regression.

3.5 Results

3.5.1 Mass

Tagged *H. guttulatus* gained significantly more mass than untagged *H. guttulatus* over the 5 day trial period (Fig. 3.1). Initial masses were between 15.6 and 35.4 g (median 20.9 g) with males significantly heavier than females (Mann–Whitney U-test, $n = 16$, $P < 0.001$) but no significant mass difference was detected between treatment groups (Wilcoxon matched pairs test, $n = 16$, $P > 0.05$). There was a significant difference in initial and final mass for tagged *H. guttulatus* (two-way repeated measures ANOVA with Bonferroni post-tests, $P < 0.001$) but

not for untagged fish ($P > 0.05$). There was a significant difference between the change in mass of tagged and untagged *H. guttulatus* (paired t-test, $n = 16$, $P < 0.001$) with tagged *H. guttulatus* gaining significant mass overall (one-sample t-test, $n = 16$, $P < 0.001$) while untagged *H. guttulatus* neither gained nor lost mass throughout the trial period (one-sample t-test, $n = 16$, $P > 0.05$). There was no significant difference detected in the change in mass between sexes (unpaired t-test, $n = 16$, $P > 0.05$).

3.5.2 Movement

Hippocampus guttulatus moved distances of between 0 and 238 cm (median 13.4 cm) during the 150 min of total observation. Distance moved by individual fish did not differ significantly from one day to another (paired Friedman test, $n = 32$, $P > 0.05$) so daily movement data were combined. Total distance moved did not differ significantly between tagged and untagged seahorses (Wilcoxon matched pairs test, $n = 16$, $P > 0.05$), but male *H. guttulatus* moved significantly greater distances than females (median distance moved: males = 33.1 cm v. females = 8.74 cm; Mann–Whitney U-test, $n = 16$, $P < 0.05$) (Fig. 3.2). There was no correlation between the distance moved and M_w of each *H. guttulatus* (Spearman rank correlation, $n = 32$, $P > 0.05$).

3.5.3 Orientation

Hippocampus guttulatus were oriented vertically the majority of the time (84% of observations). There was a significant difference in frequency of vertical orientation between days (Friedman test, $n = 32$, $P < 0.01$), so each day was analysed separately. On the first day, untagged fish were oriented vertically more often than tagged fish (median frequency of

vertical orientation day 1: untagged fish = 30 v. tagged fish = 21; Wilcoxon signed rank test, $n = 16$, $P < 0.01$), even after applying a Bonferroni correction to adjust P-values for multiple tests ($P = 0.05/5 = 0.01$). On days 2 to 5, however, there was no significant difference between tagged and untagged fish after Bonferroni correction (Wilcoxon signed rank tests, $n = 16$, $P > 0.01$).

3.5.4 Holdfast use

Hippocampus guttulatus used holdfasts the majority of the time (94% of observations) and used the rigid wire holdfasts more than the balloon ribbon (31 vs. 0.02% of observations). Other holdfasts used included the filter, the grid, the air stone, the heater, the air hose and their paired fish (36, 14, 9, 3, 0.4 and 0.1% of observations, respectively). The frequency with which fish used holdfasts in general (as opposed to using none) did not differ from day to day (Friedman test, $n = 32$, $P > 0.05$) so observations were combined for each fish. When summed observations were compared, there was no significant difference between how frequently tagged and untagged *H. guttulatus* used a holdfast (Wilcoxon matched pairs test, $n = 16$, $P > 0.05$).

3.5.5 Behavioural states

All *H. guttulatus* remained stationary most of the time (93% of all observations) and tagging had no effect on behavioural state (Fig. 3.3). Behavioural states of individual seahorses did not differ from one day to the next (Friedman tests, $n = 32$, $P > 0.05$ in all cases), so observations were combined. None of the seven behavioural states differed significantly

between tagged and untagged fish (Fig. 3.3; Wilcoxon matched pairs tests, $n = 16$, $P > 0.05$ in all cases).

3.6 Discussion

3.6.1 Syngnathid marking and tagging

External tagging with necklaces and external marking with VIFE have been the most utilized marking or tagging techniques in studies of syngnathid biology. Any long-term use of necklaces would require attachment using shrinking plastic (Vincent *et al.* 1994), and regular monitoring to ensure necklaces do not cause injury as fishes grow, whereas VIFE injected beneath the skin remains visible for years in the wild without the need for maintenance. Both techniques could be used to verify growth rates and estimate life-history variables (Matsumoto and Yanagisawa 2001, Curtis 2006b). Using many colours and injection sites with VIFE or individually numbered plastic discs on necklaces, hundreds of individual syngnathids can be differentiated to measure population-level characteristics such as total mortality, immigration, emigration and abundance. Marked animals, however, must be reliably recaptured for these techniques to be useful. This may be less difficult for the many syngnathids that are sedentary as their small home ranges may make it easier to find marked individuals (Kuitert 2000, Foster and Vincent 2004). A major limitation of external marking and tagging is that one cannot monitor individual movement continuously and archive the environmental conditions experienced by fishes (Nielsen *et al.* 2009). This problem can be overcome using electronic tags.

3.6.2 Aquarium experiments

The aquarium experiments presented here suggest that acoustic tagging technology has become small enough to be a viable technique for monitoring *H. guttulatus* and similarly sized syngnathids. Although dummy tags were used in the experiment, they were the size and mass of acoustic tags and this size seems to have had minimal effect on behaviour when attached as necklaces. Tags did not seem to affect movement, holdfast use or general behavioural state. An initial difference in vertical orientation was a short-lived response and, by itself, small differences in orientation may not matter given that wild *H. guttulatus* have been observed oriented both vertically and horizontally (personal observation).

The finding that tagged *H. guttulatus* gained more mass than untagged clearly needs more probing. Did they somehow eat more or expend less energy? In a search of other tagging studies, no others could be found that resulted in mass gain. There is no evidence that tagged *H. guttulatus* moved shorter distances (Fig. 3.2) or were less active (Fig. 3.3). On the other hand, tagged fish are the only ones that clicked (Fig. 3.3), and clicking has been associated with feeding in other seahorse species (Colson *et al.* 1998). Although further trials would be needed to determine the true cause, this limited evidence does hint that the mass difference might have been due to food intake rather than energy expenditure. In any case, mass was measured in this study to determine whether tagging reduced feeding and that at least did not seem to happen.

For short-term studies, these syngnathids seem to be able to cope with tags exceeding the 2% guideline normally used for fishes. The tags in the present study, as heavy as 5.77% of body

mass, had minimal effect on fish movement or behaviour over a 5 day period. The sedentary nature of *H. guttulatus* and many other syngnathids may allow them to carry larger tags than more active fishes without affecting their behaviour. *Hippocampus guttulatus* in the present study rarely moved, using rigid holdfasts to remain stationary. This sedentary behaviour, in combination with their unusual body morphology, allows seahorses and many other syngnathids to ambush prey and escape predation using camouflage (Foster and Vincent 2004). If such syngnathids can remain hidden and feed with a large tag attached, they may be better suited to carry heavy tags than fishes that need to swim to find prey or escape predation. The utility of the 2% guideline, however, has also been questioned for fishes that need to swim greater distances, with tags weighing up to 10% of body mass found to have no significant effect on swimming speeds of juvenile Chinook salmon *Oncorhynchus tshawytscha* (Jepsen *et al.* 2005, Brown *et al.* 2006). Indeed, the threshold in tag mass to body mass for syngnathids may not have been reached in this aquarium study, given that the *H. guttulatus* used were larger than average in the wild (Curtis and Vincent 2006). While the present study suggests these large tags are suitable for short-term studies, the tags may or may not be suitable for longer periods.

Caution should be taken before assuming that acoustic tags will have no effect on these fish in the wild. Despite the positive results from the present *ex-situ* experiment, *in-situ* experiments should follow. *In-situ* experiments should use a larger sample size to increase the power to detect any small effects of tagging that may not have been detected in the present study and could prove to be important in long-term studies in the wild. Many of the natural threats to the welfare of wild fish were not present in aquaria and results may only

apply to a specific size range of *H. guttulatus*. In the wild, fish are exposed to threats from predators, variable food resources, parasites, disease and variable environmental conditions, none of which was present in aquaria (Huntingford *et al.* 2006). Tags might interfere with a wild syngnathid's camouflage making them more vulnerable to predation or making it harder to ambush prey. The additional stress of carrying a tag might also impair the ability to fight parasites or disease. The movement constraints in the aquaria may have produced results that do not predict the effects of tagging on long-range movement *in-situ*. Before any large-scale deployment of transmitters on *H. guttulatus* or similarly sized syngnathids, experiments should be conducted to test whether tagging effects are influenced by the natural threats to which wild fish are exposed.

If acoustic tagging technology can be used to study wild syngnathids, it would help establish conservation status of data-deficient species and protect threatened species. Sedentary syngnathids may be less capable of escaping negative environmental change than more mobile species. Acoustic tags, however, could be used to follow these more sedentary fishes when exposed to change to determine their true capability for long-distance movement. Following syngnathids with acoustic tags after displacement could help identify habitats associated with settlement and those of greatest importance. Information on habitat use, movement and occurrence can be integrated into IUCN assessments of data-deficient species such as *H. guttulatus* and used to appropriately site and manage marine reserves.

Advancements in marking and tagging techniques for syngnathids have provided life history and population information that is necessary for conservation assessment and action. There

are now a variety of marking and tagging techniques, which can be used to track small fishes such as syngnathids and provide information on movement, population dynamics and behaviour. The most advanced of these is the use of electronic tags, which allow fishes to be tracked remotely and continuously with stationary receivers, allowing for precise measurement of their movement and environmental conditions. This method has been limited to large fishes in the past due to large tag sizes but here is shown to be increasingly suitable for smaller fishes. Other marking and tagging methods, such as VIFE and external tagging, cannot be used for such precise measurements but have proven equally useful in studies where fine temporal scales are not needed (e.g., estimating population abundance, verifying growth estimates or understanding population structure).

3.7 Acknowledgements

I am grateful to P. Andrade and the staff of the Ramalhete field station for their help with the aquarium facilities. L. van Walraven helped with behavioural observations. S. Foster provided invaluable comments during analysis and writing that greatly improved the chapter. The chapter was further strengthened by comments from two anonymous reviewers.

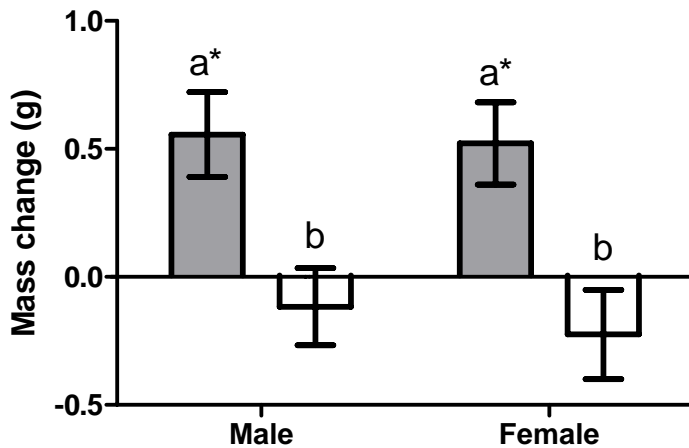


Figure 3.1 Mean \pm S.E. mass change for male and female *H. guttulatus* tagged with dummy tags (light grey bars; n = 8 in each case) compared to those that were not tagged (white bars; n = 8 in each case) over a 5 day trial period. Bars labelled with the same lower case letter are not significantly different ($P > 0.05$). *, mass change is significantly different from zero ($P < 0.05$).

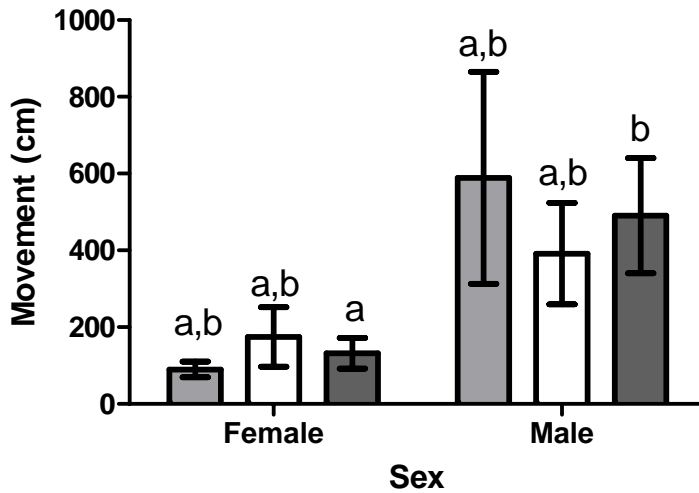


Figure 3.2 Mean \pm S.E. distance moved over 5 days by female and male *H. guttulatus* tagged with dummy tags (light grey bars; n = 8 in each case), untagged (white bars; n = 8 in each case) and both combined (dark grey bars; n = 16 in each case) when observed for 30 min each day. Bars labelled with the same lower case letter are not significantly different ($P > 0.05$).

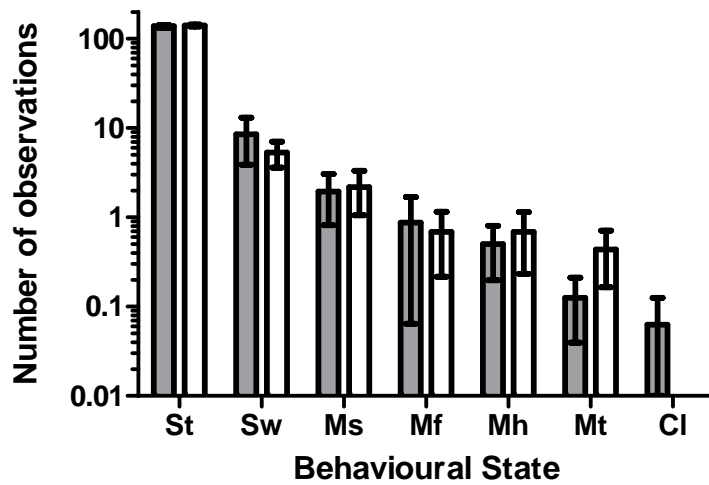


Figure 3.3 Mean \pm S.E. number of times, on a logarithmic scale, tagged (grey bars; $n = 16$ in each case) and untagged (white bars; $n = 16$ in each case) *H. guttulatus* were observed in each of seven behavioural states (St, stationary; Sw, swimming; Ms, slow body movement; Mf, fast body movement; Mh, head movement; Mt, tail movement; Cl, clicking) during 30 min focal periods per day for 5 days.

Table 3.1 Published syngnathid studies using tagging and marking techniques, with maximum standard length (L_s) and wet weight (W_w) for each species. NM = natural markings, ET = external tags, EM = external marks, IT = internal tags, BT = biotelemetric/electronic tags.

Syngnathid species	Technique used	Maximum Size		Focus of study	References
		L_s (cm)**	W_w (g)		
<i>Anarchopterus criniger</i>	EM	10.0	-----	Population dynamics	Masonjones <i>et al.</i> 2010
<i>Corythoichthys haematopterus</i>	EM	19.8	-----	Behaviour	Matsumoto and Yanagisawa 2001, Sogabe and Yanagisawa 2007a, b, 2008, Sogabe <i>et al.</i> 2007
<i>Entelurus aequoreus</i>	ET	60.0	47.5 [†]	Reproductive ecology	Vincent <i>et al.</i> 1995, Bauchot and Bauchot 1978 [†]
<i>Hippocampus abdominalis</i>	ET, EM*, IT*	35.0	44.4 [‡]	Growth, ecology, population dynamics, effect of tags	Woods and Martin-Smith 2004*, Martin-Smith and Vincent 2005, Woods 2005a*, b**
<i>Hippocampus breviceps</i>	ET	15.0	2.08 [‡]	Behaviour, ecology	Moreau and Vincent 2004 [‡]
<i>Hippocampus capensis</i>	ET	12.1	2.58 [‡]	Ecology, population dynamics, effect of tags	Le Cheminant 2000**, Bell <i>et al.</i> 2003
<i>Hippocampus comes</i>	ET	18.7	10.7 [‡]	Behaviour, ecology	Meeuwig and LaFrance 2001 [‡] , Perante <i>et al.</i> 2002
<i>Hippocampus erectus</i>	EM	19.0	14.9 [‡]	Population distribution	Masonjones <i>et al.</i> 2010, Zhang <i>et al.</i> 2010 ^{‡*}
<i>Hippocampus guttulatus</i>	ET, EM	21.5	22.5 [‡]	Growth, mortality, behaviour	Curtis and Vincent 2006 [‡] , Palma <i>et al.</i> 2008*, Garrick-Maidment <i>et al.</i> 2010
<i>Hippocampus kuda</i>	ET	30.0	14.9 [‡]	Growth	Lipton and Thangaraj 2007, Lin <i>et al.</i> 2009 [‡]
<i>Hippocampus reidi</i>	NM, ET	17.5	14.9 [†]	Behaviour, population distribution, ecology	Felício <i>et al.</i> 2006, Rosa <i>et al.</i> 2007, Castro <i>et al.</i> 2008, Freret-Meurer and Andreatta 2008, Hora and Joyeux 2009 ^{†*}

Syngnathid species	Technique used	Maximum Size		Focus of study	References
		L _s (cm)**	W _w (g)		
<i>Hippocampus subelongatus</i>	ET	20.0	-----	Behaviour	Kvarnemo <i>et al.</i> 2000, 2007
<i>Hippocampus whitei</i>	ET, EM	13.0	9.70 [‡]	Behaviour, reproduction, habitat use	Vincent and Sadler 1995, Vincent and Giles 2003 [‡] , Vincent <i>et al.</i> 2004, 2005, Harasti <i>et al.</i> 2010
<i>Hippocampus zosterae</i>	EM	5.00	0.234 [‡]	Population dynamics	Masonjones 2001 [‡] , Masonjones <i>et al.</i> 2010
<i>Nerophis lumbriciformis</i>	NM	17.0	1.95 [†]	Behaviour	Lyons and Dunne 2003 [†] , Monteiro <i>et al.</i> 2005
<i>Nerophis ophidion</i>	ET	30.0	5.93 [†]	Ecology	Vincent <i>et al.</i> 1995, Gurkan and Taşkavak 2007 [†]
<i>Phycodurus eques</i>	NM, BT	35.0	-----	Behaviour, ecology, population abundance	Connolly <i>et al.</i> 2002a, b
<i>Phyllopteryx taeniolatus</i>	NM, EM	46.0	18.2 [‡]	Behaviour, growth, reproduction, population dynamics, ecology	Kvarnemo and Simmons 2004 [‡] , Sanchez-Camara and Booth 2004, Sanchez-Camara <i>et al.</i> 2005, 2006, Martin-Smith 2011
<i>Syngnathus abaster</i>	NM	21.0	4.97 [†]	Behaviour	Verdiell-Cubedo <i>et al.</i> 2006 [†] , Silva <i>et al.</i> 2010 [*]
<i>Syngnathus acus</i>	ET	50.0	57.0 [†]	Reproductive ecology	Vincent <i>et al.</i> 1995, Valle <i>et al.</i> 2003 [†]
<i>Syngnathus floridae</i>	EM	25.0	3.96 ^{‡*}	Population dynamics	Ripley and Foran 2008 ^{‡*} , Masonjones <i>et al.</i> 2010
<i>Syngnathus fuscus</i>	ET	33.0	4.81 ^{‡*}	Behaviour, ecology	Roelke and Sogard 1993, Ripley and Foran 2008 ^{‡*}

Syngnathid species	Technique used	Maximum Size		Focus of study	References
		L_s (cm)**	W_w (g)		
<i>Syngnathus louisianae</i>	EM	38.0	-----	Population dynamics	Masonjones <i>et al.</i> 2010
<i>Syngnathus rostellatus</i>	ET	18.7 [‡]	2.83 [‡]	Reproductive ecology	Vincent <i>et al.</i> 1995, Gokoglu <i>et al.</i> 2004 [‡]
<i>Syngnathus scovelli</i>	EM	18.3	-----	Population dynamics	Masonjones <i>et al.</i> 2010
<i>Syngnathus springeri</i>	EM	38.0	-----	Population dynamics	Masonjones <i>et al.</i> 2010
<i>Syngnathus typhle</i>	ET	35.0	19.0 [†]	Behaviour	Vincent <i>et al.</i> 1994, 1995, Valle <i>et al.</i> 2003 [†]

* *ex-situ* study

** from Froese and Pauly (2012) unless otherwise indicated

[†] weight calculated from maximum L_s using reported length-weight relationship

[‡] maximum size reported in reference

Chapter 4. A sedentary fish on the move: Effects of displacement on *H. guttulatus* movement and habitat use.

