Beyond the reef:
How risk of predation shapes fish movement over sand

by

Lily Haines

B.Sc. (Hons., Journalism and Biology), Carleton University, 2016

Thesis Submitted in Partial Fulfillment of the
Requirements for the Degree of
Master of Science

in the
Department of Biological Sciences
Faculty of Science

© Lily Haines 2018
SIMON FRASER UNIVERSITY
Summer 2018

Copyright in this work rests with the author. Please ensure that any reproduction
or re-use is done in accordance with the relevant national copyright legislation.

Approval

Name:	**Lily Haines**
Degree:	**Master of Science**
Title:	**Beyond the reef: How risk of predation shapes fish movement over sand**
Examining Committee:	**Chair:** Eirikur Palsson Assistant Professor
	Isabelle Côté Senior Supervisor Professor
	Lawrence Dill Supervisor Professor Emeritus
	Ronald Ydenberg Examiner Professor
Date Defended/Approved:	June 22, 2018

Ethics Statement

The author, whose name appears on the title page of this work, has obtained, for the research described in this work, either:

a. human research ethics approval from the Simon Fraser University Office of Research Ethics

or

b. advance approval of the animal care protocol from the University Animal Care Committee of Simon Fraser University

or has conducted the research

c. as a co-investigator, collaborator, or research assistant in a research project approved in advance.

A copy of the approval letter has been filed with the Theses Office of the University Library at the time of submission of this thesis or project.

The original application for approval and letter of approval are filed with the relevant offices. Inquiries may be directed to those authorities.

Simon Fraser University Library
Burnaby, British Columbia, Canada

Update Spring 2016

Abstract

On naturally fragmented coral reefs, the reluctance of small-bodied fishes to cross sand is widely considered a predator-avoidance response, but the extent to which distance from safety and how specific predators mediate off-reef movements is unclear. Here, I use video-generated estimates to assess the degree to which sand acts as a barrier to reef-associated fish movement, and I use novel translocations to test how the presence of standardized models of native and invasive predators over sand affects the homing probability of a Caribbean damselfish, *Stegastes partitus*. The frequency of fish observed over sand fell non-linearly with distance from the nearest reef, and fish were often observed when < 50 m away (~90 fish per hour, 33 species). However, only the native predator model reduced damselfish homing probability over sand. The invasive lionfish (*Pterois* sp.) did not affect homing, suggesting damselfish are naïve to the threat of predation posed by lionfish.

Keywords: Predation risk; Movement ecology; Prey naïveté; Marine invasions; Pterois sp.; Connectivity

Acknowledgements

I am sincerely grateful to my supervisor, Isabelle Côté, for her overwhelming mentorship and guidance throughout this thesis marathon. Thank you for helping me grow as a field scientist, as a writer and most importantly, for inspiring me as a woman in science to always be brave, speak my mind and keep asking questions. Larry Dill, thank you for your ongoing feedback, comments on my study design and wonderful sense of humour – we'll get you to the Bahamas one of these days! In addition, thank you Ronald Ydenberg for agreeing to be my examiner.

Field work in Curaçao wouldn't have been possible without the incredible support of my dear friends and field assistants, Rachel Munger and Natalie Maslowski, as well as The Diveshop Curaçao and CARMABI Research Station. I'd also like to give a special shout-out to former Côté Lab members Emily Darling and Luis Malpica-Cruz for field assistance in the Bahamas, as well as the staff at the Cape Eleuthera Institute, and especially Ron Knight for help with diving logistics. A million more thank-yous to the rest of the Côté Lab and the Earth to Ocean Group for the laughs, adventures, presentation feedback, mentorship and especially help with my R-code.

I would like to thank the various funding sources that have supported my research: the Natural Sciences and Engineering Research Council of Canada, Philip and Mary McClelland and of course, Simon Fraser University.

I want to thank Cole Nakatani for always pushing me to be the best possible version of myself, and his family for all of their support. As a transplant living in the Pacific Northwest, I'll never forget all of our shared adventures: from scaling mountains in the desert, to consuming way too much Mexican food and banana cake, to spa days and late-night airport pick-ups, and of course your ever-lasting interest in scuba diving and tropical marine biology.

Lastly, I will never be able to express enough gratitude to my Mom and Dad in New Brunswick, my brother Matt in Ontario, my sister Sarah in Alberta, and my favourite dog in the world, Montgomery. Thank you for being my five pillars of support, and for always having my back, through the good time and the hard times. Cheers to our next family reunion!

Table of Contents

List of Tables

List of Figures

Chapter 1.

General Introduction

For most animals, lifetime fitness is contingent on the capacity to perceive risk of predation, and in turn, respond appropriately to avoid predators (Lima and Dill 1990; Sih 1992; Casillas-Barragán 2015). Many adaptive anti-predator behaviours exhibited by prey include alterations of prey movement patterns. Examples include behaviours that decrease predator–prey encounter rates, such as prey moving to safer habitats or at times of day when predators are less active or hungry, and behaviours that improve the chances of escaping detection by a predator, such as hiding and general reductions in activity levels (Lima and Dill 1990; Sansom et al. 2009; Casillas-Barragán 2015).

In fact, the perception of risk of predation shapes virtually every aspect of animal movement. This is particularly true in fragmented habitats such as coral reefs, where perceived risk of predation for small inhabitants such as fish is highly variable spatially. Coral reefs are naturally heterogeneous systems. They harbour over 100 million species globally (Knowlton et al. 2010), and often consist of high-complexity coral patches, which offer relative safety in the form of holes and crevices, separated by low-complexity substrata such as sand, which provides neither resources nor refuge. While many reef fish are territorial and might settle on a coral patch for life, many reef fish species are less site-attached and can move among patches. Inter-patch movement of fishes among coral patches is important as it contributes to herbivory, biomass production and nutrient transfer, which are major ecosystem processes on coral reefs (Meyer et al. 1983; Lewis and Wainwright 1985; Mumby et al. 2004). Grazing herbivores, for example, can help regulate the abundance of algae on networks of coral patch reefs within their home ranges (Morgan 2003; Meyer and Holland, 2005). In turn, schooling fish may deposit feces as they swim over patches, enriching benthic communities with ammonium, particulate nitrogen and phosphorus (Meyer et al. 1983).

However, reef fish species often appear averse to venturing over sand (Barrett 1995; Chapman and Kramer 2000; Turgeon et al. 2010). Crossing sand gaps that connect coral patches may be costly: prey are highly exposed, and have limited to no refuge. Strong intraspecific competition, territory loss and low resource availability on a home patch may nonetheless motivate coral reef fish to move to seek more favourable conditions. To evaluate the costs and benefits associated with crossing sand gaps, a coral reef fish must be able to perceive the general risk of predation associated with a habitat, and the specific risk of predation associated with specific predators.

Perceived risk of predation in sandy habitats

The reluctance of coral reef fishes to move over sand is widely considered to be a predator avoidance response. This suggests that homogeneous matrices of sand surrounding coral patches are perceived as entailing a potentially high predation risk. This potential risk was confirmed when Shulman (1985) reported that the predator encounter rate of juvenile grunts (*Haemulon* sp.) tethered over sandy "halos" (i.e., zones of bare sand around coral reefs, often created by herbivores and urchins grazing outwards from a reef) was 40% higher compared to that for prey tethered over dense seagrass beds some 20 m away.

The perceived risk of predation of swimming over sand, away from shelter, is likely to vary across contexts and individuals. Coral reef fish likely perceive a higher risk of predation associated with crossing larger sand gaps. For example, Turgeon et al. (2010) showed the homing probability of a Caribbean damselfish, *Stegastes diencaeus*, declined to less than 50 % when individuals were translocated over sand gaps wider than 3.90 m. In addition, all else being equal, smaller reef fish should perceive higher predation risk over sand than larger fishes (Sweatman and Robertson 1994; Boaden and Kingsford 2015). This suggests that there should be general patterns in observations of reef fishes over sand: fewer, but generally larger, fish at increasing distances from reefs. To my knowledge, however, there are no published estimates of adult fish movement at various distances from coral reef patches separated by stretches of open sand.

Predator recognition

Once a visual cue is perceived, fish must be able to correctly identify a threat and assess the level of risk presented by that threat in order to respond appropriately (e.g., seeking shelter, avoiding open expanses of sand, reducing activity, etc.) (Ferrari et al. 2009; Cox and Lima 2006; Salo et al. 2007). While fish might readily recognize native predators as posing a significant risk, they might not perceive the same of novel predators with which they have not co-evolved. The phenomenon of prey naiveté, or the failure to recognize novel predators and respond appropriately due to lack of experience, is thought to have facilitated the high predation rates of invasive Indo-Pacific lionfish (*Pterois* sp.) in the Caribbean (Cure et al. 2012; Kindinger 2014).