4.1 Summary

To understand how a sedentary fish responds to displacement and identify key habitat characteristics for that fish, I translocated *H. guttulatus* within their natural habitat both near (within 20 m) and far beyond (>750 m) their home range. After displacement, I located these small fish using either VIFE (near displacements) or acoustic technology (far displacements) then collected environmental data where I captured, released, and relocated them. Fish displaced far beyond home ranges (n=9) moved much greater distances (max: 150 m; mean daily: 6.4–48.2 m) than expected from known home range movements. There was evidence of homing in seahorses displaced within 20 m of home ranges, but not in seahorses displaced further away. Seahorses varied in the specific environments they moved towards but tended to move towards environments more similar in both depth and water current speed to their original capture locations than their release locations.

4.2 Introduction

As with most animals, marine fish move to access necessary resources for survival, growth, and reproduction. Moving fish should maximize time spent in high quality habitat with plentiful food and mating opportunities, while minimizing time spent in low quality habitat with high risk of predation and competition. Consequently, their movement patterns can be used to infer resources of value. Such inferences have been made in a variety of terrestrial animals (Ferguson and Elkie 2004, Garcia *et al.* 2005, Nams 2005, Loureiro *et al.* 2007). In fish, movement paths have been used to deduce the distribution of important resources for

migratory species such as tuna (e.g., Gutenkunst *et al.* 2007). However, habitat use in sedentary fish has mainly been assessed using presence-absence or density distribution data rather than movement (Johnson *et al.* 2003, Lowe *et al.* 2003), with some exceptions (e.g., Ogden and Buckman 1973, Turgeon *et al.* 2010).

Movement of a sedentary fish may provide information about what constitutes suitable and unsuitable habitat. All fish are capable of movement but for some species, including many coral reef fish, long distance movement is more common in juvenile phases, after which they remain sedentary (Sale 1991). Sedentary animals can remain within a small area (i.e., home range) because, in that location, they can access all of their needed resources: food, shelter/protection, mating opportunities, etc. When a sedentary fish leaves its home range and establishes another it may be an indication that either the needs of the fish have changed (e.g., ontogenetic range shift), or the environment (e.g., temperature, food supply) is no longer suitable. If fish are displaced far enough from their home range that they are unable to return, they will be forced to settle in a new location. If competition does not limit movement, fish should move toward (and subsequently settle in) the best habitat they can locate.

Seahorses are prime examples of sedentary marine fish. Juvenile seahorses are thought to be planktonic (Morgan 2008), and have been found attached to floating rafts of marine vegetation in the open ocean (Vandendriessche *et al.* 2005), suggesting at least some long distance dispersal in early life stages. However, once settled and mature, seahorses tend to stay within small home ranges (Vincent and Sadler 1995, Perante *et al.* 2002, Bell *et al.*

2003, Moreau and Vincent 2004, Vincent *et al.* 2005, Rosa *et al.* 2007). Adult seahorses are capable of swimming but have few reasons to travel extensively in search of resources and benefit from remaining still enough to remain unseen by predators or prey (Foster and Vincent 2004). However, shallow areas of coral reefs, seagrass beds, and mangroves inhabited by seahorses are prone to both natural (e.g., storms, strong currents) and anthropogenic (e.g., fishing, coastal development) disturbances. These disturbances may lead to either involuntary displacement of seahorses, or changes in the environment that prompt seahorses to move voluntarily.

Understanding movement and habitat use of seahorses can help to inform conservation action. The IUCN Red List includes 38 species of seahorse, of which 29 are considered Data Deficient while the rest are listed as either Vulnerable (7) or Endangered (1) (IUCN 2012). The design of management plans to protect such Vulnerable species could benefit from movement studies. For example, information about movement of *Hippocampus whitei* has led to best practice procedures for cleaning shark nets in Sydney Harbour: seahorses were attracted to the epibiotic growth on the nets and would move away when the entire net was cleaned but would stay nearby if only half of the net were cleaned at one time (Harasti *et al.* 2010). Habitat use inferred from movement studies could also be used to choose appropriate sizes and locations for spatial protection.

In this study, I translocated *H. guttulatus* to (1) determine whether this normally sedentary species would move beyond the distance of its usual home range size when placed in a new environment and (2) identify environmental features related to their movement. I exposed *H.*

guttulatus to a sudden change in environment by displacing them well beyond their home ranges then compared the source environments with the environments where they settled to explore what prompts movement and settlement. I hypothesized that after displacement *H. guttulatus* should move greater distances than suggested by their ~20 m² home ranges (Curtis and Vincent 2006), and they should move towards increasingly more suitable habitats. Therefore, the environments where they move after displacement should be more similar to original capture locations than release locations.

4.3 Methods

4.3.1 Study site

I conducted my experiments in the Ria Formosa lagoon. The shallow, estuarine lagoon is 55 km long and 6 km at its widest point with water temperatures varying seasonally between 12 °C and 27 °C (Newton and Mudge 2003). The substrate tends to be mostly bare (fine sand, coarse sand, and shell fragments), with living substrate dominated by seagrass (mainly *Cymodocea nodosa*), macroalgae, and benthic invertebrates (Curtis and Vincent 2005). However, habitat within the lagoon is temporally variable (Cunha *et al.* 2005).

4.3.2 Pilot experiment

To determine how *H. guttulatus* responded to capture and release close to their home range, I moved seahorses less than 20 m from capture locations. Between 28 June and 31 July 2007, I captured, marked, and released 17 seahorses within the same site in the Ria Formosa lagoon. I captured seahorses by hand, and marked each with a unique colour combination of VIFE (Northwest Marine Technologies, Inc. Shaw Island, WA, U.S.A.), as per Curtis and Vincent

(2006). I randomly assigned seahorses to release locations, releasing eight seahorses within 1 m of their capture location, three within 10 m, four within 15 m, and two within 20 m, all in randomly chosen directions. In the 2 weeks after release I monitored the site daily, using SCUBA to search areas of approximately 10 m² centered on each release and capture location, and recorded the position of any marked seahorses using coordinates from a tethered GPS (Garmin GPSmap 76CSx).

4.3.3 Displacement experiment

To determine how *H. guttulatus* responded to displacement where they were unlikely to return home, I released seahorses at sites within the Ria Formosa that were well beyond their home range sizes (Fig. 4.1). From 21 September to 11 November 2009, I translocated 11 *H. guttulatus* to different sites in the Ria Formosa lagoon that were between 785 and 3477 m from capture locations. I captured seahorses from six of 32 sites previously surveyed for seahorses in 2001–2002 and 2008–2009 (Chapter 2, Curtis and Vincent 2005). I chose release locations that had (n=3) and had not (n=8) been inhabited by *H. guttulatus* in 2008–2009 (Chapter 2), reasoning that these might represent sites that were and were not suitable (i.e., good and bad habitat). I displaced more seahorses to locations where seahorses had not been recorded because there were so few sites where seahorses had been found in 2008–2009 surveys. I captured seahorses by hand while SCUBA diving—easy as they remained stationary—then released them in new sites.

I attempted to capture equal numbers of males and females, differentiating sex by the presence or absence of a brood pouch (Lourie *et al.* 2004). I transported each seahorse to the

GPS coordinates of its predetermined release location by boat in an 80 l container filled with seawater. Using SCUBA, I released each seahorse on the holdfast nearest to the anchor (e.g., tube worm, seagrass blade, sponge, shell).

4.3.4 Seahorse movement

To track where seahorses moved after release, I used small (0.6×1.65 cm, 0.5 g in water), external acoustic transmitters (VEMCO model V6). I attached transmitters on cotton thread “necklaces” as used in Vincent and Sadler (1995). Ex-situ experiments have demonstrated that dummy models of these transmitters and this attachment method have minimal effect on normal behaviour of *H. guttulatus* (Chapter 3). I handled seahorses with latex gloves and kept them submerged in a seawater filled container on the boat throughout the process, which took less than 1 min. After securing the tag, I monitored the seahorses in the container for a period of 5 min before release to ensure there were no signs of distress (e.g., loss of ability to regulate buoyancy or vertical orientation and/or constant twitching or clicking).

On successive days after displacement I returned to release sites and used a VEMCO directional hydrophone (VR100-180 kHz) and receiver (VR2W-180 kHz) to locate each tagged seahorse. When a signal was detected, I maneuvered the boat in the direction of the strongest signal. At the location with the strongest signal, I used SCUBA to search the area and confirm that the tag was still attached. When I found a tagged, displaced seahorse, I recorded its location using GPS and quantified the environment at its location as I did at the capture and release locations. I removed tags either after relocating a seahorse over a 5-day

period or earlier if there were signs of distress (as per above). After tags were removed, I released seahorses at the last location I found them to minimize handling.

I used the GPS locations of confirmed sightings to map the movement of each seahorse. Using GIS software (ESRI ArcGIS 9.3), I calculated the straight line distance between each sighting location and the release location (i.e., net distance moved from the release site), distance between successive sightings, and total movement (sum of all distances between successive sightings). Since I only have point locations, with no information about the path each fish travelled between sightings, these are minimum distances moved by the fish.

4.3.5 Habitat use

At the capture, release, and tracking locations, I measured % live cover, depth, temperature, water current speed, and horizontal visibility. I centered a 1 m² square quadrat on each seahorse as a subsample of habitat used. I visually estimated % live cover (i.e., seagrass, macroalgae, benthic invertebrates) and measured depth (m), temperature (°C) and water current speed (m · sec⁻¹) within the quadrat. I estimated horizontal visibility as the furthest visible measure along a transect tape from the quadrat. While this 1 m² subsample did not allow me to characterize all of the variation in habitat used at the capture location, it allowed me to easily compare with locations where seahorses moved after displacement.

4.3.6 Analysis

I compared the minimum distances moved between sexes, between release sites (with and without seahorses), and among days after release to determine whether there was any effect

of sex, presence of other seahorses, or time. I tested for normality and constant variance within groups in the movement data (straight line and total distances). I tested for differences in movement (the maximum straight line distance and total distance moved) between sexes and between sites with and without seahorses using t-tests.

To determine whether seahorses moved towards environments more similar to where they were captured, I tested whether the differences in environmental variables between capture (original) and last known locations were less than the differences between original and release locations. I reasoned that, if seahorses moved towards successively better environmental conditions after I displaced them, the final day on which I found a seahorse should be most representative of the environment they were moving towards. Therefore, I used only the environmental data from the capture, release, and final locations in these analyses.

I first tested whether seahorses moved towards specific environmental variables (i.e., depth, temperature, visibility, water current speed, and % live cover). For each seahorse, and each environmental variable, I calculated the absolute differences between the original and release location and between the original and final location. I tested for normality and constant variance of these absolute differences, and square-root transformed temperature and % live cover to satisfy the assumptions for parametric analysis. Using one-way paired t-tests in PRISM software (Version 5.02), I tested whether the absolute differences between original and release locations were significantly greater than between original and final locations. To

account for multiple comparisons, I applied a Bonferroni correction and calculated the false discovery rate.

My second test was to identify whether seahorses move towards similar environments that can be identified through combinations of variables. To combine variables I created resemblance matrices of all combinations of variables using the Euclidean distance method in PRIMER software (Version 6.1.6). To correct for the different scales of the five variables I used the normalize function (Clarke and Gorley 2006). To compare environments among seahorses and among locations (origin, release, and final), I used the resemblance matrices to run similarity percentages (SIMPER) two-way analyses on the normalized data in PRIMER. To correct for individual variation among seahorses and test whether the environment at the final tracking location was significantly more similar to the original capture location than the release location I used the resemblance matrices to run one-way paired t-tests in PRISM.

4.4 Results

4.4.1 Pilot experiments

At least 12 of the 17 seahorses I marked and released back to their original site stayed within that site (i.e., within 20 m of their capture and release sites). Immediately after release all seahorses (in both the pilot and displacement experiment) wrapped their tail around the closest holdfast and remained there for the duration of my 5 min initial monitoring period. Of the eight seahorses I released within 1 m of their capture locations I found six at the same location (some even on the same holdfast) between 1 and 14 days later. Both of the seahorses released at 20 m, three of the four seahorses released at 15 m and two of the three seahorses

released at 10 m from their capture location returned to within 1 m of where I found them originally, all within 3 days. As no seahorses in this experiment had acoustic transmitters, I could not locate the five missing seahorses that apparently moved beyond the site.

4.4.2 Displacement experiment

I was able to locate nine of 11 tagged seahorses for 2 to 10 days after release (Table 4.1). Average daily movement per individual ranged from 6.4 m to 48.2 m (mean \pm S.E. = 13.4 ± 4.6 m). The largest distance a seahorse moved between sightings was 150.6 m over an 8 day period, with the largest daily movement being 60.8 m. Seahorses ranged in size from 3.2 to 5.0 cm in trunk length (9.0 to 17.2 cm L_S as calculated from Curtis and Vincent (2005)), and sex ratio was even (males, $n=5$; females, $n=4$). Males and females did not differ significantly in the average distance moved (unpaired t-test; net and total, $p>0.54$) nor was there a difference between sites that were with and without seahorses in 2008–2009 population surveys (unpaired t-test; net and total, $p>0.49$).

I located six tagged fish multiple times and four on successive days for up to 4 days after release. From the successive locations I was able to get an idea of where the seahorses moved from 1 day to the next. Tagged seahorses moved generally in the same direction although I found one seahorse north of the release point after the first day, further east on the second day and even further south on the third day. Another seahorse moved to the southwest of the release point on the first day and then back towards the release point on the second. I did not detect a pattern of homing behavior, with only one seahorse moving in the direction of the capture location.

After displacement, I found the nine located seahorses in a variety of different habitats (e.g., at a variety of depths, some of which were deeper and others more shallow than the release location). However, there seemed to be less variation within individual seahorses. Individual seahorses tended to move to locations with environments more similar to where I originally captured them than where I released them. In my SIMPER two-way analyses, the average squared distance (i.e., dissimilarity) among seahorses was always greater than among location type (origin, release, and final), indicating that there was more clustering of environments within individual seahorses than within each location. The clustering of environments for individual seahorses can be seen visually in multi-dimensional scaling plots (e.g., Fig. 4.2). The difference in depth (Fig. 4.3, $P_{\text{one-way}}=0.048$) and the difference in the combination of depth and water current speed (Fig. 4.4, $P_{\text{one-way}}=0.044$) was less between the origin and last location than between the origin and the release location. The difference was not significant for any other variable or combination of variables ($P>0.05$, in all cases). None of the variables or combinations of variables was significant after applying a Bonferroni correction or calculating the false discovery rate to account for multiple tests.

4.5 Discussion

In 10 days or less, the seahorses I translocated moved (a) further from their release location than the majority of seahorses I released back to their original capture location and (b) further than most adult *H. guttulatus* moved among sightings within their home range over a 3 year period in the Ria Formosa lagoon (Curtis and Vincent 2006). In my pilot experiment more than 70% of released seahorses moved 20 m or less to return home. Another study showed

that captured and released *H. guttulatus* travelled less than 40 m between tracking locations (Garrick-Maidment *et al.* 2010). The majority of seahorses I translocated moved greater distances than these seahorses that had been released back to their capture location (Table 4.1; mean \pm S.E. = 59.4 \pm 14.7 m).

Other displaced sedentary fish have moved further than expected based on their home range sizes, but such long distance movements have mainly been associated with homing (Hartney 1996, Lowry and Suthers 1998, Turgeon *et al.* 2010), which does not seem to be the case in my study. When displaced to another kelp-bed, adult blacksmith (*Chromis punctipinnis*) travelled 500 m to the kelp-bed where they were originally captured (Hartney 1996), a distance greater than expected from their typical foraging ranges of 30 m (Bernstein and Jung 1979), or their typical migration ranges of 300 m (Bray 1981). Red morwong (*Cheilodactylus fuscus*) travelled as much as 900 m back to the site of original capture when displaced to what was thought to be an unfamiliar area even though they were found to stay within areas smaller than 3639 m² (Lowry and Suthers 1998). Unfortunately, since these fish were not tagged acoustically, neither Hartney (1996) nor Lowry and Suthers (1998) could determine how far the fish that did not return to their home range might have moved in search of a new settlement site. A hypothesis for why these fish are able to return home from much greater distances than expected from home ranges is that they have enhanced orientation abilities (and unexpectedly large mental maps) due to their variable environment (Odling-Smee and Braithwaite 2003). However, the tagged seahorses in my study did not consistently move in the direction of their original capture site and it is highly unlikely that their mental maps extended even further (beyond my >700 m displacement distances) than the distance

blacksmith and red morwong travelled in earlier studies, given that seahorses have much smaller home ranges than either of those two species. It would be interesting, though, to displace *H. guttulatus* distances between those I used in my pilot and displacement experiments to determine how far their mental maps do extend.

It is unlikely that the larger than expected movement was a flight response to being captured, given the results of my pilot experiment and other studies on *H. guttulatus* (Curtis and Vincent 2006, Garrick-Maidment *et al.* 2010). The immediate behaviour of *H. guttulatus* after release was to find the nearest holdfast and remain there at least until after I left. Remaining in place seems to be a more appropriate response than flight for a fish that relies on camouflage to avoid predation (Kleiber *et al.* 2010).

Translocated seahorses moved further than expected even when placed in sites inhabited by other *H. guttulatus*. The long distance movements by seahorses placed in presumably “good” habitat could be linked to the high variability I found among seahorses. Individual seahorses were found in environments similar to where they were originally captured but these conditions were different for each seahorse. Seahorses may have adapted to the environmental conditions of the capture site and, even when placed in an environment suitable for a conspecific, they may move to locate those particular conditions. However, the majority of tagged seahorses were within a metre of another seahorse when last located, suggesting they are either attracted to the presence of other seahorses or attracted to acceptable environmental conditions as indicated by the presence of other seahorses.

I was able to identify some environmental variables of potential importance for *H. guttulatus*, although my results were hampered by low power due to the large variability among individual seahorses and a small sample size. The clustering in environments chosen by an individual seahorse but not among seahorses suggests that *H. guttulatus* were able to settle in a variety of conditions but that once individuals have settled they prefer those conditions. *H. guttulatus* tended to move to locations with depths and water current speeds similar to where they had settled before I captured them, suggesting these were important environmental variables. As suggested by Cabin and Mitchell (2000) I have presented results with and without multiple hypothesis testing to let readers judge the results for themselves. Unfortunately, the high variability among individuals in my study means that a larger sample size is needed to identify high quality environments for the species. Longer-term studies on more animals are needed to refine and test my findings but would be difficult in the Ria Formosa lagoon with the acoustic tags I used, and given the low visibility and strong currents in the lagoon.

My sample size was further limited by tagging related deaths. Even though the effects of similarly sized tags were minimal in an earlier ex-situ study (Chapter 3), two of the seahorses I tagged and displaced in the wild died. In the ex-situ study, tags weighing up to 6% of body weight had no significant effect on *H. guttulatus* movement, holdfast use, or general behavioural state and only a short-term effect on orientation (Chapter 3). The tag burden was no greater for my tagged and displaced seahorses than the seahorses used in aquaria and one of the seahorses that died in the wild was among the largest tagged so the deaths did not seem to be related to the size of the fish. The cause of death was unclear but a variety of added

stressors in the wild not present in the aquaria may have been factors (e.g., presence of predators, limited food supply). A 22% tagging mortality is not trivial, though, and I would not recommend using these tags on similarly sized fish in the wild until further longer term tagging trials are conducted.

Despite the challenges of the technology, translocation experiments with acoustic tags could be superior to presence-absence or density data to evaluate important habitat for rare species. The problem with using presence-absence data at low population densities is that it is unclear whether a species is absent because the environment is unsuitable or if it is because there are insufficient densities to colonize all suitable areas. Furthermore, at low densities it is difficult to find sufficient numbers of animals to compare density unless a large area is surveyed. By translocating animals and tracking them through areas that they reject for settlement before they settle, each animal can be used to identify preferred habitat. The approach should become easier as acoustic tags become even smaller and include greater functionality. Archival tags can already store and transmit information remotely about water temperature, depth, time, and location (Nielsen *et al.* 2009). Using archival tags with an underwater array would eliminate the need to SCUBA dive to locate tagged fish, the main problem I encountered in my study.

My study suggests that sedentary fish are capable of longer distance movement than expected. The method I have used could further reveal what conditions these animals would escape and prefer such that interventions could be made on their behalf, if necessary, to ensure population persistence. Such information is particularly pertinent for species living in

coastal environments that are changing globally (e.g., Short and Wyllie-Echeverria 1996, Hoegh-Guldberg 1999, Alongi 2002).

4.6 Acknowledgements

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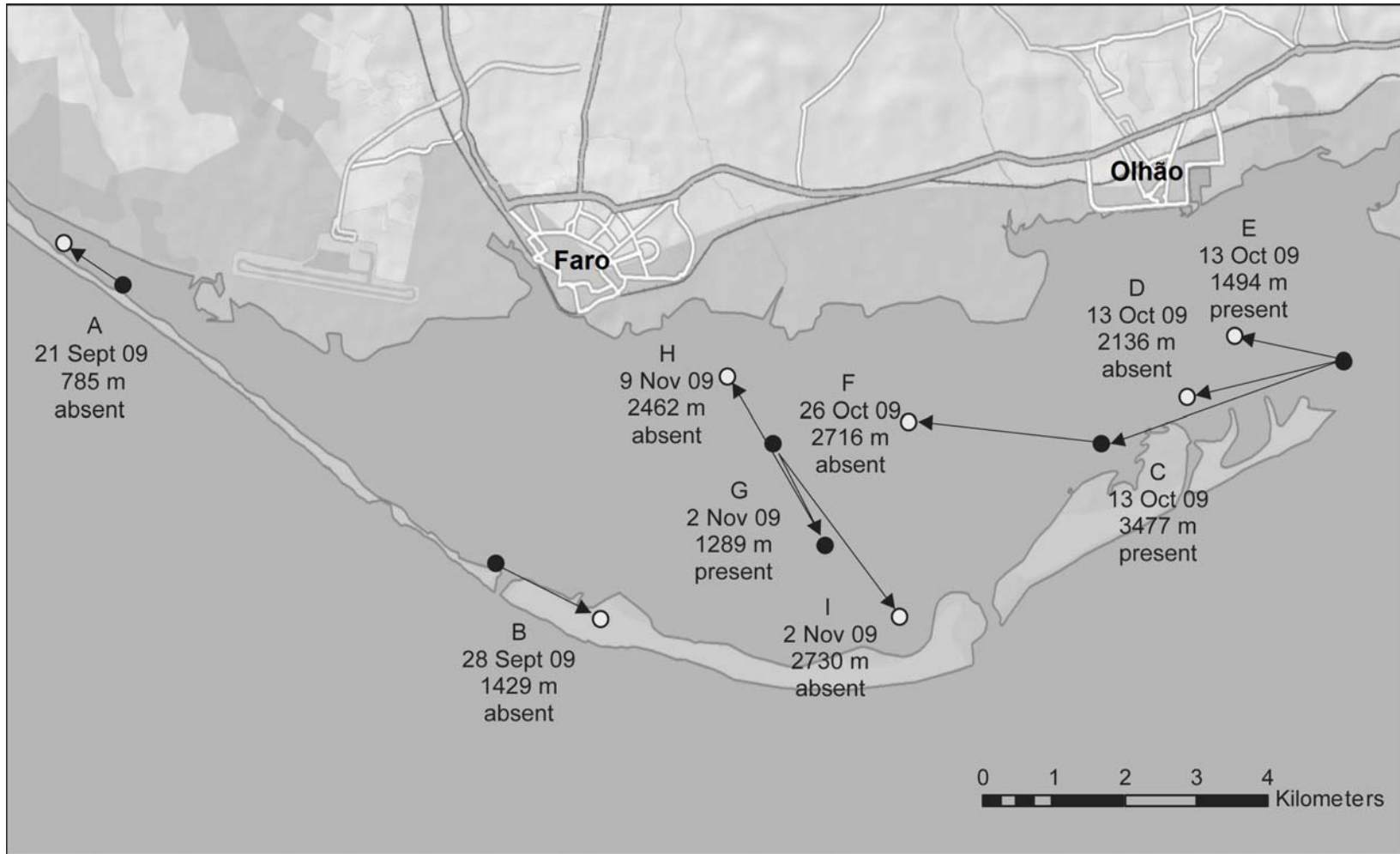


Figure 4.1 Map of the Ria Formosa lagoon showing the original capture (solid black points) and release (hollow white points) locations (with directional lines connecting each) of nine displaced *H. guttulatus* I relocated successfully. The identification letter, release date, distance between origin and release location, and whether there were seahorses present in earlier 2008–2009 population surveys at the release location (Chapter 2) are all indicated in the text beside each line. © Springer, 2012, by permission.

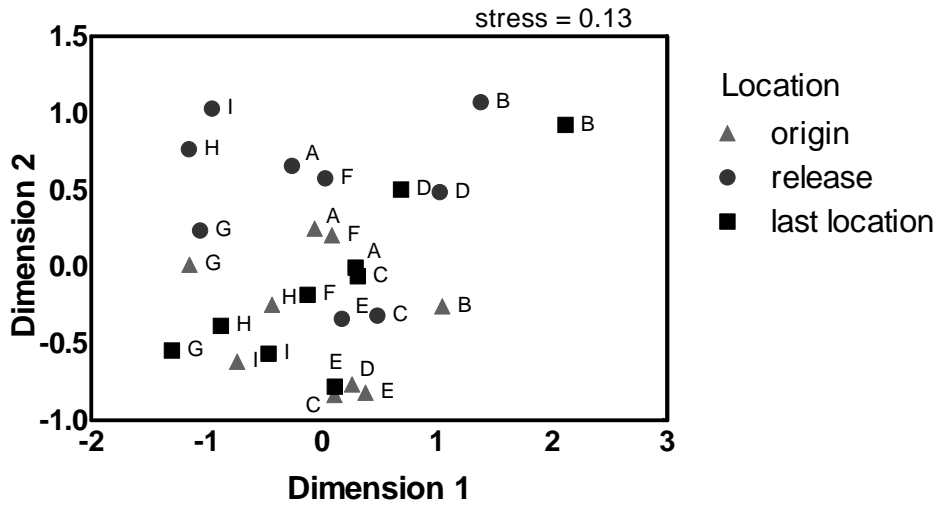


Figure 4.2 Multi-dimensional scaling plot showing the similarities between environments (depth, temperature, visibility, water current speed, and % live cover) at the original capture (triangle), release (circle) and final tracking locations (square) of nine tagged *H. guttulatus* (identified with unique letters).

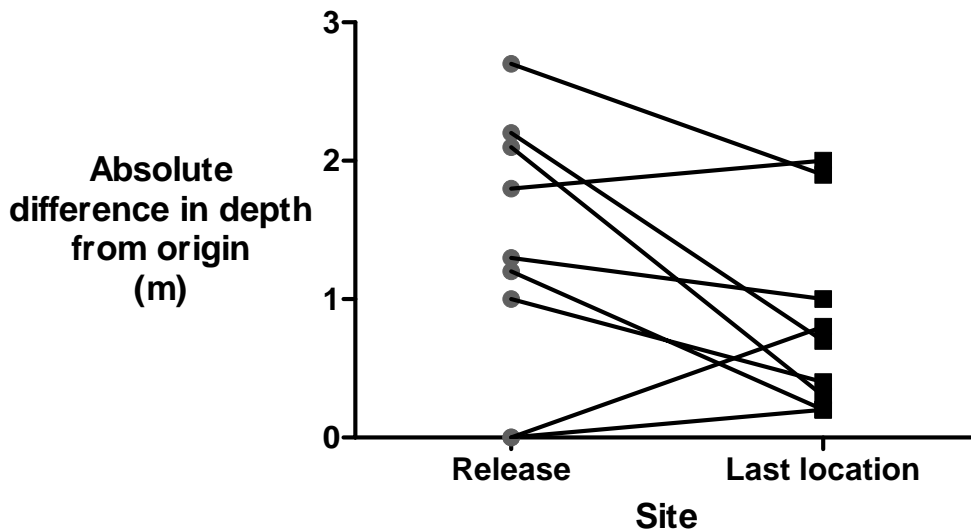


Figure 4.3 Difference in depths between the original capture location and both the release and last location of nine displaced *H. guttulatus*. Lines link data for the same individual seahorse. Downward lines indicate movement towards depths more similar to the capture location

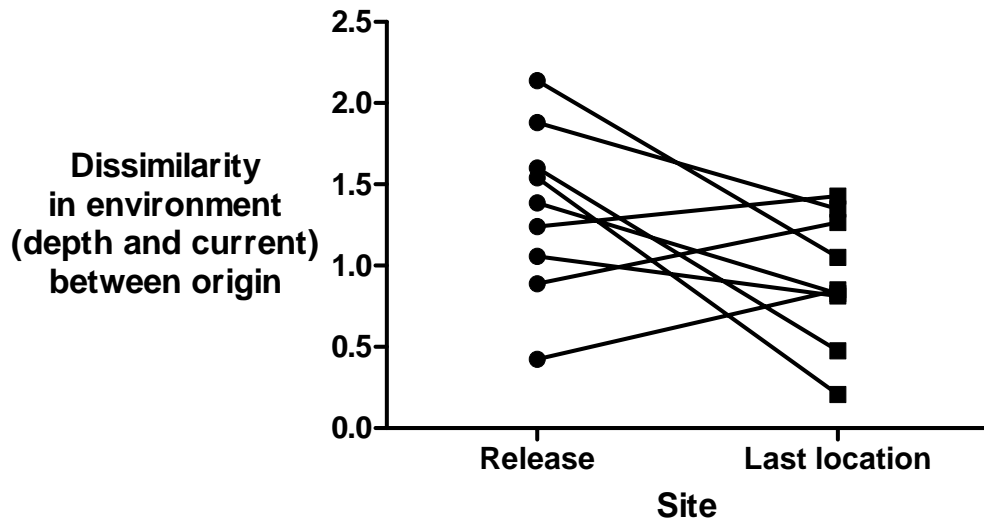


Figure 4.4 Dissimilarity in combined depth and water current speed between the original capture location and both the release and last location of nine displaced *H. guttulatus*. Dissimilarity was calculated using the Euclidean distance method.

Table 4.1 Minimum distances travelled by nine displaced *H. guttulatus*, including their sex, size (trunk length), the dates of displacement, the number of times they were located after displacement, and the date when they were last located.

Fish ID	Sex	Trunk length (cm)	Dates		# times located	Minimum distance moved (m)	
			Displaced	Last located		Total	Net
A	Female	5.0	21 Sept	01 Oct	3	150.6	150.6
B	Male	3.4	28 Sept	02 Oct	4	77.3	46.7
C	Male	3.9	13 Oct	16 Oct	3	24.6	13.3
D	Female	3.3	13 Oct	16 Oct	3	21.7	10.5
E	Male	3.2	13 Oct	15 Oct	2	16.4	7.1
F	Female	3.5	26 Oct	29 Oct	1	27.9	27.9
G	Male	3.6	02 Nov	10 Nov	1	51.2	51.2
H	Female	3.6	02 Nov	11 Nov	1	68.4	68.4
I	Male	3.4	09 Nov	11 Nov	2	96.5	96.4

Chapter 5. Thresholds in seascape connectivity: Influence of mobility, habitat distribution, and current strength on fish movement

5.1 Summary

Assessing connectivity of the marine environment is a fundamental challenge for marine conservation and planning. Much of the conceptual development in habitat connectivity has been based on terrestrial examples (i.e., from landscape ecology), with little application of those concepts to marine ecosystems. In the case of cost surface models, data limitations have hampered efforts to estimate relative costs to fish when swimming through different habitats, which are necessary for assessing seascape functional connectivity. When empirical data are few, animal movement can be simulated across artificial landscapes, allowing for systematic contrasts among landscapes with varying levels of habitat abundance and fragmentation. Here, I explore differences in the underwater environment that can affect localized movement of marine organisms and demonstrate the importance of incorporating them into seascape models. I link a fish-based cost surface model to simulated “seascape” landscapes to test interacting effects of habitat abundance, fragmentation, fish mobility and water currents on connectivity. First, I simulate movement of fish of different mobility, basing their costs of movement on available empirical data. Secondly, I explore the impact of directional water currents, relative to other factors, on movement across the seascape. In my models, all four factors (habitat abundance, fragmentation, mobility, and current) affected where fish moved. Sedentary fish were more sensitive to habitat change than more mobile fish. Swimming against water currents increased the path cost for all fish, regardless of mobility, but for less mobile fish the effect was most pronounced when habitat was scarce and fragmented. In comparison, mobile fish were more sensitive to water currents than to

habitat change. The cost of swimming against a current (of any strength) exceeded the benefit of swimming with that current, resulting in decreases in connectivity for seascapes with stronger currents. Both path measurements (length and cost) were useful in identifying marine connectivity thresholds but path cost was a better measure of connectivity: least cost paths were straight when hospitable habitat was plentiful but also when it was rare, whereas path cost increased non-linearly with habitat loss and fragmentation. Connectivity thresholds occurred when 10-50% of benthic habitat was favourable; below these thresholds there was a rapid increase in path cost. My approach indicates the importance of incorporating mobility and water currents into models of seascape dynamics; they are useful indicators of connectivity thresholds in marine environments.

5.2 Introduction

The concept of habitat connectivity has often been based on terrestrial examples (i.e., landscape ecology), but there is now a need to apply it to marine environments to understand how habitat loss, fragmentation, and degradation could affect organisms living there (Grober-Dunsmore *et al.* 2009, Foley *et al.* 2010, Boström *et al.* 2011). One of the reasons for past emphasis on landscapes compared to seascapes is the relative ease of measuring structural connectivity on land compared to underwater (Boström *et al.* 2011). While still not as easy as on land, advances in remote sensing and global positioning system technology are making it easier to quantify seascape habitat abundance and fragmentation (Moore *et al.* 2011), the two components needed to measure structural connectivity (Tischendorf and Fahrig 2000). Using such technology, habitat loss and/or fragmentation have been documented worldwide in marine habitats ranging from seagrass (Waycott *et al.* 2009, Fraschetti *et al.* 2011), coral reef

(Nyström *et al.* 2000, Bellwood *et al.* 2004), and mangrove ecosystems (Alongi 2002). In general, structural connectivity is lost when habitat is lost or fragmented (With and King 1999, With *et al.* 1999, King and With 2002, Rayfield *et al.* 2010). If losses in marine structural connectivity (arrangement of physical habitat) are creating seascapes with little functional connectivity (ability of organisms to move among the patches) there may be cause for concern, especially for species also threatened by direct exploitation and those that live in metapopulations (Hanski 1999).

Unfortunately, there are few data available to assess functional connectivity of a seascape. Whether a landscape or seascape is functionally connected for a given species depends on the distribution of habitat types (i.e., habitat structure) and the cost of moving through each type (Tischendorf and Fahrig 2000). Although a habitat can sometimes act as a complete barrier (e.g., a lake for a terrestrial animal or land for aquatic animals), more often an animal will prefer to use one habitat but can traverse others if needed (Wiens *et al.* 1997, With *et al.* 1999, Jonsen and Taylor 2000, Marsh *et al.* 2004). Some habitats may be better for foraging or have increased predation risk; tradeoffs between such opportunities and risks will influence the relative cost of moving through each habitat (Zollner and Lima 2005). Using displacement and gap crossing experiments, the relative costs of moving through one habitat over another has been estimated for several terrestrial species (reviewed in Rayfield *et al.* 2010). However, to my knowledge, similar relative costs have only been empirically measured in one marine species, the longfin damselfish (*Stegastes diencaeus* Jordan and Rutter) (Turgeon *et al.* 2010). In a homing experiment, *S. diencaeus* chose paths over coral that were between three and six times longer than straight paths over bare sand, presumably

because of increased risk of predation when travelling over sand (Turgeon *et al.* 2010). These results suggest that swimming over sand is up to six times more costly than swimming over coral for these fish.