Invasive lionfish have spread rapidly through the western Atlantic since they were first introduced to Florida in 1985, and have caused major declines in native fish recruitment and abundance on some reefs (Albins and Hixon 2008; Green et al. 2012). If prey are, in fact, naïve to these generalist carnivores, they should exhibit ineffective predator avoidance behaviours associated with movement. For example, when in the presence of lionfish, naïve prey might not seek shelter, might not reduce activity levels or might be willing to cross sand gaps as wide as when predators are absent.

Studying the reluctance of small-bodied reef fishes to cross open expanses of sand – a natural predator avoidance response – provides a novel opportunity to evaluate invasive predator recognition by native prey. So far, studies of prey naïveté to invasive lionfish have used experimental tanks that do not mimic realistic conditions, or constrained natural behaviour in the field by placing predators and/or their prey in bottles or cages (e.g., Kindinger 2014; Anton et al. 2016). The results have been perplexing and inconsistent. Typically, fear or aggression exhibited by native prey to invasive lionfish mirrors that displayed towards native non-predators or empty bottle controls (Black et al. 2014; Kindinger 2015). Some studies, however, have reported that prey fish exhibit responses to lionfish consistent with typical predator avoidance behaviour, such as reduced activity (i.e., foraging, movement; Eaton et al. 2016, Kindinger and Albins 2017) and increased time spent in shelter (Marsh-Hunkin et al. 2013). Examining natural avoidance behaviours of unconstrained fishes to invasive predators in the field (i.e., in fragmented coral reef habitats) should help paint a clearer picture of prey naïveté (Côté and Smith 2018).

Research goals

In this thesis, I first explore the degree to which sand acts as a barrier to the movement of coral reef fishes. Second, building on the commonly held assumption that coral reef fish are reluctant to cross open expanses of sand, I present a novel methodology to test whether the highly abundant Caribbean damselfish, *Stegastes* *partitus*, is naïve to the presence of invasive predatory lionfish (*Pterois* sp.). Specifically, in Chapter 2, I use video-generated estimates of hourly rates of fish observations over sand to examine how the distance that reef fish are willing to venture away from reefs co-varies with the distance to the nearest patch reef. I also examine the effect of fish body size on both the frequency with which fish are observed on sand as well as the maximum distance individual species are found away from reefs. I find that the number of fish observed over sand declines with increasing distance to the nearest coral patch, that larger species are found further from patches, and that reef-associated fish species are frequently observed (~90 fish per hour, across 33 species) over sand at distances of less than 25 m to the nearest patch. In Chapter 3, I use experimental translocations over various stretches of open sand to compare the homing probability of damselfish in the presence and absence of standardized models of a lionfish, an ecologically similar native piscivore (i.e., a black grouper; *Mycteroperca bonaci*) and a native non-piscivore (i.e., white grunt, *Haemulon flavolineatum*) in the field. I find that the grouper model alone elicited a strong predator avoidance response in homing damselfish: translocated fish were less likely to home, took longer to do so and stayed in the release shelter longer in the presence of the grouper model. In contrast, the homing behaviour exhibited by damselfish in the presence of a lionfish mirrored that observed in the presence of a non-piscivore, as well as in the absence of any model. These findings clearly demonstrate that bicolor damselfish are naïve to the threat of predation posed by invasive lionfish. Taken together, my research has direct implications for the design of fish studies in heterogeneous coral reef habitats, as well as the effective design of marine protected areas.

References

Albins MA, Hixon MA (2008) Invasive Indo-Pacific lionfish (*Pterois volitans*) reduce recruitment of Atlantic coral-reef fishes. Mar Ecol Prog Ser 367: 233–238.

Anton A, Cure K, Layman CA, Puntila R, Simpson MS, Brunso JF (2016) Prey naïveté to invasive lionfish *Pterois volitans* on Caribbean coral reefs. Mar Ecol Prog Ser 544: 257–269.

Auffret AG, Plue J, Cousins SAO (2015) The spatial and temporal components of functional connectivity in fragmented landscapes. AMBIO 44: 51–59.

Barrett NS (1995) Short- and long-term movement patterns of six temperate reef fishes (families Labridae and Monacanthidae). Mar Freshwater Res 46:853–860.

Bartholomew A, Bohnsack JA, Smith SG, Ault JS, Harper DE (2007) Influence of marine reserve size and boundary length on initial response of exploited reef fishes in the Florida Keys National Marine Sanctuary, USA. Landscape Ecology 23: 55-65.

Black AN, Weimann SR, Imhoff VE, Richter ML, Itzkowitz M (2014) A differential prey response to invasive lionfish, *Pterois volitans*: Prey naïveté and risk-sensitive survivorship courtship. J Exp Mar Biol Ecol 460: 1–7.

Brock RE, Norris JE (1989) An analysis of the efficacy of four artificial reef designs in tropical waters. Bull Mar Sci 44: 934–941.

Buechner M (1987) Conservation in insular parks: simulation models of factors affecting the movement of animals across park boundaries. Biol Conserv 41:57–76.

Casillas-Barragán I, Costa-Pereira R, Piexoto PEC (2015) Percieved predation risk decreases movement and increases aggregation of Amazon milk frog (Anura, Hylidae) tadpoles through ontogeny. Hydrobiologia 765: 379–386.

Chapman MR, Kramer DL (2000) Movements of fishes within and among fringing coral reefs in Barbados. Env Biol Fishes 57: 11–24.

Cox JG, Lima SL (2006) Naiveté and an aquatic-terrestrial dichotomy in the effects of introduced predators. Trends Ecol Evol 21: 674−680.

Côté IM, Mosquiera I, Reynolds JD (2001) Effects of marine reserve characteristics on the protection of fish populations: A meta-analysis. J Fish Biol 59: 178–189.

Côté IM, Smith NS (2018) The lionfish *Pterois* sp invasion: Has the worst-case scenario come to pass? J Fish Biol 92: 660–689.

Cure K, Benkwitt CE, Kindinger TL, Pickering EA, Pusack TJ, McIlwain JL, Hixon MA, (2012) Comparative behavior of red lionfish *Pterois volitans* on native Pacific versus invaded Atlantic coral reefs. Mar Ecol Prog Ser 467: 181–192.

DeMartini EE (1993) Modeling the potential of fishery reserves for managing Pacific coral reef fishes. Fish Bull 91:414–427.

Eaton L, Sloman KA, Wilson RW, Gill AB, Harborne AR (2016) Non-consumptive effects of native and invasive predators on juvenile Caribbean parrotfish. Env Biol Fishes 99: 499-508.

Ferrari MCO, Sih A, Chivers DP (2009) The paradox of risk allocation: a review and prospectus. Anim Behav 78: 579–585.

Gell FR, Roberts CM (2003) Benefits beyond boundaries: the fishery effects of marine reserves. Trends Ecol Evol 18: 448–455.

Green SJ, Akins JL, Maljkovic A, Côté IM (2012) Invasive lionfish drive Atlantic coral reef fish declines. PLoS ONE 7: e32596.

Hixon MA, Carr MH (1997) Synergistic predation, density dependence, and population regulation in marine fish. Science 277: 946–949.

Kindinger TL (2015) Behavioral response of native Atlantic territorial three spot damselfish (*Stegastes planifrons*) toward invasive Pacific red lionfish (*Pterois volitans*). Env Biol Fishes 98: 487−498.

Kindinger TL, Albins MA (2017) Consumptive and non-consumptive effects of an invasive marine predator on native coral-reef herbivores. Biol Invas 19: 131-146.

Knowlton N, Brainard RE, Fisher R, Moews M, Plaisance L, & Caley MJ (2010) Coral reef biodiversity. In: McIntyre A, editor. Life in the world's oceans: diversity, distribution and abundance. Chichester: Wiley-Blackwell.

Kramer DL, Chapman MR (1999) Implications of fish home range size and relocation for marine reserve function. Env Biol Fishes 55: 65–79.

Lester SE, Helpern BS, Grorud-Colvert K, Lubchenco J, Ruttenberg BI, Gaines SD, Airamé S, Warner RA (2009) Biological effects within no-take marine reserves: A global synthesis. Mar Ecol Prog Ser 384: 33–46.

Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: A review and prospectus. Can J Zool 68: 619–640.

Marsh-Hunkin KE, Gochfeld DJ, Slattery M (2013) Anti-predator responses to invasive lionfish, *Pterois volitans*: interspecific differences in cue utilization by two coral reef gobies. Mar Biol 160: 1029−1040.

Mittelbach GG, Persson L (1998) The ontogeny of piscivory and its ecological consequences. Can J Fish Aquat Sci 55:1454–1465.

Moberg F, Folke C (1999) Ecological goods and services of coral reef ecosystems. Ecol Econ 29: 215–233.