Given the dearth of empirical data, landscape ecology models have been used to simulate terrestrial animal movement across artificial landscapes (Gustafson and Gardner 1996, With and King 1999, With *et al.* 1999, King and With 2002, Adriaensen *et al.* 2003, Rayfield *et al.* 2010). Neutral landscapes and/or least cost models have been used to test the relative and interacting effects of habitat abundance and fragmentation on animal movement and dispersal (Gustafson and Gardner 1996, With and King 1999, With *et al.* 1999, King and With 2002), to test the effect of relative habitat costs on dispersal (Schadt *et al.* 2002, Adriaensen *et al.* 2003, Gonzales and Gergel 2007), and, most recently, to study the interacting effects of abundance, fragmentation, and relative costs on connectivity (Rayfield *et al.* 2010). However, these models were all parameterized using terrestrial species and environments. Such models have not yet been extended into marine environments.

While some aspects of the marine environment can be modelled similarly to terrestrial environments, there are differences in the underwater environment that may also influence movement across seascapes. Marine environments, and in particular benthic environments, can be simulated using distributions of habitat types of varying relative cost, as they are in landscape models (Boström *et al.* 2011). However, the buoyancy of water means that fish do not need to expend much energy to remain upright or move vertically compared with terrestrial organisms (Alexander 1982), and body forms can be more streamlined to make

forward movement more efficient (Lindsay 1978). Another difference is the presence of ocean currents, which can have a large influence on connectivity of marine populations through larval exchange (Trembl 2008), and potentially also through movement of adult fish. Water currents can impart directionality to the seascape, making it easier for fish to move more in one direction than another. Currents can also allow for fish to be sedentary, bringing food to ambush predators (e.g., seahorses; Foster and Vincent 2004). Lifestyles of fish thus range from highly sedentary to highly mobile. This wide range in mobility is reflected in their various swimming modes, which categorize fish based on the amount of undulation vs. oscillation and the main fin used for propulsion (Lindsay 1978). In general it should be less costly for a more streamlined fish to cross inhospitable habitat (e.g., escape higher predation risk environments), and to swim against a current. However, it is unknown how the functional connectivity of a seascape might be affected by differences in fish mobility and water currents when habitat is lost and/or fragmented.

I created a marine-based seascape model to test the potentially interacting effects of habitat abundance, habitat fragmentation, fish mobility, and water current on the optimal (i.e., least cost) movement paths of simulated marine benthic fishes. I focused on marine benthic fishes because they have greater contact with habitat that can easily be visualized in terms of patches of good and bad habitat. However, these models may be equally applicable to pelagic fishes. My first question was how movement paths would differ among fishes with different levels of mobility when crossing seascapes with various amounts and fragmentation of habitat. To simplify my model I used only two habitats: an inhospitable habitat (IH) with a higher relative cost and a hospitable habitat (HH) with a lower relative cost. I based my

initial relative costs of moving through IH vs. HH on movement data from *S. diencaeus* (Turgeon *et al.* 2010). I assumed that faster swimming fish could move through IH more quickly, thus spending less time exposed to risks (e.g., predation) that make IH more costly. Therefore, I simulated movement of less and more mobile fish respectively by increasing and decreasing relative costs of moving through IH. My second question was how water currents across a seascape would additionally affect these movement paths. I simulated the effect of directional water currents by increasing the cost of moving in one direction.

To compare movement paths among simulated fishes I used two metrics: path length and path cost. Path length of least cost paths (Gonzales and Gergel 2007) and analogous metrics, such as “effective distance” (Adriaensen *et al.* 2003) or “spatial deviation of least cost links” (Rayfield *et al.* 2010), have been used to assess effects of habitat on simulated terrestrial animal movement and landscape connectivity. If an animal is unaffected by different habitat types, its path should be a straight line regardless of how those habitats are distributed. However, if there are perceived differences among habitat types, increased spatial heterogeneity should result in more convoluted paths. More convoluted paths (i.e., of greater length) should be more costly if all else is equal, but path cost will also depend on the type of habitat along the path (Gonzales and Gergel 2007). It could be better to take a route that is longer than an alternative, but passes through better habitat. If the path cost is too great, the seascape will no longer be functionally connected because the cost of moving will outweigh its benefit. Higher cost paths therefore represent lower connectivity.

I had three main hypotheses about how movement paths would be affected by mobility, habitat distribution and current. Habitat abundance (total amount of IH vs. HH) and fragmentation (dispersion of HH) should affect how often a fish needs to choose between the two habitat types, while fish mobility and current strength should affect which of the two is chosen in each case. Therefore, my first hypothesis was that all four factors (abundance, fragmentation, fish mobility, and current strength) will affect both the length and cost of fish movement paths. My second hypothesis was that less mobile fish should take longer and more costly paths than more mobile fish since the cost of moving through IH will be greater and they will be more likely to choose a convoluted route through HH. Swimming against a current should result in greater differences between paths of less and more mobile fish. Fish should move greater distances along more costly paths when forced to swim against stronger currents and along straighter, less costly paths when swimming with a current. My third and final hypothesis was that there will be thresholds in connectivity at intermediate levels of habitat abundance and fragmentation (as measured by length and cost of the path) and that those thresholds will depend on both the fish mobility and water current strength. Such thresholds have been found in the spatial distribution of least cost links for simulated terrestrial animals (Rayfield *et al.* 2010), but their relationship with mobility and current strength have not been explored.

5.3 Methods

5.3.1 Rationale and modeling assumptions

To test how habitat abundance, fragmentation, fish mobility, and current strength affect habitat connectivity, I ran a four factor factorial experiment. I used neutral landscape models

(NLMs) to create landscapes with specific levels of habitat abundance and fragmentation (Gustafson and Gardner 1996, Wiens *et al.* 1997, With 1997, With *et al.* 1999, With 2004, Gergel 2005, Gardner and Urban 2007), and least cost analysis to model fish movement across the seascape (Adriaensen *et al.* 2003, Rayfield *et al.* 2010). Using NLMs enabled direct control over landscape pattern in a way not possible in the field.

Instead of simulating dispersal, I chose to simulate fish movement as homing (with a known source and destination). Despite the fact that many terrestrial and aquatic taxa are highly territorial or exhibit high site fidelity and thus return to a home location (i.e., homing) (Kelt and Van Vuren 1999, Kramer and Chapman 1999, Bélisle and St. Clair 2002, Perry and Garland 2002), landscape ecology models tend to simulate animal movement as dispersal (e.g., Gustafson and Gardner 1996, With and King 1999, King and With 2002, Gonzales and Gergel 2007, Rayfield *et al.* 2010), rather than homing (e.g., Desrochers *et al.* 2011).

Modelling homing animals rather than dispersing animals allows for a more explicit test of habitat costs and landscape structure because a straight path represents the null model (no influence of habitat amount or configuration). By releasing an animal at a specific site (origin) and knowing that it is motivated to return home (destination), the path of the animal can be predicted without the need to guess (and simulate) the reasons for and/or drivers of dispersal.

5.3.2 Parameterizing habitat costs for fish of differing mobility

I used three different relative costs of moving through IH vs. HH to represent homing fish of varying mobility. My first relative cost (6:1) was based on longfin damselfish (*S. diencaeus*)

(Turgeon *et al.* 2010). Damselfish (Family Pomacentridae) are labriform swimmers that use pectoral fins as the main source of propulsion (Lindsay 1978). In the spectrum of adult fish movement, labriform swimmers are neither the worst nor the best swimmers. To reflect fish species that are more and less mobile, I used relative costs of 1.5:1 and 12:1 (i.e., half the minimum and twice the maximum for the range found in *S. diencaeus*; Turgeon *et al.* 2010).

Among the many fish families that are more and less mobile than damselfish, I will use Serranidae (sea basses and groupers) and Sygnathidae (seahorses, pipefish, pipehorses, and seadragons) to illustrate my research. Serranids are subcarangiform swimmers (Froese and Pauly 2012), using their caudal fin for propulsion for more efficient swimming (Lindsay 1978). Sygnathids tend to be less efficient amiiform swimmers (Froese and Pauly 2012), undulating their dorsal fin to move forward (Lindsay 1978). Species from all three illustrative families maintain territories or home ranges and have strong site fidelity (Pomacentridae: Luckhurst and Luckhurst 1978, Norman and Jones 1984, McGehee 1995, Turgeon *et al.* 2010; Serranidae: Robinson *et al.* 2008, March *et al.* 2010, Mason and Lowe 2010, Lino *et al.* 2011; Sygnathidae: Perante *et al.* 2002, Moreau and Vincent 2004, Sanchez-Camara and Booth 2004, Curtis and Vincent 2006).

5.3.3 Creating seascapes and cost surfaces

Using the software Qrule (Gardner and Walters 2001, Gardner and Urban 2007), I created two dimensional neutral seascapes with theoretical distributions of IH and HH habitats.

Using neutral seascapes (i.e., null models) enabled me to explore general relationships between landscape structure (habitat abundance and fragmentation) and my other two factors.

My seascape grids were 128 x 128 cells in size with fractal distributions of habitat (Gardner and Urban 2007). I produced seascapes with five levels of HH abundance (10, 20, 30, 50, and 70% of cells), with the remaining proportion of cells as IH. I varied the fragmentation of cells using three levels of spatial contagion ($H = 0.1, 0.5, 0.7$). I created 100 replicates of each combination of abundance and fragmentation (1500 total seascapes).

I transformed neutral seascapes into cost surfaces using the cost values associated with my simulated fish (Table 5.1). I assigned a cost value of one to all HH cells and differing costs based on mobility (1.5, 6, and 12) to all IH cells using GIS and scripting (ESRI ArcGIS 10; Python 2.7). Applying the three costs to the 1500 seascapes resulted in 4500 cost surfaces.

5.3.4 Modelling the effect of ocean currents

I simulated the effects of water currents on fish movement by making it more costly to move in one direction across the seascape. Using the Path Distance tool in ArcGIS 10, I added a horizontal factor (eastward 90° current) to each cost surface. The cost of moving from one cell to another on the seascape was dependent on both the cost associated with each cell (from the cost surface) and the cost associated with the direction of movement between cells. It was least costly to move in an easterly direction (horizontal factor = 1). The cost associated with movement in all directions other than eastward (i.e., relative angle = 0°) was dependent on the slope of the horizontal factor graph (Fig. 5.1), with a maximum cost when fish moved in a westerly direction (relative moving angle = 180°). I varied the slope of the horizontal factor graph to represent effects of different current strengths.

I simulated the effects of four current strengths based on the ratios of oxygen consumption when swimming against currents (MO_{2-MAX}) versus oxygen consumption at rest (MO_{2-REST}). I was able to find oxygen consumption data for pomacentrids but not for serranids or syngnathids. The oxygen consumption for ten damselfish species was between 3.63 and 7.71 times greater when swimming against currents than when at rest (Johansen and Jones 2011). I therefore simulated the effects of directional water currents which were four and eight times more costly to swim against than to swim with by using horizontal factor graph slopes of 0.0222 and 0.0444 respectively. It should be noted that these are relative costs (as in the habitat costs) rather than current speeds. The cost of swimming against a water current of a given speed could differ among fishes. To simulate a wide range of costs I included the effects of one weaker and one stronger current than represented by the damselfish data, using slopes of 0.0111 and 0.0888 (twice and six times as costly to swim against currents respectively).

I examined the effects of swimming both with (positive) and against (negative) currents by starting fish at western and eastern edges of the seascape respectively (i.e., the release point in a homing study). I compared positive and negative currents at each of the current strengths, simulating the effects of eight currents (i.e., -16, -8, -4, -2, +2, +4, +8, +16). I applied the eight currents to the 4500 cost surfaces to simulate movement of fish across 36000 seascapes.

5.3.5 Determining homing path cost and length

I simulated movement of fish across each seascape using least cost path models. These models find the optimum path (i.e., least costly) between an origin and a destination given the cost of moving through each cell along the path. For the positive current simulations I set the destination (i.e., the “home” location in a homing study) as the centre point of the eastern edge of the seascape and for the negative current simulations I set the destination as the centre of the western edge. Using the Cost Path tool in ArcGIS 10, I calculated the (1) overall cost and (2) length of the optimum path across the seascape as my two measures of connectivity.

5.3.6 Statistical analyses

To determine how connectivity was influenced by habitat abundance, fragmentation, fish mobility and water current I used a four-factor ANOVA (Crawley 2007). I tested the associations between my two measures of connectivity (path cost and path length) and my four factors. I analysed the main effects, two-way interactions, and any higher-order interactions. I tested for normality and constant variance throughout and assumptions of parametric tests were met. I further examined the interactions between variables visually by plotting the interaction between the response variables (path length and path cost) and habitat abundance at each combination of habitat fragmentation, mobility, and current strength.

To further differentiate the relative importance of the four factors and their interactions, I sequentially compared models with and without each factor or their interacting effects. I used the minimum adequate model (i.e., generalized linear model with all significant factors from

the four-factor ANOVA) for comparison. I then created generalized linear models removing each of the significant interacting effects or main effects (and any higher-order interactions containing that effect) but including all other effects. I compared each of the reduced models with the minimum adequate model using an ANOVA. I judged the relative importance of each effect based on the relative change in deviance when that effect was removed (Larson-Hall 2010). For ease of comparison I standardized deviances by division with the lowest change in deviance. Effects with larger relative changes in deviance were considered more important.

5.4 Results

5.4.1 Importance of four factors

As expected, habitat abundance, fragmentation, fish mobility, and water current all significantly influenced both the path cost and path length. However, these associations are highly dependent on their interactions as well (Table 5.2). The only non-significant result was that the four-way interaction did not significantly affect path length. Based on relative changes in deviance, water current was of greatest relative importance, followed by fish mobility (difference in habitat cost), then habitat abundance. Habitat fragmentation seems less important than any of the second-order interactions involving the other three factors. The pattern of relative importance for main effects was similar for both path length and path cost. For the three most important factors, higher-order interactions were of successively less importance.

5.4.2 Path length vs. path cost

When seascapes are mostly composed of favourable benthic habitat ($HH > 50\%$) trends in path length and path cost are similar but when favourable habitat becomes scarce the two trends diverge (Fig. 5.2 vs. 5.3). If there is plenty of good (i.e., hospitable) habitat available, fish are able to take straight paths to their destinations and because it is of good quality (e.g., with shelter from predators) it is not very costly to move through: path length and path cost are minimal. Fish take the longest detours (i.e., maximum path length) when there are intermediate amounts of good quality habitat available ($HH = 20-50\%$). The peak thresholds in path length seem to coincide with sudden increases in path cost as the habitat becomes less hospitable. Path cost continues to increase exponentially as habitat quality declines but path length actually decreases when good quality habitat is rare: fish are forced to move through inhospitable habitat because that is all that is available but travel directly to their destination to minimize the time spent travelling through it.

The position of peak thresholds in path length, and consequent increases in path cost, illustrate the interaction between hospitable habitat abundance and fragmentation. When the habitat is not very fragmented (Fig. 5.2a), most fish take longest paths when 20% of the habitat is hospitable. However, when the habitat is more fragmented (Fig. 5.2b and 5.2c), fish take longest paths when the habitat is more hospitable ($HH = 30\%$). When habitat is fragmented, it seems more difficult for fish to find paths through the rare good habitats available, decreasing the functional connectivity of the seascape.

5.4.3 Differences in fish mobility

Fish mobility affected the position of the peak threshold in path length and the magnitude of (but not the general pattern in) path cost. The patterns in path length were more similar for the two less mobile fish, although the least mobile fish consistently took longer routes to their destination (Fig. 5.2). Compared with the less mobile fish, the most mobile fish took relatively straight paths (and of relatively low cost) regardless of the amount of favourable habitat (Figs. 5.2 and 5.3). The longest detours for the most mobile fish were much shorter than those taken by less mobile fish and they took those long detours when the habitat was more hospitable (HH = 50%) than in less mobile fish (HH = 20-30%). It seems that for more mobile fish, since there is less difference between good and bad habitats, minimizing path length also minimizes path cost (Fig. 5.2 vs. 5.3). Less mobile fish were more sensitive to changes in the amount and fragmentation of hospitable habitat: the cost of crossing the seascape increased non-linearly as hospitable habitat was lost and/or fragmented and the increase was greatest in the least mobile fish (Figs. 5.3 and 5.4).

5.4.4 Additional impact of current

Although the general pattern in path cost is similar regardless of whether the seascape has current or not (Fig. 5.4 vs. 5.3), the magnitude of the path cost depends on the current strength. For each combination of fragmentation, fish mobility, and current, the path cost decreases when habitat becomes more hospitable (i.e., it is less costly to cross a seascape if hospitable habitat is abundant). Path costs increase when fish swim against stronger currents and decrease when they swim with stronger currents. However, the increase in path cost for

fish swimming against the current was much greater than the decrease in path cost for fish with swimming with the current, even for the same current strength (Fig. 5.4).

Path cost is most sensitive to current strength when fish are of lower mobility and the hospitable habitat is highly fragmented (Fig. 5.4c). For more mobile fish (Fig. 5.4g-i), swimming against a strong current increases the path cost substantially but the cost for a given current strength is relatively consistent even when habitat is lost and/or fragmented. My model predicts that more mobile fish would be more sensitive to changes in current strength than changes in habitat abundance or fragmentation.

5.5 Discussion

5.5.1 Sedentary fish are more sensitive to habitat change

As expected, my model predicted that highly mobile fish should be less sensitive to changes in habitat. If fish are able to swim through inhospitable areas quickly to minimize risks of predation or other threats (for example the groupers in my model), a higher level of connectivity should be maintained regardless of habitat abundance or fragmentation. Of the 53 serranid species listed on the IUCN Red List as threatened or Near Threatened, habitat loss or degradation is a major threat for only 13 (IUCN 2012). In contrast, less mobile fish (for example the seahorses in my model) should be highly sensitive to changes in habitat. Adult seahorses are sedentary fish: they use camouflage to avoid predation and ambush prey (Foster and Vincent 2004). A major threat to these sedentary fish is habitat loss and degradation (Vincent *et al.* 2011), which may be exacerbated by their sedentary nature

(Curtis 2004). Of the 14 threatened or Near Threatened syngnathid species, all are threatened by habitat loss or degradation (IUCN 2012).

5.5.2 Mobility affects connectivity thresholds

I found results that suggest critical thresholds in fish mobility at intermediate habitat abundances, consistent with terrestrial research and recommendations for conservation. Habitat and mobility thresholds have been discussed thoroughly in terrestrial literature (reviewed in Swift and Hannon 2010), but their exploration in marine environments is lacking (Grober-Dunsmore *et al.* 2009), with some notable exceptions (e.g., Mumby and Hastings 2008). In terrestrial simulations, the effects of habitat loss on connectivity tend to be non-linear, with sudden declines in dispersal success when habitat is reduced by 50-90% (Swift and Hannon 2010). I found similar thresholds, with maximum path lengths and sudden increases in path cost occurring when 50-80% of hospitable habitat is lost. Both results correspond with theoretically based recommendations for spatial protection of 10-50% (mean 30%) of marine habitat (Gell and Roberts 2003).

Mine is the first study to indicate that connectivity thresholds should be influenced by the interaction of fragmentation and relative cost of inhospitable habitat (i.e., mobility) together. Previous studies have shown separately that, when habitat is lost, ecological thresholds are reached earlier (i.e., with more hospitable habitat remaining) when the habitat is also fragmented (With *et al.* 1999) or when inhospitable (matrix) habitat is more costly (Fahrig 2001). My results suggest that thresholds for less mobile fish (higher relative cost) should be reached earlier when habitat is fragmented, but thresholds for mobile fish should be

unaffected by fragmentation. A greater proportion of habitat might need to be protected for less mobile fish to maintain connectivity when habitat is fragmented.

Interestingly, my results suggest that at least 30% of marine habitat should be protected in order to maintain connectivity regardless of fish mobility or habitat fragmentation, but further empirical data would help refine my model predictions. While I have attempted to model effects of habitat change on a variety of fish using different relative habitat costs, empirical data were available only for a single species, *S. diencaeus* (Turgeon *et al.* 2010). My relative costs were less extreme than those used in many terrestrial simulations where the relative cost of good vs. bad habitat was up to 100:1 (reviewed in Rayfield *et al.* 2010). However, *S. diencaeus* are highly territorial (Cheney and Côté 2003) and may be exposed to high predation risk when crossing over sand, as are other coral reef fish (Sweatman and Robertson 1994). These traits would suggest that, compared with other species, damselfish should have a relatively high cost of moving through inhospitable habitat, yet they chose paths 5.9 times longer to avoid open sand (Turgeon *et al.* 2010). A fish species which would detour 100 times longer would have to be exposed to much greater predation risk or be extremely habitat specific. I feel my estimations are reasonable but further field studies are needed to estimate the actual relative costs for fish species with a broader range of mobility to improve and test my model predictions.

5.5.3 Path cost better reflects structural connectivity than path length

As an index of connectivity, path cost may be more indicative than other metrics of animal movement paths. A variety of movement path measurements have been used as indices of

connectivity, including path length (With *et al.* 1999, Adriaensen *et al.* 2003, Gonzales and Gergel 2007), tortuosity (With *et al.* 1999), net displacement (With *et al.* 1999) or spatial deviation of least cost links (Rayfield *et al.* 2010). In my models, path cost increased when habitat was lost and/or fragmented, as would be expected from an inverse index of connectivity (decreasing connectivity with habitat loss and fragmentation) (Mönkkönen and Reunanen 1999). However, paths were short (i.e., relatively straight) when the habitat was pristine or when it was degraded, with a peak in path length at intermediate habitat abundance. When good habitat is abundant and available, fish can move in straight paths exclusively through good habitat. When good habitat is rare, paths are also relatively straight because the only option is to move through bad habitat and a straight path minimizes time spent in that habitat. Even though both paths are straight, the increased energetic cost (or increased risk of predation, lack of foraging opportunities, etc.) of moving exclusively through inhospitable habitat should reduce the chances that fish will cross a seascape, thereby reducing functional connectivity, as indicated by the increase in cost but not the decrease in path length. Unfortunately, while path cost is easy to calculate in simulated data, it would be difficult to measure in the wild.

5.5.4 Water currents are as important as habitat to marine connectivity

My modeling approach helped address the potential impacts of prevailing currents relative to other factors. By simulating homing fish I could assume that I knew the destination and did not need to incorporate further behavioural traits and additional complex assumptions for which there is usually limited data. Dispersal behaviour is generally poorly understood (Ray *et al.* 2002, Revilla *et al.* 2004), and dispersal data are difficult to collect (Koenig *et al.*

1996). Furthermore, random walk models inaccurately predict dispersal for a variety of taxa including butterflies (Jones *et al.* 1980, Pe'er *et al.* 2004), rattlesnakes (Duvall and Schuett 1997), lynx (Revilla *et al.* 2004), sea cucumbers (Purcell and Kirby 2006), and squirrels (Gonzales and Gergel 2007). Behavioural traits unconnected to landscape structure (conspecific attraction, prior knowledge, competition, or predation; Brooker *et al.* 1999, Pearson *et al.* 1999, Gautestad and Myrsetrud 2006) create uncertainty in such approaches. Modelling homing fish allowed me to add water current to previous factors examined in landscape ecology models without having to deal with behavioural uncertainties. However, my model predictions may be limited to fish that migrate between known areas. More complex modeling may be needed to develop more broadly applicable predictions for fish.

Water current could affect functional connectivity as much or more than habitat structure in marine systems. The effect of water current depended on fish mobility: in less mobile fish, water currents had their strongest effect when habitat was scarce and fragmented, while more mobile fish were sensitive to changes in current strength but not to changes in habitat abundance or fragmentation. Regardless of mobility, for a given current strength the cost of swimming against a current outweighed the benefit of swimming with it, resulting in an overall negative effect on connectivity. The loss in connectivity with stronger currents could have implications for source-sink dynamics and marine metapopulations if they are connected through movement of less mobile species. If populations within a metapopulation are connected by bidirectional current flow, a decline in habitat abundance or an increase in habitat fragmentation could isolate populations of less mobile species more easily than if

there was no current. However, fish could also time their movements to periods when currents are favourable, thus minimizing energetic costs of moving between habitat patches.

As with all models, my simulations were meant to focus on specific factors and were simplifications of a more complex reality. I created a model of what fish might do under a specific set of circumstances. I assumed that fish mobility was directly related to the cost of moving through habitats. In reality, the cost of moving through a habitat will depend on a suite of life history, ecological, and behavioural characteristics that influence predation risk (e.g., trophic level), competition (e.g., territorial behavior), food availability (e.g., foraging strategy), or energetic costs (e.g., movement behavior). I also focused on benthic fish species for my examples. While it is easy to imagine benthic habitat as habitat patches, pelagic habitat also has structure and my model could be adapted for pelagic fish. My models of water current strengths would actually be more applicable to fish that swim within the water column because fish can escape water currents by staying close to the benthos or by staying within habitats that buffer the effects of the current. A more realistic model for benthic marine fishes would simulate currents that change according to habitat types. Lastly, I focused on movement of adult fish. Some studies have suggested that adult movement can be as important to connectivity as larval dispersal in some species and locations (Mora and Sale 2002, Di Franco *et al.* 2012). However, the prevailing thought has been that most marine fish populations are connected by movement of early life stages (Williams *et al.* 1984, Roberts 1997, DiBacco *et al.* 2006). Larval fish phases tend to move passively on ocean currents so my seascape model would be far less applicable to these early life stages. My model would

only predict a small proportion of connectivity in marine fish with large amounts of larval exchange.

My study is an early attempt to adapt a technique originally intended for landscape ecology to a seascape and test the effect of an additional factor that could affect animal movement in the marine environment. While landscape ecology is increasingly being applied to seascapes (Boström *et al.* 2011), this is the first use of neutral landscape and least cost modeling specifically focused on the marine environment. Incorporating fish of differing mobility and water currents into seascape models has proven important in exploring patterns in marine connectivity. Technological advancements will become even more important in improving our ability to measure pattern in marine habitats (Moore *et al.* 2011), and study fish movement and behaviour (Nielsen *et al.* 2009), creating opportunities to further adapt landscape ecology models into increasingly realistic models of seascape processes.

5.6 Acknowledgements

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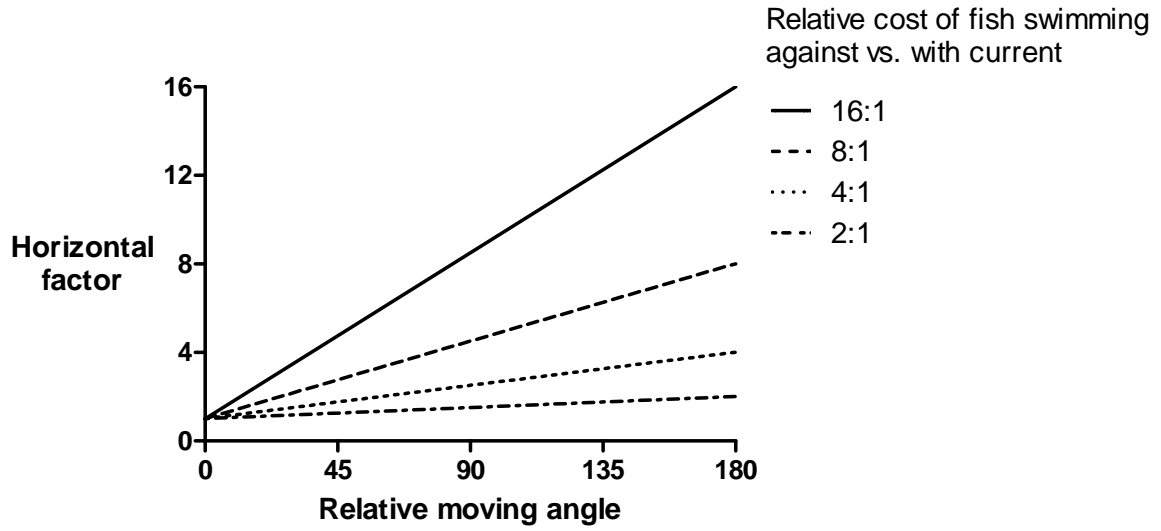


Figure 5.1 The horizontal (directional) cost incurred by simulated fish swimming in directions relative to easterly water currents (relative moving angle = 0) of various strengths (2:1, 4:1, 8:1, and 16:1 indicate successively greater current strengths).

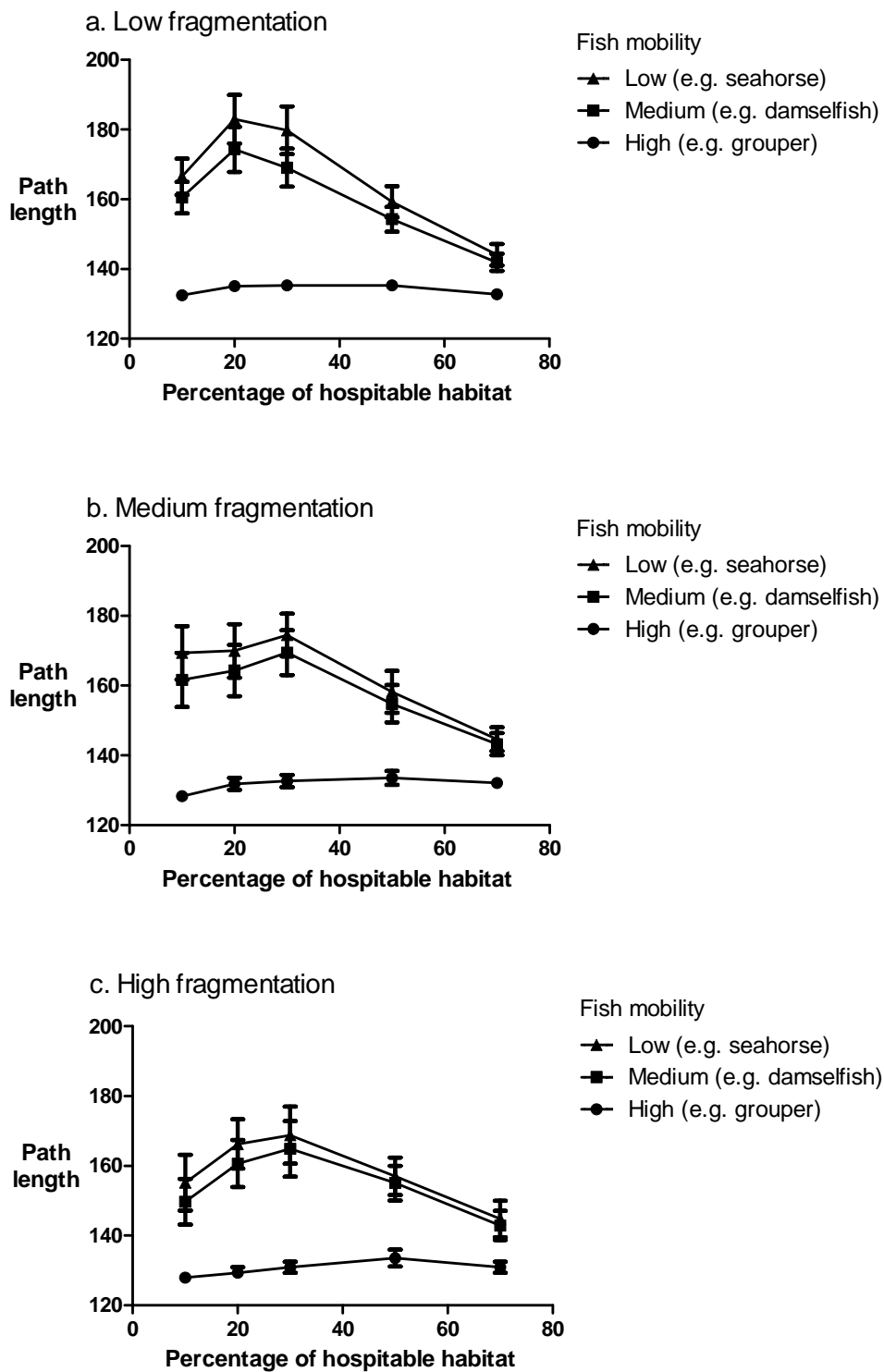


Figure 5.2 Average path lengths (\pm 95% CI) of simulated fish with three levels of mobility moving across artificial seascapes with different percentages of hospitable habitat at low (a, $H=0.1$), medium (b, $H=0.5$), and high (c, $H=0.75$) levels of fragmentation.

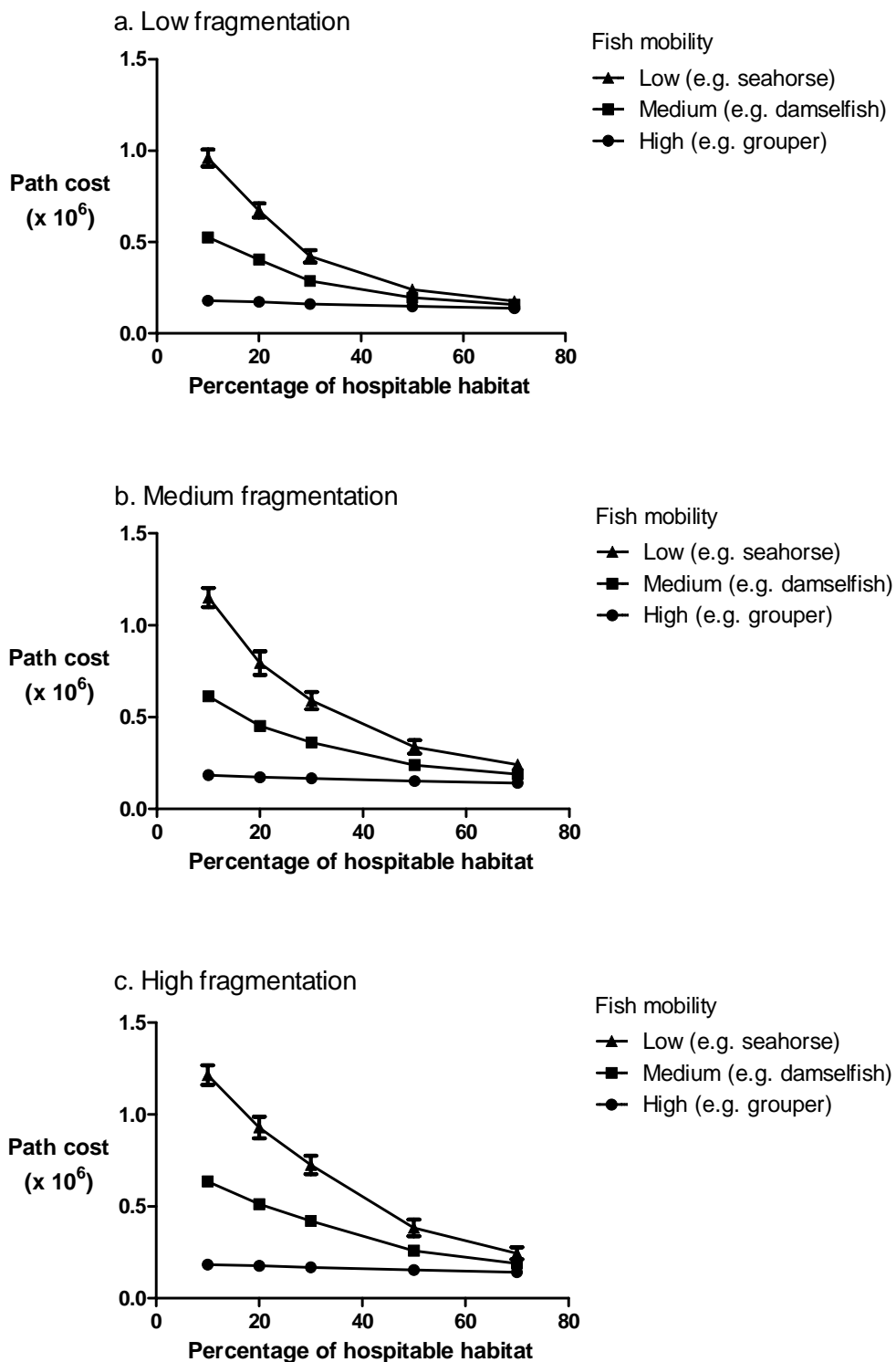


Figure 5.3 Average path cost (\pm 95% CI) of simulated fish with three levels of mobility moving across artificial seascapes with different percentages of hospitable habitat at low (a, H=0.1), medium (b, H=0.5), and high (c, H=0.75) levels of fragmentation.