Ogden JC, Buckman NS (1973) Movements, foraging groups, and diurnal migrations of the striped parrotfish *Scarus croicensis* Bloch (Scaridae). Ecology 54 :589–596.

Polacheck T (1990) Year round closed areas as a management tool. Nat Res Model 4: 327–354.

Rowley RJ (1994) Marine reserves in fisheries management. Aquat Conserv Mar Freshwater Ecosyst 4: 233–254.

Sale PF, Cowen RK, Danilowicz BS et al (2005) Critical science gaps impede use of no-take fishery reserves. Trends Ecol Evol 20: 74–80.

Sale PF, Steel WJ (1989) Temporal variability in patterns of association among fish species on coral patch reefs. Mar Ecol Progr Ser 51: 35–47.

Salo P, Korpimaki E, Banks PB, Nordstrom M, Dickman, CR (2007) Alien predators are more dangerous than native predators to prey populations. Proc R Soc B 274: 1237−1243.

Sambrook K, Jones GP, Bonin MC (2016) Life on the edge: Coral reef fishes exhibit strong responses to habitat boundary. Mar Ecol Prog Ser 561: 203 – 215.

Sansom A, Lind J, Cresswell W (2009) Individual behavior and survival: the role of predator avoidance, foraging success, and vigilance. Behav Ecol 20: 1168–1174.

Scharf FS, Juanes F, Rountree RA (2000) Predator size–prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. Mar Ecol Progr Ser 208: 229–248.

Selig ER, Casey KS, Bruno JF (2012) Temperature-driven coral decline: the role of marine protected areas. Glob Change Biol 18: 1561–1570.

Shulman MJ (1985) Recruitment of coral reef fishes: effects of distribution of predators and shelter. Ecology 66: 1056–1066.

Smith CL, Tyler JC (1975) Succession and stability in fish communities of dome-shaped patch reefs in the West Indies. Amer Mus Novit 2572: 1-18.

Sweatman HPA, Robertson DR (1994) Grazing halos and predation on juvenile Caribbean surgeonfishes. Mar Ecol Progr Ser 111: 1–6.

Syms C, Jones GP (2000) Disturbance, habitat structure, and the dynamics of a coral-reef fish community. Ecology 81: 2714-2729.

Turgeon K, Robillard A, Grégoire J, Duclos V, Kramer DL (2010) Functional connectivity from a reef fish perspective: behavioral tactics for moving in a fragmented landscape. Ecology 91: 3332–3342.

Chapter 2.

Exposed: Effects of body size and distance on off-reef movement by fish

Abstract

Sand is widely perceived to be a strong barrier to fish movement, especially for fishes inhabiting coral reef patches, but the extent to which fish size and distance from safety mediate off-reef movements is unclear. Using underwater video cameras placed at varying distances from patch reefs, I estimated the frequency of strongly reef-associated fish swimming over sand. The hourly number of reef fish observed over sand fell abruptly and non-linearly with distance from the nearest coral patch. Fish were frequently observed over sand when < 50 m from the nearest reef patch (~90 fish observed per hour, of 33 species), while movement was reduced to < 1 fish per hour when the nearest reef was more than 140 m away. Larger species were found further from the nearest reef patch, but they were not observed on sand more frequently than smaller species. These findings have implications for the design of studies on patch reefs, since they suggest that patches that are less than 280 m apart are connected by frequent movement and might not be independent replicates for many fish species, especially larger ones. My results are also relevant for the design of marine protected areas. They highlight the fact that fish movement is frequent only between patches that are in relatively close proximity, suggesting that habitat discontinuities a few hundred metres wide might be an easy way to define protected area boundaries to minimise rates of fish straying into unprotected habitat.

Introduction

Sand is widely perceived to be a strong barrier to fish movement, especially for fishes inhabiting coral reef patches (Ogden and Buckman 1973; Barrett 1995; Chapman and Kramer 2000). The reluctance of reef fish to cross expanses of sand has been examined directly or indirectly in various ways. For example, some mark-recapture studies found that many coral reef fish rarely move between reefs separated by sand

(Chapman and Kramer 2000), while some tagged fish followed by telemetry clearly avoided sandy substratum (Popple and Hunte 2005; Meyer et al. 2010). In contrast, some studies of recolonization of depopulated patch reefs surrounded by sand suggest fish readily move between nearby patches and that inter-patch gaps of as much as 100 m are needed to provide at least a partial barrier to fish movement (Brock et al. 1979; Syms and Jones 2000). In general, sandy expanses and other habitats with very low structural complexity offer few food resources, limited shelter and potentially high risk of predation (Shulman 1985; Sweatman and Robertson 1994). The latter is confirmed experimentally by the heavy mortality of small coral reef fishes tethered over sand at the reef edge (Shulman 1985; Sweatman and Robertson 1994).

If risk of predation is a factor in the decision of fish to venture on sand, away from reefs, then their willingness to do so should vary with distance from safety and with body size. Indeed, studies of fish homing after translocation have revealed distinct threshold distances for sand gap crossing (e.g., Ogden and Buckman 1973; Hixon and Beets 1993). Turgeon et al. (2010), for example, demonstrated by means of translocations that the probability that small (< 10 cm TL) damselfish crossed a sand gap to return to their territory declined steeply with gap width, dropping to near zero for gaps of more than 4 m when there was a safe, over-reef detour route and of more than 8 m when no such route existed. Body size might also be an important determinant of the likelihood of crossing sand because predation is strongly size-dependent in aquatic systems (Sheldon et al. 1972; Dickie et al. 1987). The range of prey fish sizes consumed increases with predator body size (Mittelbach and Persson 1998; Scharf et al. 2000). The continued inclusion of small fish in the diet of increasingly large predatory fishes means that, in general, risk of predation is likely to be highest on small fishes. Conversely, risk of predation should diminish as fish become larger, leading to a greater readiness to move away from the safety of cover.

Understanding fish movement over sand is important. Such movements, when they result in the transfer of individuals from one patch to another, have a direct effect on meta-population dynamics, which in turn has implications for the design of ecological and behavioural studies (e.g., how far apart should reefs be to be considered separate populations?) as well as the configuration of marine protected areas (e.g., how likely are different fish species to stray beyond reserve boundaries?). Yet, to my knowledge, there are currently no empirical estimates of the number and species of reef fish observed between coral reef patches separated by various stretches of inhospitable habitat.

In this study, I examined the effects of distance to the nearest coral reef patch and fish body size on the frequency of fish observed over sand. To do so, I set underwater video cameras on sand at varying distances from the nearest patch reef to obtain snapshots of the numbers of individual fish and range of reef-associated species observed on sand. I predicted that the hourly number of fish seen over sand might increase with species body size, but decline with increasing distance from the nearest patch. To place my findings in context, I also carried out a systematic review of ecological and behavioural studies of fish on coral reef patches to estimate the inter-reef distances most widely considered to confer isolation between fish populations. My results reveal that nearby reef patches are likely connected by the movement of adult fishes of a wide range of reef-associated species.

Materials and methods

Ethics statement

The study conforms to the guidelines of the Canadian Council on Animal Care and was approved by the Simon Fraser University Animal Care Committee (permit B1077B-13). The field work was conducted under a permit from the Bahamas Department of Marine Resources to the Cape Eleuthera Institute.

Literature survey

To place my findings in context, I first conducted a literature survey to estimate the range and frequency distribution of inter-patch distances used in studies of adult fish behaviour and ecology on tropical coral reef patches over the last 20 years. I followed the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA, Moher et al. 2009) guidelines (see Fig. A1), and used both Web of Science (WOS) and Aquatic Sciences and Fisheries Abstracts (ASFA) as search engines. I retrieved all papers returned by a search that used the following key words in either the title or abstract: fish AND coral AND (patch OR bommie). I limited my search to the years 1996-2016. Excluding duplicates, conference proceedings, reviews and letters, my combined search from WOS and ASFA generated 528 research papers. To be included, a study had to (1) focus on coral reef fish, (2) include multiple natural coral reef patches as study sites, and (3) carry out analyses in which patches were considered independent replicates or populations (i.e., the unit of analysis was reef or population). A total of 485 papers were deemed to be not relevant based on their title, abstract and methods (Fig. A1). From the remaining 43 papers, I recorded the minimum inter-reef distance (in m) reported and also noted when this information was not given. The details of all papers examined are given in Table A1. I obtained from Fishbase (Froese and Pauly 2016) the maximum body size of species considered in the studies that reported minimum inter-patch distances.

Video data collection

The field study was conducted in Rock Sound, a large, shallow bay (average depth: 3.3 m) at the southern tip of Eleuthera Island, The Bahamas. Dozens of patch reefs of varying sizes are spread across the bay, interspersed in a matrix of sand and sparsely distributed seagrass, sponges and gorgonians. The location of the majority of patches was recorded by GPS over several years, yielding a relatively complete distribution map of reef patches.

I identified 20 pairs of reef patches that were each other's nearest neighbours. Half-way between each pair of patches, as determined by a hand-held GPS unit, I deployed two GoPro (Hero 3, White Model) cameras, each strapped to a 1 kg lead weight and placed back-to-back and perpendicular to the axis connecting the patches. Distances between nearest-neighbouring patches ranged from 2.75 m to 4330 m, thus the distance of cameras to the nearest patch varied from 1.4 m to 2165 m. The 170^{o} field of view of each camera therefore provided close to a 360^{o} view around the mid-point between the patches. The cameras recorded video continuously for 70-180 min. Horizontal visibility on all recording days was 25-30 m. A single recording was made at each site between 13 and 27 January, 2013. All recordings were made between 10h00 and 16h00 to limit variation in light levels and time of day effects.

I scored 60 min of each video, starting 5 min after the start of recording to eliminate the initial period of disturbance caused by the snorkelers and the departing boat, and ending before the disturbance of the returning boat and camera retrieval. All videos were scored blindly with respect to distance from the nearest patch. From each video, I noted the species identity and number of individuals. Because fish were not marked, it is possible that some individuals might have crossed the field of view more than once. When recognizable individuals (i.e., because they had specific marks, were rare species or on the basis of school size) were observed multiple times, they were recorded only once. I considered only swimming fishes; burrowing fishes (e.g., pikeblennies (*Chaenopsidae*), garden eels (*Congridae*), jawfishes (*Opistognathidae*) were not recorded. Because of the lack of calibration measures along the long depth of field, it was not possible to assess fish size accurately. I therefore did not distinguish between juveniles and adults.

Analyses

First I calculated the percentage of studies that did not report minimum inter-patch distances, as well as the percentage of papers that used coral reef patches less than 50 m apart, based on the 43 papers included in my literature survey of studies of fish behaviour and ecology on patch reefs, I used a regression analysis to determine whether fish maximum length (i.e., obtained from Fishbase; Froese and Pauly 2016) co-varied with the minimum inter-patch distance selected in each study.

Next I classified all fish species observed on video as either ‘strongly’ or ‘weakly’ reef-associated on the basis of published descriptions of typical habitat use (e.g., Humann 2014) and personal experience. I defined strongly reef-associated species as those that are predominantly found on or along the margins of coral reef patches and are therefore not expected to occur far from reefs during the day. Weakly reef-associated species were defined as those that occur occasionally on reefs but may also be found in other shallow-water habitats. Some fish species, particularly grunts (family *Haemulidae*), undertake daily movements, resting on reefs during the day and foraging off-reef at night (Meyer and Schultz 1985, Appeldoorn et al. 2009). I deemed these species to be strongly reef-associated because they would not be expected to be seen over sand during my daytime recordings. Although I initially report all fish species observed on the video recordings, I carried out subsequent analyses only on the ‘strongly’ reef-associated species (n = 33 species; Table A2).

I generated an hourly observation frequency for each site by summing the total number of fish recorded in 60 min across both cameras in a pair. I also calculated species-specific mean observation frequencies for fish species that were recorded from at least three sites (n = 8 species; Table A3). This analysis was de facto limited to the 8 sites that were less than 25 m from the nearest patch because species-specific observations were essentially zero at sites further away from the nearest patches (see Results). The sites contributing to each fish species' mean observation frequency varied from species to species, minimising the risk of spatial autocorrelation.

I noted the maximum distance to the nearest patch for each species observed (n = 33 species). It is important to note that this is a minimum estimate since fish captured on video might have left from a reef patch that was further than the patch nearest to the video camera.

Because I could not accurately estimate the length of fish on the videos, I collated size information from two sources. First, I obtained the maximum body length (total length, cm) of the species I observed from Fishbase (Froese and Pauly 2016). Second, I calculated mean adult lengths of the species I observed from a large database of fish surveys carried out from 2011 to 2015 across 16 patches in Rock Sound (including nine patches included in this study). The two sets of lengths were highly correlated ($r^2 = 0.62$, n = 33 species, $p < 0.001$; see Table A2). I therefore present the results using mean lengths derived from reef patches, since these sizes are likely to be more representative of the fish observed on my videos.

I used a generalized linear model (with negative binomial distribution to account for overdispersion of the data and a log-link) to determine whether distance to the nearest patch affected the overall hourly frequency of fish observed over sand. I also sought to examine the influence of fish body size (i.e., mean species-specific body lengths derived from long-term patch surveys) on species-specific observation frequencies. I used linear model analyses to test whether the mean species-specific hourly observation frequency (derived from 8 sites; rate ~ length) and, separately, the maximum distance each strongly reef-associated species was found from the nearest patch (derived from all 20 sites; maximum distance ~ length), co-varied with species mean total length.

Results

Inter-reef distances in studies of reef fish ecology and behaviour

I retrieved 43 published papers that focused on the ecology or behaviour of adult fish on natural coral reef patches. Thirty-eight percent of these papers (16 studies) did not report the minimum distance between the reef patches studied. For the rest, minimum inter-reef distances ranged between < 50 m to more than 1000 m, with 48 % of studies using reef patches that were less than 50 m apart (Fig. 1; Table A1).

Eleven of the studies that did report minimum inter-patch distances focused on multiple fish families (Table A1). The remaining 16 studies of adult fishes were about 10 species (mainly damselfishes (n = 5), groupers (n = 2), gobies (n = 1) and wrasses (n = 1); Table A1). Fish maximum length did not co-vary with the minimum inter-patch distance used in studies ($r^2 = -0.07$, $F_{1,14} = 0.01$, $p = 0.911$), and there was much variation among studies. For example, minimum inter-patch distances in studies of adult damselfishes (all 9-13 cm total length) varied from 3 to 40 m (Table A1). In contrast, patches in studies of wrasses (14 cm TL) were only separated by 5 to 8 m (Table A1) and gobies (just 4 cm TL) were studied on patches separated by 50 m.

Frequencies of reef fish over sand

I recorded a total of 55 fish species, from 21 families, on sand at varying distances from the nearest reef patch (Table 1). Of these, 33 species in 10 families were considered to be strongly reef-associated and therefore expected to be observed very close to reef patches. The maximum distance from a patch reef at which these reef fish species were observed ranged from 140 cm for sharpnose puffer, *Canthigaster rostrata*, to more than 2 km for yellowhead wrasse, *Halichoeres garnoti* (Table 1). The latter is clearly an overestimate explained by the fact that yellowhead wrasse were often seen associated with small, isolated, individual coral colonies, away from reef patches. Omitting this species, the log maximum distance a fish species was observed from a patch reef increased with body length ($r^2 = 0.18$, $F_{1,35} = 9.05$, $p = 0.005$; Fig. 2). Strongly reef-associated families, including grunts and one species of parrotfish, were observed as far as 85.5 m from the nearest coral patch (Fig. 2). At this distance, white grunts (*Haemulon plumierii*), white margates (*Haemulon album*) and redband parrotfish

(*Sparisoma aurofrenatum*) were each observed one to two times in one hour. In contrast, the yellowtail snapper (*Ocyurus chrysurus*), a weakly reef-associated species, had the highest observation rate of 373 fish per hour at 85.5 m from the nearest reef.

Overall observation frequencies varied from zero to just over 1500 fish per hour. The frequency of fish sightings declined steeply and non-linearly with increasing distance from the nearest reef patch (Fig. 3). Observation frequencies are predicted to be ~ 90 fish per hour at sites 50 m from the nearest reef. This value is reduced to ~ 20 fish per hour at sites 100 m from the nearest reef, and beyond 140 m from the nearest reef patch, observation rates are predicted to drop to <1 fish per hour.

There were sufficient data (i.e., from more than three sites) to calculate species-specific observation frequencies over sand for eight strongly reef-associated species for sites less than 25 m from the nearest reef patch. These species included two species of grunts, one angelfish, three parrotfishes and two grouper species, which ranged in total length from 17 to 41 cm (Tables A2, A3). White grunts (*Haemulon plumierii*) had the highest mean observation frequency, at approximately 68 per hour. Species-specific observation frequencies did not co-vary with mean body size ($r^2 = 0.24$, $F_{1,7} = 3.23$, $p = 0.12$).

Discussion

In this study, I asked to what extent expanses of open sand present barriers to coral reef fish movement. As predicted, I found that the frequency of reef-associated fish observed swimming over open sand decreased with increasing distance to the nearest coral patch. In contrast to my expectation, fish body size did not influence observation frequency over sand. However, the maximum distance at which coral reef fish were observed from the nearest patch reef was positively related to fish body size, suggesting that larger species did cross larger expanses of sand. Taken together, I highlight the fact that adult fish movement of a wide range of reef-associated species is frequent between nearby coral patches, but rare at distances greater than a few hundred metres from the closest reef. These results have implications both for the design of ecological and behavioural studies on patch reefs and for the design of marine protected areas in fragmented habitats.