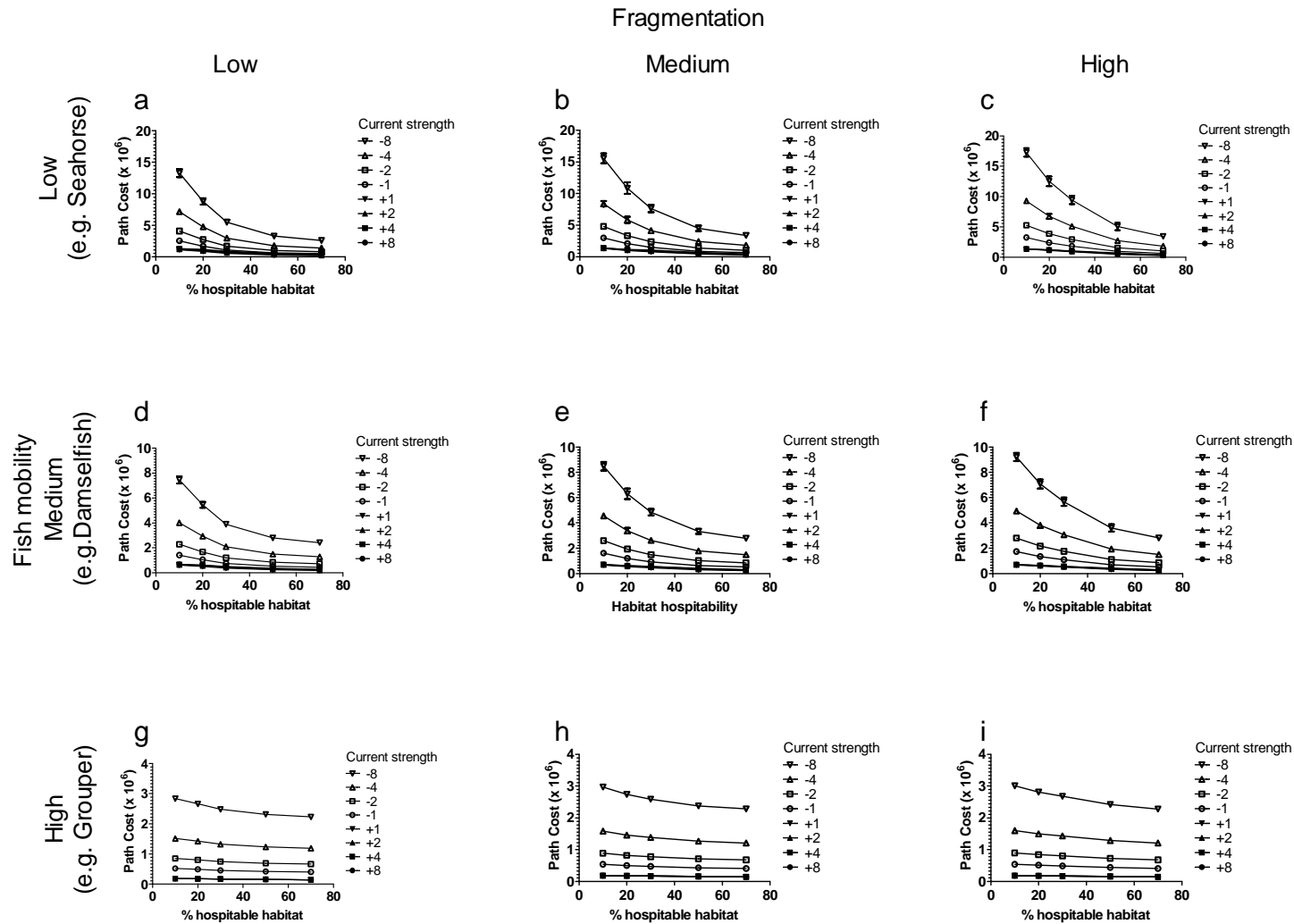


Figure 5.4 Average path costs (\pm 95% CI) of simulated fish with different mobility moving across artificial seascapes with different percentages of hospitable habitat at low (a, $H=0.1$), medium (b, $H=0.5$), and high (c, $H=0.75$) levels of fragmentation and with varying current strengths.

Table 5.1 Relative costs of moving through inhospitable habitat (IH) vs. hospitable habitat (HH) used in simulations of fish with varying mobility.

Mobility	Cost of IH: HH	Example family	Swimming mode
Low	12:1	Syngnathidae (seahorses, pipefish, pipehorses, and seadragons)	Amiiform
Medium	6:1	Pomacentridae (damsel fish)	Labriform
High	1.5:1	Serranidae (sea basses and groupers)	Subcarangiform

Table 5.2 Results of a four-factor ANOVA testing the effects of hospitable habitat abundance (ABUND), hospitable habitat fragmentation (FRAG), relative cost of inhospitable habitat vs. hospitable habitat (COST), and seascape current strength (CURR) on the path length and total cost of paths of artificial fish moving across a seascape, with comparisons of the relative change in deviance associated with each factor.

Source	D _f	Path Length			Path Cost		
		F-ratio	P value	Relative Δ Deviance	F-ratio	P value	Relative Δ Deviance
ABUND	4	1410	<0.0001	233	13400	<0.0001	277
FRAG	2	394	<0.0001	56	1710	<0.0001	79
COST	2	8650	<0.0001	385	32800	<0.0001	295
CURR	8	4000	<0.0001	673	49300	<0.0001	799
ABUND*FRAG	8	78.3	<0.0001	39	71.2	<0.0001	64
ABUND*COST	8	189	<0.0001	53	3960	<0.0001	107
ABUND*CURR	32	154	<0.0001	108	2250	<0.0001	161
FRAG*COST	4	62.8	<0.0001	33	551	<0.0001	67
FRAG*CURR	16	3.53	<0.0001	29	326	<0.0001	71
COST*CURR	16	190	<0.0001	77	4470	<0.0001	161
ABUND*FRAG*COST	16	11.0	<0.0001	3	24.7	<0.0001	2
ABUND*FRAG*CURR	64	2.70	<0.0001	3	17.4	<0.0001	3
ABUND* COST*CURR	64	21.1	<0.0001	22	649	<0.0001	57
FRAG* COST*CURR	32	1.94	0.001	1	99.3	<0.0001	5
ABUND*FRAG*COST*CURR	128	0.38	1.00	N/A	5.77	<0.0001	1
Residuals	3645						

Chapter 6. Movement-biased threats to extinction risk in marine benthic fish: A comparative analysis

6.1 Summary

Increasingly, marine conservation has focused on identifying particularly vulnerable marine species through life history, ecological, or behavioural proxies, and then using this information to prioritize conservation efforts. The capability and extent of individual adult movement has been linked to vulnerability in some terrestrial animals but such a link has not been examined in marine species. Individual movement (i.e., capability, extent, and frequency) is likely to influence a marine fish's exposure to and ability to escape from threats, but such relationships depend on the nature and scale of movement and the type of threat. In this chapter, I used published data to test whether there is a relationship between indices of individual movement (aspect ratio, home range size, or frequent long distance movement) and species' vulnerability (extinction risk, as gleaned from the IUCN Red List) among marine benthic fish species. I also tested whether the importance of mobility on species' vulnerability depended on the dominant threat type (fishing or habitat degradation). I discerned that only the broadest scale movement metric (frequent long distance movement) is related to extinction risk, and that this relationship depends on the threat to which species are exposed: among species subject to direct exploitation, those that migrate or disperse beyond home ranges after initial settlement are at greater extinction risk than those that do not. However, the converse is true among species threatened by habitat degradation. When vulnerability information is unavailable, my results could help guide data collection towards species that may be of high extinction risk because of their movement (or lack thereof). Such

prioritization is of particular importance for marine organisms since so many species are Data Deficient or have yet to be assessed on the IUCN Red List.

6.2 Introduction

When direct information on vulnerability is limited, biological correlates of extinction risk can be used to identify particularly vulnerable marine species (Dulvy *et al.* 2003, Dulvy *et al.* 2004, Reynolds *et al.* 2005a, Olden *et al.* 2007, Hutchings *et al.* 2012). Claims that marine species cannot go extinct because of their high fecundity and large dispersal capabilities are proving incorrect (Reynolds *et al.* 2005a). Recent evidence suggests that aquatic species are as vulnerable to extinction as terrestrial animals (Dulvy *et al.* 2003), if not more so (Jenkins 2003). Unfortunately, there is limited information available to assess the vulnerability of most described marine fishes (Vié *et al.* 2009). However, among fishes with sufficient data, there seem to be relationships between vulnerability and certain life history, ecological, and behavioural traits; large size, late maturity, high trophic level, slow growth, demersal behaviour, and longevity all increase the risk of population depletion in marine fishes (reviewed in Reynolds *et al.* 2005a). Such traits could be used as proxies for extinction risk to help identify and prioritize conservation efforts towards species in need of protection.

Movement characteristics of individuals have been linked to vulnerability in some terrestrial animals but such a link has not been examined in marine species. Bat species that are less capable flyers (as indicated by smaller wing aspect ratios: wingspan squared divided by wing area) are at greater risk of extinction (Jones *et al.* 2003), and primates with larger extents of normal movement (i.e., larger home ranges) are more vulnerable to anthropogenic threats

(Harcourt 1998). However, the greater permeability of marine environments and mobility of marine species (Carr *et al.* 2003) makes it difficult to extrapolate from terrestrial results. The only spatial trait that has been linked to vulnerability in marine animals is species range (i.e., species with larger ranges are less vulnerable; Hawkins *et al.* 2000). However, species range depends not only on the movement of individuals but also on the number and spread of individuals (i.e., population size and distribution; Lester *et al.* 2007).

Individual movement (i.e., capability, extent, and/or frequency) is likely to influence a marine fish's exposure to and ability to escape from threats such as habitat degradation. Animals survive detrimental threats in one of two ways: acclimatizing or escaping. All else being equal, when unable to acclimatize, species with individuals capable of moving beyond a threat should be more successful than species with less mobile individuals (de Juan and Demestre 2012). Fish that have larger extents of normal movement may be more capable of escaping threats or may be less exposed if threats affect only a portion of their home range. However, a larger home range may also be indicative that larger areas are needed to acquire resources for survival, growth, and/or reproduction. Fish requiring a larger area could be more vulnerable as it is more likely that a threat will reach at least part of the area needed. Species with individuals that frequently move beyond home ranges (through migration or otherwise) could escape short-term threats that affect those home ranges. However, long distance movements crossing multiple habitats could also expose fish to a greater number of potential threats.

The degree to which mobility affects vulnerability to extinction may depend on the type of threat. In general, the greatest threat to marine fish is exploitation, followed by habitat loss and/or degradation, pollution, and invasive species (Jackson *et al.* 2001, Reynolds *et al.* 2005a, Kappel 2005). These threats can affect fish in different ways in relation to body size. For example, exploitation impacts larger fish more than smaller fish while habitat degradation and invasive species do not (Olden *et al.* 2007).

In this chapter I tested whether individual movement correlates with extinction risk among marine benthic fish. I focused on bottom-dwelling species because they are more likely than their pelagic counterparts to be exposed to exploitation and habitat degradation - the two main threats to marine species (Hutchings 2000, Hutchings 2001, Stobutzki *et al.* 2001, Denney *et al.* 2002). I collated published data on three metrics that collectively capture capability, extent, and frequency of movement respectively: fin aspect ratio (fin height squared divided by fin area, as a proxy for swimming capability), home range size, and whether a species moves beyond its home range frequently or not. I focused on species assessed on the IUCN Red List and used Red List Categories as relative indicators of extinction risk. Since mobility could either have a positive or negative effect on extinction risk (as described above), I used an empirical survey approach to develop hypotheses rather than speculating with a priori ones (Peters 1991). I first tested whether each movement metric was related to extinction risk regardless of threat type. I then tested whether any such relationships differ among fish threatened by exploitation and those threatened by habitat degradation.

6.3 Methods

6.3.1 Data

Vulnerability to extinction risk

For information on the vulnerability of fish species I relied on the IUCN Red List (IUCN 2012). The IUCN Red List assigns each evaluated species to one of eight categories, using the best data available and standard, rigorous criteria: Data Deficient (DD), Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), Critically Endangered (CR), Extinct in the Wild (EW), or Extinct (EX). I compared mobility across species in each category other than Data Deficient, where extinction risk is uncertain. Throughout my analyses I treated the extinction risk data as an ordinal response variable since I could assess only relative levels of extinction risk from the Red List categories. I ranked the Red List categories from low to high extinction risk as follows: LC = 1, NT = 2, VU = 3, EN = 4, CR = 5, EW = 6, EX = 7. Since my response variable was ordinal, I used non-parametric comparisons of movement and extinction risk throughout (Mooers *et al.* 2008).

I focused my search of the IUCN database on coastal, benthic, ray-finned fishes found in marine habitats. I limited my search to coastal benthic fish (i.e., species on the IUCN Red List with a habitat type of “Marine Neritic”) because they are most vulnerable to the multiple threats of fishing and habitat degradation (Hutchings 2000, Hutchings 2001, Stobutzki *et al.* 2001, Denney *et al.* 2002). I further limited my search to ray-finned fishes (Class = Actinopterygii) because they are the most thoroughly assessed fish class, which facilitated phylogenetic comparisons. Since marine and freshwater environments pose different threats to fishes, resulting in different vulnerabilities (Olden *et al.* 2007, Reynolds *et al.* 2005a,

Reynolds *et al.* 2005b), I only included marine fish (i.e., I excluded freshwater, anadromous and catadromous species). I included fish from all oceans (Location = All FAO Marine Areas), and assessments on the IUCN Red List website completed between 1996 and 2011. For species that have been assessed more than once, I used the latest assessment available.

After analyzing all fish (regardless of threat type), I sought to establish whether relationships differed depending on major threat type. I repeated each analysis on two subsets of species, based on their threats: those species threatened only by direct exploitation and, separately, those threatened only by habitat loss/degradation. I used the IUCN Red List's twelve major threat types (IUCN 2012) to distinguish species threatened only by direct exploitation from those threatened only by habitat loss/degradation. I used only one IUCN major threat type (Biological resource use) to designate species threatened by direct exploitation but I assigned a threat type of habitat loss/degradation to species with any of several major threat types that affect habitat (Table 6.1).

Movement metrics

I used FishBase (Froese and Pauly 2012) and published literature to obtain movement data for a subset of marine benthic species identified in my IUCN Red List search. I chose species using a stratified random sampling approach to ensure at least 10% of all species within each fish family were represented. I collected data on three indicators of individual movement: (1) aspect ratio, (2) home range size, and (3) frequency of long distance movement.

1. Aspect ratio

I used aspect ratio as a proxy for swimming ability. The size and shape of the fin providing propulsion governs how much water can be displaced for forward momentum, and is thus an indicator of swimming capability. Fin aspect ratio is calculated as fin height squared divided by fin surface area (Pauly 1989, Sambilay 1990, Fulton *et al.* 2005). Fish with larger aspect ratios tend to have higher metabolic rates (Pauly 1989), and swim faster (Sambilay 1990). I initially searched for aspect ratio data for each species on FishBase. When it was unavailable on FishBase, I calculated aspect ratio of the main propulsive fin from photographs using image processing software (Image J; Abramoff 2004).

2. Home range size (m²)

I used home range size as an indicator of the extent of normal movement in fish. An animal's home range is the area where it moves on a daily basis, excluding dispersal or migratory movements (Burt 1943). Although there are many ways of measuring home range size (e.g., Kernel methods: Worton 1989; Minimum convex polygons: Burgman and Fox 2003; Convex-hull: Getz and Wilmers 2004), they all provide a relative estimate of the routine movement of individuals. I searched published literature databases (e.g., Web of Science and Google Scholar) using each species name and "home range" and included all measures of home range. If several estimates were available, I calculated a mean.

3. Frequency of long distance movement (infrequent/frequent)

I identified species that are known to move beyond home ranges frequently (at least once per year), and those that are known to stay within home ranges for most of their lives (except

perhaps juvenile dispersal), as a coarse metric for frequency of long distance movement. Some marine fish remain in home ranges after an initial longer dispersal (Sale 1991), while others disperse or migrate beyond home ranges more regularly, often to spawn (McKeown 1984, Hinch *et al.* 2006). I searched published literature databases using the species name and variants of "migration" and "dispersal" to find evidence of how frequently a fish species moves beyond their home ranges. Although most of what I found referred to "migration", it is difficult to know what that means because some definitions of migration are very general while others include a list of requirements which must be met, only one of which is movement beyond normal home ranges (McKeown 1984, Hinch *et al.* 2006). To remain consistent, I categorized species as "frequent long distance movers" if there was evidence of movement beyond home ranges (daily movements) at least once per year and "infrequent long distance movers" if there was evidence to suggest that they do not move beyond home ranges once settled as adults.

I considered including swim speed and swimming mode (as in Lindsay 1978) as additional metrics of movement but ultimately chose not to because (a) too few data were available, and (b) both are somewhat captured by aspect ratio. While swim speed is a more direct measure of swimming capability than aspect ratio, I was able to find swim speed data for only one coastal benthic species on the IUCN Red List. Nevertheless, aspect ratio is a reasonable proxy for swim speed since the two are correlated (Sambily 1990). Swimming modes (e.g., anguilliform, subcarangiform, carangiform) are categorized based on the proportion of undulation vs. oscillation and which fin(s) are used for propulsion (Lindsay 1978). Swimming modes could be assigned to many of the species identified in my IUCN Red List

search but it is somewhat subjective, as is the ranking of swimming modes in order of swimming capability. Furthermore, a key variable in assigning swimming mode is the fin shape (Lindsay 1978), which is partly captured using aspect ratio.

6.3.2 Analyses of extinction risk vs. movement

Since body size is related to vulnerability in marine fishes (Reynolds *et al.* 2005a, Olden *et al.* 2007) I used residual values, in addition to uncorrected metrics, to control for body size in my analyses. For body size of each species I obtained maximum length data from FishBase. In some cases these were standard lengths and in others they were total lengths. All three of the movement metrics were related to body size. Longer fish have larger aspect ratios (Spearman rank $r = 0.167$, $P = 0.0021$), and larger home ranges (Spearman rank $r = 0.704$, $P < 0.0001$). Fish that make frequent long distance movements are also generally longer (Mann-Whitney $U = 1058$, $P < 0.0001$). To correct for body size, I used the standardized residuals from the linear (aspect ratio and home range) or logistic (frequent long distance movement) regression in analyses of movement and extinction risk. For the two continuous variables (aspect ratio and home range) the residuals are body-size-corrected versions of the original metrics. However, for the binary variable (frequency of long distance movement) the residuals are continuous variables that represent predictions of the probability that a fish will move long distances given their body size rather than the discrete, original metric (frequent or infrequent long distance movement). For clarity, I will refer to this latter “body-size-corrected” metric as the probability of long distance movement.

I analysed relationships between movement and extinction risk first using the raw species data (i.e., treating each species as an independent data point), which allowed me to use all species in the analysis. I tested whether there was a relationship between either aspect ratio or home range (the two continuous metrics) and extinction risk using Spearman rank correlations. I compared extinction risk between infrequent and frequent long distance movers using Mann-Whitney U-tests. For each of the body-size-corrected metrics, I used Spearman rank correlations to relate movement to extinction risk.

In addition to the raw species analyses, I compared movement and extinction risk using independent contrasts to minimize phylogenetic non-independence (Harcourt 1998, Purvis *et al.* 2000, Dulvy and Reynolds 2002, Keane *et al.* 2005). This matched pairs approach involved contrasting pairs of species that were closely related but differed in extinction risk (Reynolds *et al.* 2005b). Because not all species could be paired with another closely related one, this analysis reduced the amount of data I could use. However, independent contrasts account for any pseudoreplication caused by closely related species having similar life history, ecology and behaviour (Purvis 2008). Phylogeny has not been resolved for many of the Actinopterygian clades I consider here; therefore, I chose pairs based on taxonomy rather than phylogenetic trees (*sensu* Reynolds *et al.* 2005b). I chose species pairs from the same genus when possible ($n = 31$ pairs), and from the same family otherwise ($n = 36$ pairs). Most pairs comprised a species of least concern (LC) and a species in one of the other extinction risk categories. I tested whether differences in continuous movement metrics (aspect ratio, home range, their body-size-corrected metrics, and probability of long distance movement) are correlated with differences in extinction risk between pairs using Spearman rank

correlations. I tested whether extinction risk differs between infrequent and frequent long distance moving species (uncorrected frequent long distance movement data) within pairs using Wilcoxon matched pairs tests.

6.4 Results

6.4.1 General data trends

I found 1865 marine benthic fish species on the IUCN Red List that fell into one of five extinction risk categories (LC, NT, VU, EN, or CR). None were classified as extinct in the wild or extinct. Most were classified as Least Concern (1680 spp.), followed by Vulnerable (99 spp.), Near Threatened (60 spp.), Endangered (15 spp.), and Critically Endangered (11 spp.). More species were threatened by fishing (658 spp.) than habitat degradation (224 spp.), although some of these were threatened by both (131 spp.). A further 439 marine benthic fish species were classified as Data Deficient and thus were uninformative for my analyses.

I found individual movement and body size data for a subset of 367 species found on the Red List. Of the species with mobility data, 97 were threatened only by fishing while 34 were threatened only by habitat degradation (41 spp. were threatened by both and 195 spp. by neither). Of the three mobility metrics, I was able to collect most data on aspect ratio (349 spp.), less information about the frequency long distance movement (133 spp.), and little home range data (26 spp.). Aspect ratios ranged from 0 (e.g., *Chiloconger dentatus*, a conger eel, which moves via undulations of its body rather than a fin) to 4.42 (*Caranx vinctus*, a jack), with a median of 1.39. Home range sizes ranged from 26.5 m² (*Halichoeres poeyi*, a wrasse) to 42500 m² (*Achoerodus gouldii*, another wrasse), with a median of 1675 m². I

identified more species as frequent long distance movers (80 spp.) than infrequent long distance movers (51 spp.).

6.4.2 Movement and extinction risk

Frequency of long distance movement was related to extinction risk in marine benthic fish, but only after considering whether a species was threatened by direct exploitation or habitat degradation (Table 6.2). There was no general association (i.e., before separating species by threat type) between extinction risk and frequency of long distance movement, regardless of whether I compared infrequent and frequent long distance movers or the probability of long distance movement (i.e., accounting for body size), using all species or phylogenetic pairs. However, there were opposite relationships between frequency of long distance movement and extinction risk for species threatened by fishing versus those threatened by habitat degradation (Fig. 6.1). When threatened by fishing, species that move beyond their home ranges at least once per year were at greater extinction risk; however, when threatened by habitat degradation species that tend to stay within home ranges after initial settlement were at greater risk. Independent contrasts by threat type were not possible because there was so little information on long distance movement for species pairs only threatened by fishing ($n = 2$) or habitat degradation ($n = 0$).

There was no relationship between aspect ratio or home range size and extinction risk, regardless of the type of analysis or threat type (Table 6.2). Neither aspect ratio nor home range size was correlated with extinction risk using the species data or independent contrasts. Unlike frequency of long distance movement, there was no relationship even when I

separated species by threat type. I had insufficient data to test the relationship between home range and extinction risk within species pairs threatened by habitat degradation.

6.5 Discussion

My study is the first to directly test whether individual movement can act as a proxy for vulnerability to extinction risk in marine fish. Such proxies could be used to identify species of conservation concern before they become endangered. Past studies have shown that larger, longer-lived, late-maturing, slow growing, demersal marine fish (Reynolds *et al.* 2005a), that spawn infrequently (Jager *et al.* 2008), are at greater risk of extinction. I have shown that whether a fish moves beyond home ranges after initial settlement (to disperse or migrate) can also influence extinction risk.

My results support past studies that highlight the importance of knowing what threatens an animal when judging its vulnerability to extinction risk (Owens and Bennett 2000, Olden *et al.* 2007). The relationship between fish size and extinction risk depends on the type of threat: larger fish are more vulnerable than smaller fish to direct exploitation but not to habitat degradation (Olden *et al.* 2007). Similarly, I found that the relationship between frequency of long distance movement and extinction risk differed for marine fish imperiled by different threats. Fishing seems to affect highly mobile species (i.e., those that regularly disperse or migrate beyond established home ranges) more than sedentary ones (i.e., those that remain within home ranges as adults); whereas habitat degradation seems to affect sedentary species more. While my results for fished species are similar to those found for body size (Olden *et al.* 2007), and I found a relationship between body size and whether a

fish moves long distances (beyond home ranges) as an adult, relationships between long distance movement and extinction risk persisted even after attempting to account for body size. Even though the residuals I used to account for body size actually represent a slightly different metric than the original one, the fact that both metrics identified the same relationships suggests that frequency of long distance movement is a biological correlate of extinction risk irrespective of body size.

The different effects of fishing and habitat exploitation could be due to the relative spatial and temporal scales of the two threat types. Fishing and other forms of exploitation are widespread and can be at multiple spatial and temporal scales (e.g., inshore artisanal fishers vs. offshore industrial fleets). In some cases, species that move long distances may actually be leaving relatively protected areas (e.g., marine protected areas), exposing themselves to greater fishing pressure along dispersal or migration routes. Some threat types associated with habitat loss and degradation are also widespread (e.g., pollution), but the associated effects can generally be avoided by moving to less hazardous areas nearby.

To my knowledge, there have not been any studies like this one that directly compare frequency of long distance movement (dispersal or migration) and extinction risk in terrestrial animals or freshwater fishes, though evidence suggests that non-migratory birds and butterflies are more vulnerable to extinction than migratory ones. A greater percentage of non-migratory birds are threatened or near-threatened (23%) compared with migratory birds (11%; Kirby *et al.* 2008), largely as a result of habitat loss or degradation (BirdLife International 2004). Similarly, non-migratory British butterflies threatened by habitat

loss/degradation and climate change have declined more than migratory ones (Warren *et al.* 2001). These observations for birds and butterflies echo my results for fishes threatened by habitat degradation.

Hypothesized mechanisms for increased extinction risk in non-migratory birds and butterflies may offer some insight into drivers behind my results for fishes, especially if the majority of species I identified as long distance movers were actually true migrants (as in Hinch *et al.* 2006). Four hypotheses have been posited for why non-migratory species seem to be at greater extinction risk: 1) non-migratory birds have smaller species ranges than migratory birds so smaller scale threats can affect the entire species (Kirby *et al.* 2008); 2) population declines are easier to recognize in non-migratory birds than in migratory birds (especially given their larger species ranges) so they only appear to be at great extinction risk (Kirby *et al.* 2008); 3) migration has evolved as an adaptive mechanism to cope with seasonally unfavourable conditions so non-migratory birds are less flexible in responding to habitat changes than migratory birds (Kirby *et al.* 2008); 4) non-migratory butterflies tend to be habitat specialists, which could make them less flexible in responding to habitat change (Warren *et al.* 2001). The first two hypotheses should be equally important to fish threatened by exploitation or habitat degradation. If migratory fish gain resilience by virtue of having large species ranges, this resilience should exist for all threats. Likewise, inaccuracies of vulnerability in migratory species are problematic irrespective of the threat. In contrast, the last two hypotheses are specific to habitat degradation and imply little about vulnerability to direct exploitation in absence of environmental change. These latter two hypotheses allow for

my differential results for fishing and habitat degradation and may be worth further exploration.

Unfortunately, it is currently difficult to test hypotheses of why long distance movement is related to extinction risk in marine fishes because of the scarcity of movement data for most fish species on the Red List. The dearth of movement data in marine fishes meant that I had small sample sizes for home range and migration analyses, even when using my full dataset. Sample sizes declined further when I disaggregated the data by threat type, making it impossible to test whether home range size and extinction risk are related among species threatened by habitat loss/degradation. Although phylogenetic comparisons seemed most appropriate for my approach (Harvey and Pagel 1991, Purvis 2008), the lack of movement data was exacerbated by similarities among closely related species pairs, making such analyses difficult. Further disaggregation to test whether frequency of long distance movement is related to extinction risk through other biological traits (e.g., habitat specificity) would be impossible because of these already small sample sizes.

When movement data are available, phylogenetic conservatism in frequency of long distance movement may actually help in identification and conservation prioritization of particularly vulnerable marine fish species. Among fish families that had information on the frequency of long distance movement for more than one species, only 24% had at least one species that moved long distances and at least one species that did not. If we can assume that most closely related species share this movement trait (i.e., either move long distances or do not) it could help in prioritizing data collection towards species most likely in need of protection. Sister

taxa of mobile species (i.e., those that migrate or disperse) should be prioritized if they are being fished whereas sister taxa of sedentary species (i.e., those that rarely move beyond home ranges) should be prioritized if threatened by habitat loss/degradation. Such prioritization is of particular importance for marine species given that there are so many Data Deficient and unassessed species compared with birds or mammals. Among species assessed on the IUCN Red List, 439 marine benthic fish species (24%) were Data Deficient. In comparison, only 63 bird species were data deficient in 2010 (Butchart and Bird 2010). Furthermore, unlike birds and mammals, most marine species have not been assessed (Vié *et al.* 2009).

My study was a global scale analysis and may only pick up global (or at least large) scale phenomena, which might explain why only my broadest metric was related to extinction risk. The three movement metrics I used are on different spatial and temporal scales. Dispersal and migration are generally on broader spatial scales than home range movements and longer temporal scales than aspect ratio (as a proxy for swimming speed/capability). Long distance and long duration movements have the potential to help fish escape localized, short-term threats and/or connect distant populations. Frequency of long distance movement could be related to species extinction risk because it is a broader scale metric than either aspect ratio or home range size. If there were enough data on regional scales to examine the relationship between movement and extinction risk, perhaps finer scale metrics like home range and aspect ratio would be recognized.

Table 6.1 IUCN major threat categories (IUCN 2012), indicating which were included in analyses of marine benthic fish species threatened by direct exploitation or habitat loss/degradation.

IUCN major threat #	IUCN major threat category	Direct exploitation	Habitat loss/degradation
1	Residential and commercial development		✓
2	Agriculture and aquaculture		✓
3	Energy production and mining		✓
4	Transportation and service corridors		✓
5	Biological resource use	✓	
6	Human intrusions and disturbance		✓
7	Natural system modifications		✓
8	Invasive and other problematic species and genes		
9	Pollution		✓
10	Geological events		
11	Climate change and severe weather		
12	Other options		

Table 6.2 Results of species comparisons and matched pair analyses, testing whether individual movement metrics (aspect ratio, home range, or frequency of long distance movement) are related to extinction risk for marine benthic fish species threatened by all threat types, fishing, or habitat loss/degradation, as defined on the IUCN Red List (IUCN 2012).

Metric	Analysis	Body-size corrected?	Threatened by?	Test used	n	Test statistic	P-value
Aspect ratio	Species comparisons	No	All threat types	Spearman rank	349	0.0118	0.827
			Fishing		96	1.62×10^{-5}	1.00
			Habitat degradation		34	-0.284	0.104
		Yes	All threat types		339	0.0102	0.851
			Fishing		95	-0.0401	0.699
			Habitat degradation		31	-0.295	0.107
	Matched pairs	No	All threat types		93	-0.0543	0.605
			Fishing		30	0.0615	0.747
			Habitat degradation		17	0.0276	0.916
		Yes	All threat types		93	-0.0705	0.502
			Fishing		30	0.0474	0.804
			Habitat degradation		17	0.0276	0.916

Metric	Analysis	Body-size corrected?	Threatened by?	Test used	n	Test statistic	P-value
Home range	Species comparisons	No	All threat types	Spearman rank	26	0.348	0.0814
			Fishing		14	0.464	0.0948
			Habitat degradation		2	Insufficient data	
		Yes	All threat types		26	-0.134	0.515
			Fishing		14	0.0411	0.889
			Habitat degradation		2	Insufficient data	
	Matched pairs	No	All threat types		8	0.482	0.243
			Fishing		4	0.775	0.333
			Habitat degradation		0	Insufficient data	
		Yes	All threat types		8	0.148	0.752
			Fishing		4	0.258	0.750
			Habitat degradation		0	Insufficient data	
Frequency of long distance movement	Species comparisons	No	All threat types	Mann-Whitney	51/80 ^a	1679	0.0507
			Fishing		25/24 ^a	142	0.0004*

Metric	Analysis	Body-size corrected?	Threatened by?	Test used	n	Test statistic	P-value
Frequency of long distance movement	Species comparisons	No	Habitat degradation	Mann-Whitney	3/7 ^a	0	0.0144*
		Yes ^b	All threat types	Spearman rank	131	-0.111	0.208
			Fishing		49	0.292	0.0419*
	Habitat degradation	10	-0.892		0.0011*		
	Matched pairs	No	All threat types	Wilcoxon matched pairs	6	-18	0.0708
			Fishing		2	Insufficient data	
			Habitat degradation		0	Insufficient data	
		Yes ^b	All threat types	Spearman rank	6	-0.820	0.0583
			Fishing		2	Insufficient data	
			Habitat degradation		0	Insufficient data	

*Significant at an alpha of 0.05

^aSample sizes for species with infrequent and frequent long distance movement respectively

^bBody-size-corrected metric actually represents a probability of long distance movement given a species body size

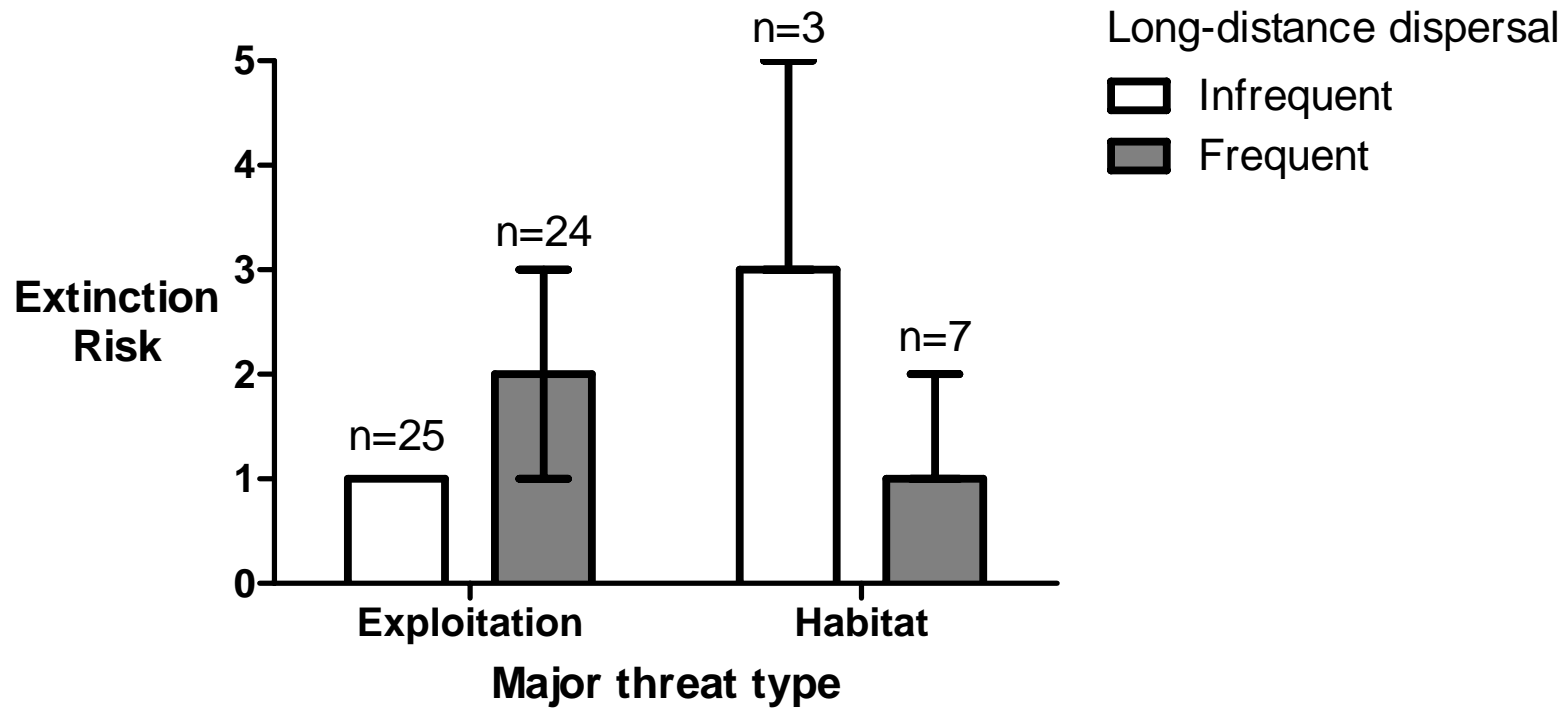


Figure 6.1 Extinction risk (median with interquartile range) for marine benthic fish species that move long distances (beyond home ranges) either infrequently (settling after an initial dispersal) or frequently (more than once per year), and are threatened by direct exploitation or habitat degradation. Extinction risk was coded using Red List categories ordered from low to high extinction risk as follows: LC = 1, NT = 2, VU = 3, EN = 4, CR = 5, EW = 6, EX = 7.

Chapter 7. General discussion and conclusions

7.1 Overview

My thesis identified general relationships between movement and vulnerability in marine fishes, which could help prioritize conservation, while raising further questions about the additional effects of habitat specialization and environmental variability. In my first few data chapters (Chapters 2, 3, and 4), I focused on a sedentary seahorse species, *H. guttulatus*, because of a need to understand how limited movement in seahorses contributes to their vulnerability to extinction (Curtis 2004). Such sedentary fishes could be at greater extinction risk if their limited movement is associated with habitat specialization (Dulvy *et al.* 2003), or a reduced capability of moving beyond home ranges to escape threats (Curtis 2004).

However, the dynamic seagrass habitats of the Ria Formosa lagoon could promote greater flexibility in habitat use and/or movement in *H. guttulatus* than suggested by their sedentary nature. In my latter data chapters, I tested, across species, whether individual movement could be associated with differences in either habitat connectivity (Chapter 5), or vulnerability to extinction risk (Chapter 6) among sedentary and more mobile fishes. My major findings were as follows:

- I determined that *H. guttulatus* habitat associations were not necessarily stable over time or space (Chapter 2). The variability in habitat relationships I found among seahorses (Chapter 4) may indicate some flexibility in the population to cope with habitat change.
- I found that displaced *H. guttulatus* (tracked using acoustic tags tested in Chapter 3) move far beyond typical home range distances and move towards familiar depths and

current strengths (Chapter 4). These results suggest individuals might be capable of escaping at least small-scale changes, and may need to do so if depths or currents change.

- I developed a model that predicted habitat loss and fragmentation should have a greater effect on habitat connectivity of sedentary fish than on more mobile fish (Chapter 5), suggesting that sedentary fish may be more sensitive to habitat loss and fragmentation.
- I established that, among marine benthic fish species threatened by habitat degradation, sedentary fish (those that remain within their home ranges as adults) seem to be at greater extinction risk than mobile species (those that migrate or disperse). Conversely, among species threatened by exploitation, mobile species seem to be at greater risk (Chapter 6).

In the following sections, I integrate the major results from my five data chapters and relate them to other work in ecology, behaviour, and conservation. I begin by explaining how my collective results address each of my research questions. I then discuss some of the strengths and limitations of my dissertation research. I end with my thoughts on the broader implications of this research and some suggestions for future research directions.