The movement of reef fishes that are strongly associated with coral patches appears to be constrained by patch isolation (Chapman and Kramer 2000; Meyer et al. 2010). In my network of patch reefs, the hourly number of reef fish observed over open expanses of sand fell abruptly and non-linearly with increasing distance to the nearest reef patch. There was extensive movement of fish over sand between reef patches that were less than 50 m apart (i.e, < 50 m to nearest patch; ~550 fish observed per hour across all species; ~90 fish per hour for strongly reef-associated species); in contrast, I usually recorded only 1-2 fish per hour between reef patches that were separated by wider distances. The shape of the overall relationship between movement and distance I uncovered across 33 reef fish species mirrors, though on a larger scale, that documented by Turgeon et al. (2010) for one Caribbean damselfish. Longfin damselfish (*Stegastes diencaeus*), a strongly territorial species, never crossed sand gaps of more than ~8 m (Turgeon et al. 2010). The four species of damselfish observed in my non-manipulative study (i.e., sergeant major *Abudefduf saxatilis,* blue chromis *Chromis cyanea*, beaugregory *Stegastes leucostictus* and cocoa damselfish *S. variabilis*) also only crossed narrow gaps (up to ~ 3 m; Table 1), as did wrasses (up to ~4 m; Table 1) – another family of coral reef fishes commonly studied on patch reefs.

Fish aversion to crossing sand might be linked to risk of predation. Given the strongly size-structured nature of predatory interactions in marine systems (Sheldon et al. 1972; Dickie et al. 1987), I expected small-bodied species to be under greater risk of predation away from shelter (e.g., Boaden and Kingsford 2015), and hence to venture less frequently away from reefs, and across narrower expanses of sand, than larger species. Indeed, predation risk can trigger a wide range of non-lethal, behavioural alterations in prey, including remaining closer to shelter (Madin et al. 2016). I confirmed that smaller reef-associated species were seen less far from reef patches than larger species, but adult body size was not a determinant of observation frequency. There might have been error in my assessment of these variables that could have masked a relationship. For example, I used mean species body size from a number of reef patches in the study area because I could not accurately measure fish size on the videos. In addition, maximum distance swum by a species might have been underestimated if fish started or ended their travel further away than the patch nearest to the video camera, or overestimated if there were small patches of non-reef habitats (e.g., seagrass or gorgonians) that provided cover along the way. It is possible that the willingness to cross sand is partly linked to feeding ecology, with species that rely on resources readily found off reefs (e.g., plankton, sponges, soft corals) being more likely to cross sand to forage (Meyer et al. 2010). Alternatively, a positive relationship between observation frequency over sand and body size perhaps should not have been expected if species abundance on patch reefs influences observation rate. The relatively low abundance of large-bodied species (e.g., Jennings and Mackinson 2003) might depress observation frequency as much as their propensity to venture off the reef increases it. Because I could not identify the departure and arrival patches of fishes observed on video, I could not measure species abundance on the relevant reefs.

Although many fish species might be reluctant to cross sand, some do, which has implications for studies of reef fishes on coral patches. Table 1 shows my estimates of distance to the nearest coral patch (i.e., maximum distance crossed) for all species, strongly and weakly reef-associated, observed on video. The range of over-sand distances crossed by fish species is important in the context of observational and experimental studies. My survey of studies of fish behaviour and ecology on coral patch reefs (Fig. 1) showed two major trends: (1) nearly half of the studies (i.e., 48 %) chose units of replication (i.e., patches) that were less than 50 m apart, and (2) 38% of studies did not report inter-patch distances at all. Previous authors have assumed patch reefs separated by a few metres of sand are relatively isolated systems (Smith and Tyler 1975; Sale and Steel 1989; Turgeon et al. 2010). Sale and Steel (1989), for example, argued that coral patches act as 'islands' for reef fish, where juveniles and adults live sedentary lifestyles following larval settlement. I found no relationship between fish maximum length and minimum inter-patch distance used in published studies (Table A1) suggesting that, in general, studies that focus on large species don't necessarily use reef patches that are further apart than studies dealing with small species. In turn, many studies considered entire fish assemblages. Of the 20 community-level studies that focus on adult fishes (Table A1), six used patches separated by ≤ 50 m of sand – a distance at which some 90 fish per hour were predicted to travel between my similarly distant study patches – and eight did not report inter-patch distances. Moreover, only three community studies used minimum inter-patch distances that were larger than 140 m – the distance at which observed fish traffic among patches was expected to drop to less than 1 fish per hour in my study. This threshold distance might be location- and/or assemblage-specific, but I believe that, taken together, these observations suggest that neighbouring patches might often not act as independent replicates for examining fish populations.

Finally, my findings are also relevant for the design of marine protected areas. The fact that individuals of many reef fish species were observed traveling over sand supports the notion that the movement of post-settlement individuals can be an important process influencing the distribution, demography, and persistence of marine populations (Pittman and McAlpine 2003; Freiwald 2012; Tamburello and Côté 2014). Some significant connectivity among habitat patches can be realised through adult rather than larval movement. However, the non-linear nature of fish willingness to cross sand in relation to distance from cover gives managers an easy way to define protected area boundaries (Barrett 1995; Kramer and Chapman 1999; Meyer and Holland 2005) to minimise rates of fish straying into unprotected habitat.

Figures

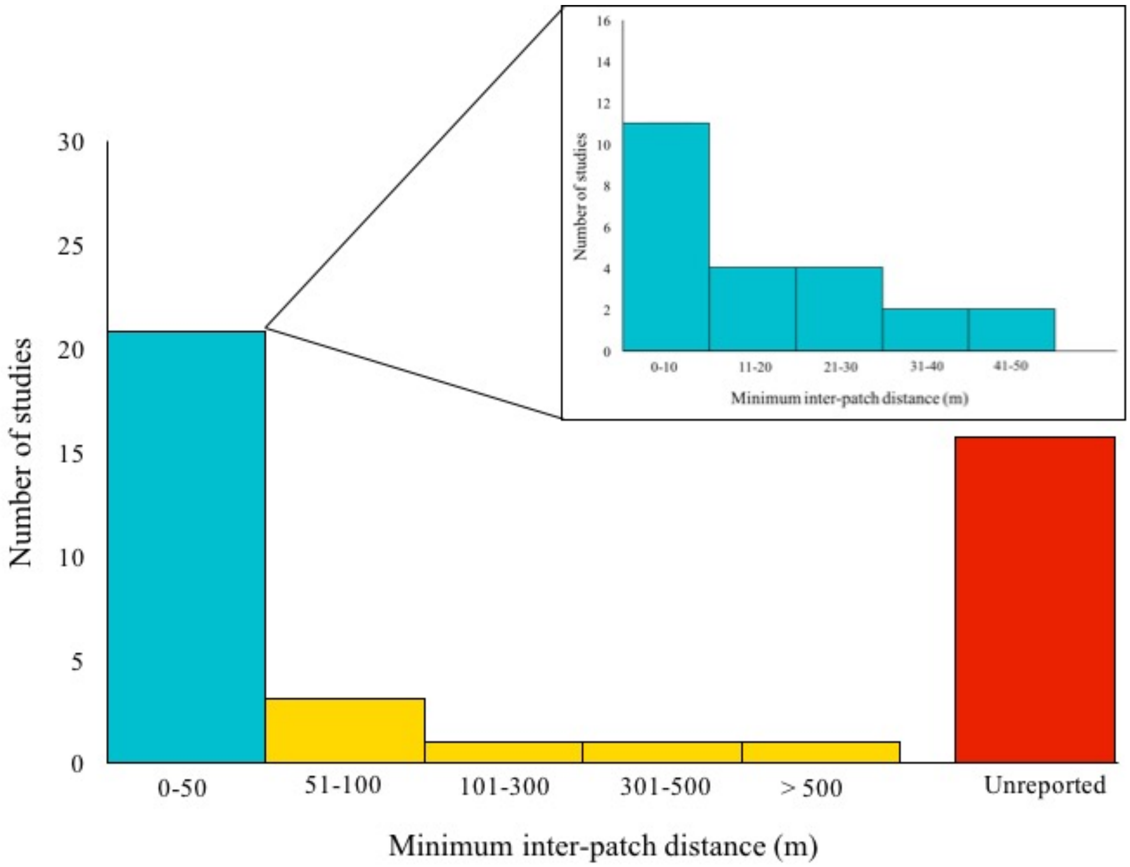


Figure 1 Inter-patch distances in studies of reef fish behaviour and ecology. Frequency distribution of minimum distances between coral reef patches recorded in 43 studies published between 1996 and 2016. Sixteen studies did not report inter-reef distances

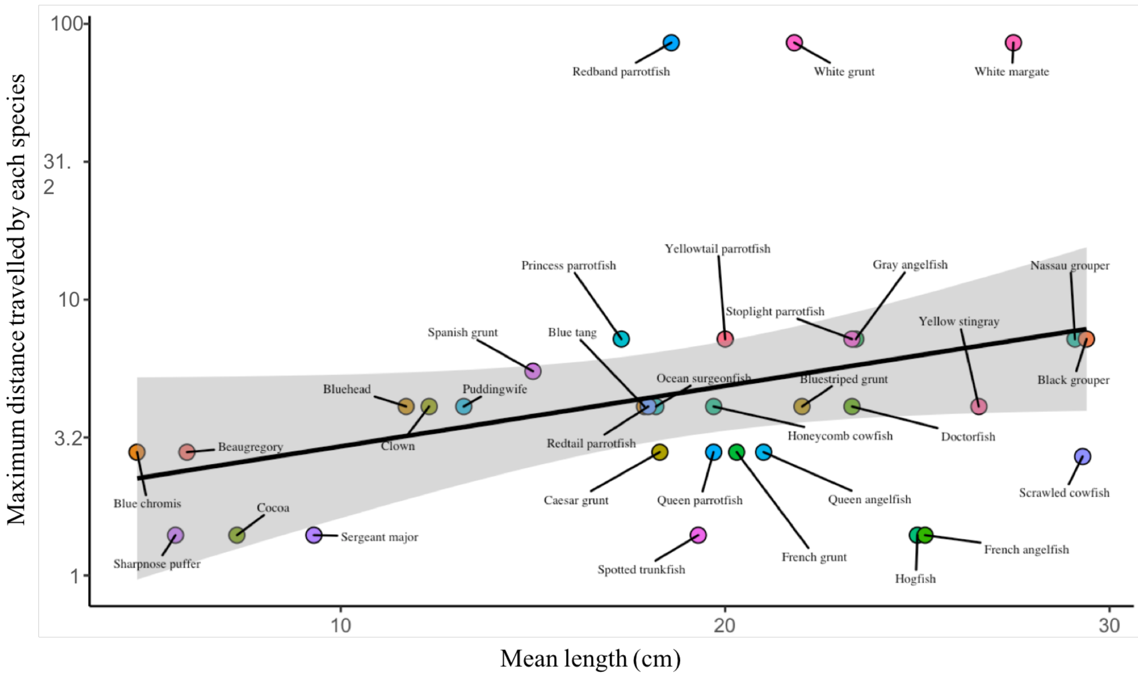


Figure 2 Relationship between maximum distance at which strongly reef-associated fish species were observed from a patch reef and species mean length on Eleuthera patch reefs. The solid line is the line of best fit (ln(maximum distance) = 0.42*mean length + 0.01), and the grey area represents the 95% confidence interval. N = 33 species

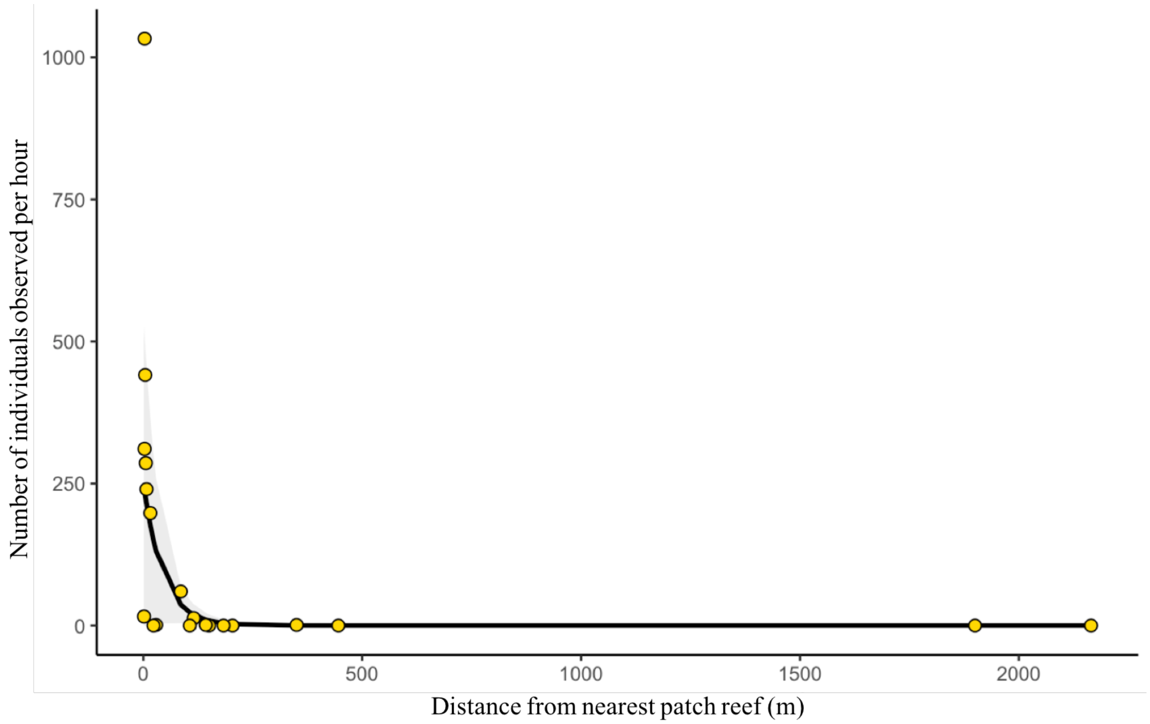


Figure 3 Relationship between the hourly rate of sand crossing by coral reef fishes and distance to the nearest coral reef patch in Eleuthera, The Bahamas. Sand crossing rates were measured by video at the mid-point between 20 pairs of nearest-neighbouring reef patches. The solid line is the line of best fit for the top generalized linear model (with negative binomial distribution and a log-link) identified by AICc (equation: number of individuals observed per hour = exp(-0.022*distance from the nearest patch) * exp(5.53)). The shaded area represents the 95% confidence interval

Tables

Table 1 Fish species observed on sand, away from coral reef patches, in Eleuthera, The Bahamas. The number of sites (out of 20) at which each species was recorded is given, as well as the maximum distance from the nearest patch reef for each species. * indicates strongly reef-associated species or families that were included in further analyses

Family	Species	Maximum distance from patch reef (m)	Number of sites
Teleosts			
*Acanthuridae (surgeonfishes)	*Acanthurus bahianus*	4.1	4
	A. coeruleus	4.1	5
	A. chirurgus	4.1	5
Balistidae (triggerfishes)	*Canthidermis sufflamen*	115	5
Carangidae (jacks)	*Carangoides bartholomaei*	86	2
	Caranx hippos	86	1
	Caranx latus	16	1
	Caranx ruber	115	11
Epiphidae (spadefishes)	*Chaetodipterus faber*	2.7	1
*Haemulidae (grunts)	*Haemulon carbonarium*	2.8	1
	H. flavolineatum	2.8	1
	H. macrostomum	5.5	2
	H. parra	86	6
	H. plumierii	86	9
	H. sciurus	4.1	5
Labridae (wrasses)	*Halichoeres bivittatus*	2165	14
	**H. garnoti*	2165	7
	**H. maculipinna*	4.1	6
	**H. radiatus*	4.1	5
	**Lachnolaimus maximus*	0.6	1
	**Thalassoma bifasciatus*	4.1	5
	Xyrichtys martinicensis	1900	1
Lutjanidae (snappers)	*Lutjanus analis*	85.5	7
	L. griseus	16	3
	L. synagris	85.5	4
	Ocyurus chrysurus	85.5	6
Mullidae	*Pseudupeneus maculatus*	5.5	1

(goatfishes)			
*Ostraciidae	*Acanthostracion polygonius*	12	1
(box/trunkfishes)	*A. quadricornis*	0.8	1
	Lactophrys bicaudalis	0.8	1
*Pomacanthidae	*Holacanthus ciliaris*	2.9	3
(angelfishes)	*Pomacanthus arcuatus*	7.2	5
	P. paru	0.8	1
*Pomacentridae	*Abudefduf saxatilis*	0.8	1
(Damselfishes)	*Chromis cyanea*	2.8	1
	Stegastes leucostictus	2.9	1
	S. variabilis	0.8	1
*Scaridae	*Scarus taeniopterus*	7.2	4
(parrotfishes)	*Sparisoma aurofrenatum*	86	2
	Sp. chrysopterus	4.1	5
	Sp. rubripinne	7.2	2
	Sp. viridae	7.2	5
Scombridae (mackerels)	*Scomberomorus regalus*	115	1
*Serranidae	*Epinephelus striatus*	7.2	5
(groupers)	*Mycteroperca bonaci*	7.2	4
Sparidae	*Calamus bajonado*	86	1
(porgies)	*C. calamus*	86	2
	C. penna	0.8	1
	C. pennatula	0.6	1
Sphyraenidae (barracudas)	*Sphyraena barracuda*	16	3
*Tetraodontidae (pufferfishes)	*Canthigaster rostrata*	0.4	1
Elasmobranchs			
Carcharhinidae (requiem sharks)	*Carcharhinus perezi*	5.5	3
Dasyatidae (whiptail stingrays)	*Dasyatis americana*	2.7	1
Ginglymostomatidae (nurse sharks)	*Ginglymostoma regalis*	115	3
*Urotrygonidae (round stingrays)	*Urobatis jamaicensis*	4.1	2

References

Appeldoorn, R., A. Aguilar-Perera, B. Bouwmeester, G. Dennis, R. Hill, W. Merten, C. Recksiek, and S. Williams. 2009. Movement of fishes (Grunts: Haemulidae) across the coral reef seascape: A review of scales, patterns and processes. Carib J Sci 45:304-316.