7.2 Major findings and implications

In this section I return to the three research questions I posed in my introductory chapter. Fish can survive habitat loss and degradation either by acclimatizing to the new conditions or escaping to a new location with better conditions. If neither is possible, a species will be

vulnerable to extinction. I quantified habitat associations, movement, and vulnerability, respectively, to address how a sedentary fish might respond to habitat loss and degradation: acclimatizing, escaping or dying.

7.2.1 Habitat associations are flexible in *H. guttulatus* populations but not for individuals

The wide range of habitats used by *H. guttulatus* in the Ria Formosa lagoon could afford their populations some flexibility in coping with variability and habitat loss/degradation. Marine habitat specialists may be prone to extirpation or extinction. Among 133 known marine extirpations or extinctions, 27 were linked to habitat specialization (Dulvy *et al.* 2003). However, *H. guttulatus* populations in the Ria Formosa lagoon seem to be habitat generalists. None of the environmental characteristics I measured was consistently associated with population changes (Chapter 2), densities (Chapter 2), presence (Chapter 2) and movement (Chapter 4). Furthermore, the habitat associations I found differed from earlier surveys (Curtis and Vincent 2005). In addition to the many stationary holdfasts used by these fish (Curtis and Vincent 2005), I found a large number of seahorses wrapped around mobile purple sea urchins (*Paracentrotus lividus*). This association could provide important habitat and protect individuals from predators when other cover is unavailable. Habitat generalization should be favoured in dynamic environments (Levins 1968) and could help *H. guttulatus* cope with the natural variability of the Ria Formosa lagoon (Cunha *et al.* 2011), as well as any unpredictable change due to habitat loss and degradation (Owens and Bennett 2000, Harcourt *et al.* 2002, Krauss *et al.* 2003).

Differences in habitat use across individuals could mean individuals find it difficult to acclimatize to change but could also increase population flexibility (Svanbäck *et al.* 2008). If individual *H. guttulatus* were complete habitat generalists, I would have expected displaced individuals to either stay where they were released or move in a random direction with respect to environmental characteristics (i.e. any location is suitable). Instead, tagged *H. guttulatus* moved towards locations with similar depth and current speed to where they were found (Chapter 4). This variation among individuals could have masked any habitat associations in my UVC surveys. Intra-population variability in behaviour and habitat use has been found in other marine fishes (Hammerschlag-Peyer and Layman 2010, Abrantes and Barnett 2011), terrestrial mammals (Edwards *et al.* 2011), birds (Shanahan *et al.* 2011), and reptiles (Rosenblatt and Heithaus 2011). Such variability can allow for a wider range of habitats to be used (Rosenblatt and Heithaus 2011), ensuring that fine scale habitat changes affect only parts of the population. However, those parts of the population that are affected may still need to move, if changes exceed individual tolerances.

7.2.2 *H. guttulatus* can move further than their small home ranges would suggest

The relatively long-distance movement shown by *H. guttulatus* might help them escape threats such as habitat loss and degradation, when they are unable to acclimatize to new conditions. Displaced *H. guttulatus* travelled an average of ten times the diameter of known home ranges (Chapter 4; based on estimates of home range size by Curtis and Vincent (2006)). Other sedentary fishes have managed to move far beyond what is expected in order to return to home ranges (Hartney 1996, Lowry and Suthers 1998), but *H. guttulatus* movements did not appear to be associated with homing (Chapter 4). While distances moved

by tagged seahorses were impressive in comparison to home ranges, they were still only on magnitudes of tens to hundreds of metres, which may only allow them to escape small-scale habitat change. However, due to constraints in using the newly available technology, I was able to track these fish only for short durations. Longer term tracking may reveal an even greater capacity to escape degrading habitat. In addition to escaping harmful habitat change, seahorses may need to move long distances to re-mate, particularly in exploited populations. Most seahorses are monogamous at least within a breeding season (Foster and Vincent 2004), which reduces the need to repeatedly find mates. However, in overexploited populations seahorses can be widowed. Given their typically patchy distributions (Foster and Vincent 2004) re-mating could require long distance movements in these fishes, the scale of which would depend on the scale of patchiness.

In the short-term, seahorse movements appear to be related to survival (e.g. search for cover), but over time they should move to locate suitable conditions for longer-term processes (e.g. growth and reproduction). When first released, seahorses moved to what seemed to be the first available holdfast, but over time they apparently moved to increasingly familiar conditions. They were often found with another seahorse on the final tracking day (Chapter 4). Longer term tracking would be invaluable in better understanding the drivers of movement.

7.2.3 Sedentary fish are more vulnerable to habitat loss/degradation (but less vulnerable to exploitation) than more mobile fish

Even though *H. guttulatus* shows some capacity to deal with small levels of change, seahorse populations seem prone to drastic population fluctuations and could be more vulnerable to threats such as habitat loss and degradation when those populations decline. Populations of the two European seahorse species in the Ria Formosa lagoon were once among the densest known in the world (Foster and Vincent 2004, Curtis and Vincent 2005). However, by 2008/2009 there were 94% fewer *H. guttulatus* (and 76% fewer sympatric *H. hippocampus*) than recorded in 2001/2002 (Chapter 2). This decline was not the first instance of a seahorse decline in the apparent absence of exploitation or obvious environmental change. In the Derwent estuary, Australia, populations of the big-bellied seahorse, *H. abdominalis* declined 79 to 98% over 3.5 years (Martin-Smith and Vincent 2005). Although those populations have since increased (K. Martin-Smith, personal communication), it may be particularly difficult for many seahorse species to recover from declines if their monogamous mating pattern, their slowness to re-mate when widowed, and their reduced brood sizes with new partners (Foster and Vincent, 2004) generate Allee effects. In general, lower density populations are more vulnerable to demographic or environmental stochasticity (Fagan *et al.* 2001). Declines, and subsequent increased vulnerabilities, could result in the extinction of less wide ranging species than *H. guttulatus* or *H. hippocampus* (e.g., *H. capensis*, which is found only in three South African estuaries; Czembor and Bell 2012).

If Data Deficient marine fish species are known to be threatened by either habitat loss/degradation or exploitation, the nature of a species' mobility might serve as a proxy for

extinction risk. My comparative analysis (Chapter 6) suggests that conservation efforts should be prioritized towards sedentary species (those that remain within their home ranges as adults) when they are affected by habitat loss or degradation, and mobile species (those that disperse or migrate as adults) when they are affected by exploitation. This proxy can now be added to the growing list of biological correlates for marine fish; large size, long lifespan, late maturity, slow growth, demersal behaviour, and infrequent spawning have all been associated with high extinction risk (Reynolds *et al.* 2005a, Jager *et al.* 2008). Multiple proxies of extinction risk can be used to prioritize data collection towards – and action for – species that are most likely to be of conservation concern. Such proxies could be particularly useful for marine fish conservation because the conservation status of thousands of marine fish species have yet to be assessed (Vié *et al.* 2009). Limited data availability meant that I was unable to explore further the reasons why sedentary fish might be more vulnerable to habitat loss and degradation than more mobile fish. However, my seascape models (Chapter 5) predicted that habitat loss and fragmentation should have a greater effect on habitat connectivity of sedentary fish than of more mobile fish. Lowered habitat connectivity could lead to increased vulnerability in these species. Empirical testing of my predictions could reveal whether sedentary fish are more sensitive to habitat change in reality.

Marine protected areas (MPAs) are effective tools to protect sedentary fish from fishing, but my results suggest the possibility that they might be most needed for protection of mobile fish. MPAs are the most highly touted tools for protection of marine life from exploitation (Jones 2002). If sited around home ranges of sedentary fish, MPAs should be highly effective at protecting their populations from fisheries (DeMartini 1993, Kramer and Chapman 1999).

However, my comparative analyses indicate that, in general, there is a greater need to protect mobile fish from fisheries (Chapter 6). Most MPAs have been quite small compared to the distances travelled by migratory and dispersing fish, but recently there has been an increase in giant marine protected areas ($> 100,000 \text{ km}^2$), which should protect even highly mobile tuna and shark species (Jones 2011). Instead of protecting very large areas, another approach would be to create networks of MPAs, at key locations for migratory fish, similar to the networks of important birding areas used for migratory land- and waterbirds (Kirby *et al.* 2008).

7.3 Strengths and limitations of the dissertation research

Having addressed my three original research questions, I now turn to discussing strengths of my dissertation and some challenges I encountered. The latter may assist others considering similar studies.

A major strength of my dissertation is the breadth of approaches and analytical techniques I employed to shed new light on the habitat use, movement, and vulnerability of seahorses, their relatives, and other sedentary fishes. I conducted UVC surveys to evaluate the habitat associations of *H. guttulatus* with presence-absence and density data at several spatial and temporal scales (Chapter 2). Collecting data on multiple scales could prevent future problems like the ones I encountered in comparing my data to previous surveys, in light of drastic population declines. Such declines are a reality when working with species of conservation concern and should be anticipated when planning field studies. Another approach I took to evaluate habitat associations was displacement experiments (Chapter 4). The advantage of

using displacement experiments was that I could assess habitat use on an individual basis, with each displaced seahorse providing data on relative suitability of several environments. It was only through these experiments that I was able to recognize that individuals were moving towards specific habitat characteristics. In addition to field techniques, I designed a seascape model using techniques borrowed from landscape ecology (Chapter 5) to predict how fish of differing mobility might be affected by habitat loss and fragmentation. I then used a broad-scale comparative analysis (Chapter 6) to test general relationships between movement and vulnerability to specific threats.

Each of my approaches involved some challenges, from complications associated with collecting data underwater to dealing with data limitations for marine fishes in general. In my field-work, I was faced with strong currents, high turbidity, strong winds, and large waves, limiting the time that could be spent underwater. I was able to complete surveys during that time, but tracking seahorses was problematic. Both my seascape modeling and comparative analysis suffered from limitations in available data. I was forced to parameterize cost in my model, making inferences around data from a single damselfish species (*S. diencaeus*) because that was all that was available (Turgeon *et al.* 2010). It would be preferable to use empirical data for all three simulated fish to test such general trends. My comparative analysis was based on data from 367 marine fish species, but little information was available for each movement metric. For example, I was only able to find home range data for 26 species. The limited data I found reflects the global dearth of biological knowledge available for marine fish. Only approximately 11% of described fish species have been assessed on the IUCN Red List as compared with nearly 100% of mammals and birds (Vié *et al.* 2009,

Zamin *et al.* 2010), and most of those fish data are for exploited species (Reynolds *et al.* 2005a). It is difficult to know whether data from such a small, potentially biased proportion of species is representative of all fish species. The expansion of this database will be important to making more informed conservation decisions.

Technology may overcome some of the hurdles of collecting data underwater, but it is still in its infancy. Advances in scuba and acoustic tagging technologies were important for my research, but even smaller tags would have been preferable for my displacement experiments. Tagged *H. guttulatus* behaved no differently than untagged fish in aquaria, but there were deaths of tagged individuals when released in the wild. When smaller tags become available, the use of a hydrophone array would reduce the main problems I encountered with active tracking of tagged *H. guttulatus*. However, such technology would not support research in the Ria Formosa lagoon, because of the shallow depths and potential for fouling. Unfortunately, these new technologies are prohibitively expensive, especially for conservation organizations with budgets already stretched between costs of collecting data to inform decisions and costs of implementing conservation plans. Fortunately, there are cheaper, lower-tech options for marking individuals (e.g., VIFE), that can be used when active tracking is not necessary (reviewed in Chapter 3).

A final limitation of my research was that, although I used a variety of statistical techniques to detect correlations in habitat use, movement and vulnerability, I could not detect causation. In the short-term, the urgency for conservation justifies rapid action on patterns alone, but some understanding of causation is important for comprehensive remedial action. The

generalized linear models and mixed effects models I used to analyze my survey data indicated that *H. guttulatus* used habitats that were deeper and warmer than uninhabited locations (Chapter 2), but did not indicate whether the fish were there because of those warmer temperatures or water depth. The resemblance matrices I used to analyze movement of individual *H. guttulatus* with respect to habitat indicated that seahorses moved towards locations that were similar in depth and current speed to their original capture locations (Chapter 4), but did not indicate whether they moved to those locations because of those characteristics or some other characteristic correlated with them. Finally, the Spearman rank correlations, Mann-Whitney U-tests, and independent contrasts I used in my comparative analyses indicated that extinction risk differs between sedentary and mobile fish on a broad scale (Chapter 6) but I cannot discount the possibility that there are other factors driving those relationships. To detect causation, manipulative experiments are needed that vary each of the relationships in a predictable way and examine the consequences. It would be difficult to manipulate underwater environments in the wild to test these relationships, but aquarium experiments would enable direct testing of how seahorses respond to specific changes in habitat.

7.4 Future research

Despite some limitations, I was able to shed light on how seahorses and other sedentary fishes might respond to habitat loss/degradation, raising further questions of significance for seahorses, their relatives, other sedentary fish, marine fish more generally, and even perhaps terrestrial organisms.

For seahorses, the big question that remains unanswered from my research is why there were such drastic declines in populations, seemingly without any associated exploitation or measured habitat change. My main hypotheses are that seahorse populations declined in the Ria Formosa because of a reduction in recruitment and/or an environmental change that was not measured. A relatively low-tech approach that could test these hypotheses would be to mark existing populations in the lagoon with VIFE, and monitor individuals over time. VIFE techniques have been used successfully to study population dynamics of seahorses and related syngnathid species for long periods with minimal effect (reviewed in Chapter 3). The use of mark-recapture methods would allow for estimates of both recruitment (immigration) and mortality (death), two of the four demographic rates (in addition to birth and emigration) that drive local population dynamics (Hixon 1998). Juvenile *H. guttulatus* spend approximately eight weeks in the plankton before settling in coastal areas (Boisseau 1967), in which case any new additions to a local population would be recruits (immigrants) rather than births. Although capable of longer distance movement than suspected (Chapter 4), it seems unlikely that *H. guttulatus* population declines would be solely due to adult emigration. However, using colour coded VIFE at each location would determine whether adult seahorses move between locations. Solving the mystery of these declines in unexploited populations is particularly important for exploited seahorse species. Without this knowledge, it is difficult to estimate the true effects of exploitation (O'Donnell 2011).

Beyond seahorses, my research raised questions about how environmental variability and habitat specialization might affect the relationship between movement and vulnerability to threats in marine fishes. In terrestrial insects, there seems to be a close connection between

mobility and specialization (Warren *et al.* 2001, Brouwers and Newton 2009). Theory suggests that less stable (more dynamic) habitats should favour generalists (Levins 1968) and habitat specialists are susceptible to habitat degradation (Brouat *et al.* 2004). Comparisons among and within sedentary and mobile species living in habitats of varying stability could help disentangle interacting relationships among environmental variability, habitat specialization, movement, and vulnerability in marine fishes. There are currently not enough data on fish movement to add habitat specialization as one more level of complexity. However, what data are available can be used to identify candidate marine fish species for each combination of habitat specialization and movement (i.e., sedentary specialists, sedentary generalists, mobile specialists, and mobile generalists). If habitat specialization is conserved among closely related species, as seems to be the case in movement metrics (Chapter 6), focusing data on congeneric or confamilial species could guide data collection for this analysis.

In my broad-scale comparative analysis, I focused on species threatened either by habitat loss/degradation or exploitation, but the relationships I found could add insight into the effects of other significant threats such as invasive species. After fishing and habitat loss/degradation, invasive species are among the greatest threats to marine fishes (Jackson *et al.* 2001, Reynolds *et al.* 2005a, Kappel 2005). However, in my search of the IUCN Red List for marine benthic fish species (Chapter 5), I found only 24 fishes listed with invasive species as a major threat type; an insufficient number to explore extinction risk relationships related to that threat. Based on terrestrial work, though (in which there are relatively more data), I suspect that relationships will largely depend on the type of invasive plant or animal

and the mechanism of threat involved (e.g. introduced predator vs. habitat effects).

Comparisons among terrestrial birds would suggest that an invasive predator would have a greater effect on large birds (similar to exploitation effects) while an invasive organism that limits available habitat would have a greater effect on small birds (similar to effects of habitat loss/degradation) (Owens and Bennett 2000). If those relationships are consistent in marine species, I would expect invasive predators would have a greater effect on mobile fishes while invasive algae (for instance) would have a greater effect on sedentary fishes. To determine whether the effect of invasive species is biased towards sedentary or mobile fish may require further separation of the threat by the mechanism involved.

The key to understanding vulnerability to certain threats in marine fish, particularly broad-scale, gradual ones like climate change, may be in understanding movement of early life stages rather than adult stages. Climate change has been linked to species range shifts (Perry *et al.* 2005), but species range shifts usually occur over multiple generations and involve the movement of larvae. The general consensus has been that most marine fish populations are connected by long distance movements of larvae or other early life stages, travelling on ocean currents (Roberts 1997). That would suggest that adult movement has relatively little importance to population persistence. However, more recent studies have suggested that larvae do not move as far as posited (Almany *et al.* 2007), and post-settlement movement may be as important as juvenile dispersal in some species and locations (Di Franco *et al.* 2012). In the past, it has been difficult to track the movement of small juvenile fish to determine the extent of movement in early life stages, limiting the data available (Mora and Sale 2002). However, new advances in genetics and microchemistry could make it easier to

determine the relative roles of juvenile and adult movement in population movement and survival (Almany *et al.* 2007, Planes *et al.* 2009).

Since most terrestrial animals are mobile only in adult phases it may actually be easier to test relationships between mobility and vulnerability in sedentary terrestrial animals. Similar displacement experiments could be used to induce movement in a normally sedentary terrestrial animal, and test the flexibility of its habitat associations. Furthermore, comparative analyses between mobility and vulnerability in these species could reveal whether the trends I found extend beyond the marine environment. Among marine and terrestrial taxa alike, animals that mature later are at greater extinction risk (Hutchings *et al.* 2012). It would be worth testing whether sedentary species are at greater extinction risk more generally as well. Whereas habitat loss is the second greatest threat to marine life, it is the greatest threat to many terrestrial animals (Vié *et al.* 2009), so could be particularly useful as a proxy for extinction risk in terrestrial species. In at least some taxa, the relationship between movement and habitat specificity needs to be teased apart first (Warren *et al.* 2001), which could be easier in birds and mammals than other taxa because of the greater availability of data (Vié *et al.* 2009, Zamin *et al.* 2010).

7.5 Concluding thoughts

We will never manage to gather an exhaustive and comprehensive compilation of data regarding every organism inhabiting Earth. Perhaps then, it is more important to find the most effective proxies and subsampling methods to determine the best ways to conserve and protect the natural evolution of all the organisms within specific ecosystems. I believe one

useful approach is to take an organism-centric view of the world, to understand the resources and ecosystem use at the scale of the organism themselves. I have applied this technique to my own dissertation research and feel that it has offered great insight into the necessary resources of many sedentary organisms in the ocean. My overarching hope is that research will continue to expand upon this knowledge, allowing all animals to thrive under the best possible conservation practices.

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