Barrett NS (1995) Short- and long-term movement patterns of six temperate reef fishes (families Labridae and Monacanthidae). Mar Freshwater Res 46:853–860.

Boaden AE, Kingsford MJ (2015) Predators drive community structure in coral reef fish assemblages. Ecosphere 6:1-33.

Brock RE, Lewis C, Wass RC (1979) Stability and structure of a fish community on a coral patch reef in Hawaii. Mar Biol 54:281-292.

Burnham K, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, NY, p 488.

Chapman MR, Kramer DL (2000) Movements of fishes within and among fringing coral reefs in Barbados. Env Biol Fishes 57:11–24.

Chateau O, Wantiez L (2009) Movement patterns of four coral reef fish species in a fragmented habitat in New Caledonia: implications for the design of marine protected area networks. ICES J Mar Sci 66:50–55.

Davies CR (2000) Inter-reef movement of the common coral trout, *Plectropomus leopardus*. Research Publication 61: Great Barrier Reef Marine Park Authority, Townsville, Australia.

Dickie LM, Kerr SR, Boudreau PR (1987) Size-dependent processes underlying regularities in ecosystem structure. Ecol Monogr 57:233–250.

Frederick J (1997) Post-settlement movement of coral reef fishes and bias in survival estimates. Mar Ecol Progr Ser 150:65–74.

Freiwald J (2012) Movement of adult temperate reef fishes off the west coast of North America. Can J Fish Aquat Sci 69:1362–1374.

Froese R, Pauly D (2016) Fishbase: World Wide Web electronic publication. Available at www.fishbase.org (accessed 10 September 2016).

Hixon MA, Beets JP (1993) Predation, prey refuges, and the structure of coral-reef fish assemblages. Ecol Monogr 63:77-101.

Humann P (2014) Reef Fish Identification - Florida Caribbean Bahamas, 4th edition. New World Publications, Jacksonville, FL, p 548.

Jennings S, Mackinson S (2003) Abundance–body mass relationships in size-structured food webs. Ecol Lett 6:971–974.

Kramer DL, Chapman MR (1999) Implications of fish home range size and relocation for marine reserve function. Env Biol Fishes 55:65-79.

Madin EMP, Dill LM, Ridlon AD, Heithaus MR, Warner RR (2016) Human activities change marine ecosystems by altering predation risk. Global Change Biol 22:44-60.

Meyer, J. L. and E. T. Schultz. 1985. Migrating haemulid fishes as a source of nutrients and organic matter on coral reefs. Limnol Oceanogr 30:146-156.

Meyer CG, Holland KN (2005) Movement patterns, home range size and habitat utilization of the bluespine unicornfish, *Naso unicornis* (Acanthuridae) in a Hawaiian marine reserve. Env Biol Fishes 73:201–210.

Mittelbach GG, Persson L (1998) The ontogeny of piscivory and its ecological consequences. Can J Fish Aquat Sci 55:1454–1465.

Moher D, Liberati A, Tetzlaff A, Altman DG, The PRISMA Group (2009) Preferred Reporting Items for Systematic Reviews and Meta-Analyses: The PRISMA Statement. PLoS Med 6:e100097.

Ogden JC, Buckman NS (1973) Movements, foraging groups, and diurnal migrations of the striped parrotfish *Scarus croicensis* Bloch (Scaridae). Ecology 54:589–596.

Ogden JC, Ehrilick PR (1977) The behavior of heterotypic resting schools of juvenile grunts (Pomadasyidae). Mar Bio. 42: 273-280.

Overholtzer-McLeod KL (2006) Consequences of patch reef spacing for density-dependent mortality of coral-reef fishes. Ecology 87:1017–1026.

Pittman SJ, McAlpine CA (2003) Movements of marine fish and decapod crustaceans: process, theory and application. Adv Mar Biol 44:205–294.

Popple ID, Hunte W (2005) Movement patterns of *Cephalopholis cruentata* in a marine reserve in St Lucia, WI, obtained from ultrasonic telemetry. J Fish Biol 67:981-992.

Sale PF, Steel WJ (1989) Temporal variability in patterns of association among fish species on coral patch reefs. Mar Ecol Progr Ser 51:35–47.

Scharf FS, Juanes F, Rountree RA (2000) Predator size–prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. Mar Ecol Progr Ser 208:229–248.

Sheldon RW, Prakash A, Sutcliffe WH (1972) The size distribution of particles in the ocean. Limnol Oceanogr 17:327–340.

Shulman MJ (1985) Recruitment of coral reef fishes: effects of distribution of predators and shelter. Ecology 66:1056–1066.

Smith CL, Tyler JC (1975) Succession and stability in fish communities of dome-shaped patch reefs in the West Indies. Amer Mus Novit 2572:1-18.

Sweatman HPA, Robertson DR (1994) Grazing halos and predation on juvenile Caribbean surgeonfishes. Mar Ecol Progr Ser 111:1–6.

Syms C, Jones GP (2000) Disturbance, habitat structure, and the dynamics of a coral-reef fish community. Ecology 81:2714-2729.

Tamburello N, Côté IM (2014) Movement ecology of Indo-Pacific lionfish on Caribbean coral reefs and its implications for invasion dynamics. Biol Inv 17:1639-1653.

Turgeon K, Robillard A, Grégoire J, Duclos V, Kramer DL (2010) Functional connectivityfrom a reef fish perspective: behavioral tactics for moving in a fragmented landscape. Ecology 91:3332–3342.

Chapter 3.

Homing decisions reveal naïveté of Caribbean damselfish to invasive lionfish

Abstract

Prey naïveté, or the failure of prey to recognize non-native predators due to a lack of co-evolutionary history, is thought to underpin the large impact of invasive Indo-Pacific lionfish (*Pterois* sp.) on coral reef fish populations in the western Atlantic. Most previous studies of lionfish recognition have taken place in experimental tanks that did not mimic natural conditions or used bottle or cage field designs that constrained natural behaviour. To alleviate these issues, I compared the homing patterns of experimentally translocated Caribbean bicolor damselfish (*Stegastes partitus*) in the presence and absence of standardized models of a lionfish, of an ecologically similar native piscivore (black grouper; *Mycteroperca bonaci*), and of a native non-piscivore (white grunt, *Haemulon flavolineatum*) in the field. The native grouper model elicited a strong predator avoidance response: translocated damselfish became unlikely to home when released beyond ~2 m from their territory and took longer to do so. In contrast, damselfish facing a lionfish model exhibited similar homing behaviours to those of damselfish in the presence of a non-piscivorous grunt and in the absence of any model. Fish length and translocation distance also influenced homing: damselfish stopped homing when released more than 5.6 m away from their territory and larger individuals crossed wider sand gaps. Overall, my findings suggest bicolor damselfish are naïve to the threat of predation presented by invasive lionfish. More broadly, I highlight a novel experimental translocation approach to evaluate behavioural responses of native prey species to novel predators under realistic field conditions.

Introduction

Most animals move within and among habitat patches during their lifetime. Movement among patches is often important for ecosystem-level processes, such as herbivory, biomass production and nutrient transfer (Meyer et al. 1983; Lewis and

Wainwright 1985; Mumby et al. 2004), but it is underpinned by individual decisions. How an individual perceives the costs and benefits associated with inter-patch movements is influenced by both extrinsic factors, such as inter-patch distance, matrix quality, and resource availability, and characteristics that are intrinsic to the individual, such as mobility, perceptual range, and body size (Turgeon et al. 2010). Many of these factors ultimately shape the perception of risk of predation – a key consideration in movement decisions (Lima and Dill 1990).

While individuals might readily recognize native predators as posing a significant risk, they might not perceive the same of predators with which they have not co-evolved. The evolutionary phenomenon of prey naiveté occurs when prey species exhibit no or ineffective anti-predator behaviour towards novel predators. Maladaptive responses to novel predators might include agonistic reactions, failure to reduce fitness-related activities that entail reductions in vigilance (i.e., foraging, mating), and not seeking or moving away from refuges (Helfman 1989; Knapp and Matthews 2000). Invasive predators might therefore inflict disproportionately high mortality on naïve prey that are unfamiliar with the archetype and hunting strategies of their pursuer (Diamond and Case 1986; Cox and Lima 2006; Sih et al. 2010).

In naturally fragmented coral reef habitats, the reluctance of small-bodied reef fishes to move over open expanses of sand is widely considered to be a predator avoidance response (Sweatman and Robertson 1994; Turgeon et al. 2010). Homogeneous matrices of sand surrounding coral patches offer low structural complexity and limited or no refuge from predators (Brock and Norris 1989; Syms and Jones 2000), which deters fish movement because of the perceived heightened predation risk. If willingness to cross sand is indeed tied to perceived risk of predation, then distance to safety, body size and predator recognition should be key determinants of the decisions of reef fish to move over sand. Translocations and gap-crossing experiments have shed light on the effects of distance to safety on reef fish movement. Studies of recolonization of depopulated patch reefs surrounded by sand show that inter-patch gaps as small as 10 m can provide at least a partial barrier to fish movement (Brock and Norris 1989; Syms and Jones 2000). Turgeon et al. (2010) further reported the homing probability of translocated longfin damselfish (*Stegastes diencaeus*) declined sharply and steeply as sand gap distances between coral patches increased beyond 3.90 m. In addition, given that smaller fishes are prey to a wider range of predators than larger fishes (Mittelbach and Persson 1998; Scharf et al. 2000), perceived risk of predation should be higher for smaller prey, making them less likely to venture over open sand. To my knowledge, however, no study has evaluated how the recognition of predation risk affects coral reef fish movement. One should expect anti-predator decisions affecting movement to be contingent on accurate assessment of the risk posed by larger fishes.

In this study, I used a natural predator avoidance behaviour – the reluctance of reef fish to move across open sand gaps (e.g., Turgeon et al. 2010) – as a novel assay to test prey naiveté to an invasive fish predator, the Indo-Pacific lionfish (*Pterois* sp.). Since 1985, lionfish have spread at an unparalleled rate through the northwestern Atlantic, Caribbean Sea and Gulf of Mexico (Whitfield et al. 2007; Schofield 2009; Betancur-R et al. 2011). These generalist carnivores have caused major reductions in native fish recruitment and abundance on some reefs (Albins and Hixon 2008; Green et al. 2012). Prey naiveté is thought to have facilitated the high predation rates of lionfish in the invaded range (Côté and Smith 2018). However, so far, most studies of lionfish recognition by native coral reef fish have taken place in experimental tanks that did not mimic natural conditions (e.g., Marsh-Hunkin et al. 2013) or have used field designs that severely constrained natural behaviour by confining lionfish and/or their prey in bottles or cages (e.g., Kindinger 2014; Anton et al. 2016). To alleviate these issues, I conducted experimental translocations in the wild to compare the homing probability of damselfish in the presence and absence of standardized models of native and non-native, piscivorous and non-piscivorous fishes.

Specifically, I asked how the likelihood that translocated damselfish would cross a sand gap to return to their territory, and the threshold distance they were willing to cross, changed in the presence and absence of an invasive lionfish, of an ecologically similar native piscivore (i.e., a grouper) and of a native non-piscivore (i.e., a grunt). I predicted that damselfish would be less likely to home as perceived risk of predation increased, that is with smaller body size (Mittelbach and Persson 1998; Scharf et al. 2000), increasing translocation distance over sand (Helfman and Winkelman 1997; Turgeon et al. 2010), as well as in the presence of a native predator. The presence of a native predator should also elicit avoidance behaviours in translocated damselfish (Cox and Lima 2006), such as longer times spent seeking or using shelter, swimming farther to avoid proximity to the predator and swimming faster. These adaptive responses should be absent if damselfish are naïve to the threat posed by invasive lionfish.

Materials and methods

Ethics statement

The study conforms to the guidelines of the Canadian Council on Animal Care and was approved by the Simon Fraser University Animal Care Committee (permit 1234B-17).

Study sites and species

I conducted my field study on 132 coral reef patches along the west coast of Curaçao, one of the leeward islands of the Netherlands Antilles, between June and August 2017. The first sighting of lionfish in Curaçao was reported on 27 October 2009 (de Léon et al. 2013), and lionfish are now widely distributed on reefs around the island (personal observations). My reef patches were distributed across eight sites (number of patches per site: 1 – 29). The patches were small (mean area ± SD: 1.15 ± 0.60 m2), in shallow water (mean depth ± SD: 3.22 ± 1.26 m2) and were separated from each other by open expanses of sand and sparse seagrass. Each patch was occupied by at least one adult bicolor damselfish (*Stegastes partitus*), although most patches supported small aggregations of three or more individuals.

Bicolor damselfish are strictly diurnal planktivores. They form small colonies of up to 20 individuals, which are organised in size-based social hierarchies (Myrberg 1972), and both sexes aggressively defend small territories above which they feed (Hogan et al. 2012). The males are polygynous and provide parental care of the eggs, which they defend vigorously against potential predators such as wrasses (Knapp and Warner 1991). Territory acquisition and protection are therefore critical for foraging and reproduction of bicolor damselfish, which should generate motivation in translocated fish to return home. Bicolor damselfish have been shown to exhibit anti-predator responses (e.g., reduced feeding and chasing activity) in the presence of model predators, particularly when predators are large and nearby (Helfman and Winkelman 1997).

Translocations and experimental treatments

Using SCUBA, I translocated a total of 154 individuals, each only once, over sand gap widths varying from 1 m to 7 m. For each translocation, one diver captured a bicolor damselfish in a scoop net and measured its total length to the nearest 0.1 cm. To do so, we marked the tip of the snout and the tip of the longest lobe of the caudal fin on a PVC dive slate and measured the linear distance between each mark. Only sexually mature adults (i.e., individuals ≥ 3.0 cm TL; Almada-Villela et al. 2003) were used in this study, and if capture was unsuccessful after five minutes, we moved to a new patch to avoid inducing high levels of stress on the focal individual. After size measurement, the diver immediately released the focal fish on a small pile of six pieces of coral rubble (i.e., the 'release site') set up at a predetermined, straight-line distance over sand from the outer edge of the focal fish's home patch. The release site was always closer to the individual's home patch than any alternative areas of refuge. Upon the release of a translocated fish, a second diver recorded the time spent by the fish in the release site prior to homing, and the time spent swimming from the release site to the home patch. Simultaneously, the first diver traced the homing path of the focal damselfish on a dive slate, noting the position of recognizable landmarks (e.g., coral pieces, shoots of seagrass, etc.). Fish that remained in the release site for the whole observation period (30 min), or that began to defend a new patch, were considered to not have homed (Turgeon et al. 2010). If homing was successful, we measured the length of the focal fish's homing path, as depicted on the hand-drawn map. At the end of each translocation, I counted the total number of bicolor damselfish on the patch, excluding the focal individual. I also recorded depth and, using measuring tape, determined the length and width of the home patch. A small number of patches (n = 22) were used for two translocations because of the limited number of suitable territories. In these instances, we waited at least 20 days before revisiting patches a second time and caught a fish of a different size from the first caught at that site.

Each translocated fish was assigned haphazardly to be a control (N = 45 damselfish) or exposed to one of three model treatments (N = 36–37 damselfish per treatment). In the control configuration, I placed a 30-cm Plexiglass rod vertically in the sand, 50 cm from the release site, along the most direct route between the release site and home patch. In the model treatments, one of three formalin-preserved, resin-coated models was attached to the vertical rod, 20 cm above the sand: (1) a French grunt

(*Haemulon flavolineatum*; non-piscivore treatment), (2) a black grouper (*Mycteroperca bonaci;* native piscivore treatment) or (3) a lionfish (*Pterois* sp., invasive piscivore treatment) (Fig. B1). All models were the same size (35 cm TL; i.e., more than three times the size of the largest damselfish used in this study, and hence piscivores were potential predators of all translocated damselfish), with their pectoral fins oriented in a strike pose to mimic foraging behaviour, since damselfish have been shown to be sensitive to both predator size and posture (Helfman 1989). A pilot experiment revealed that the homing probability of bicolor damselfish (n = 12 individuals) was significantly reduced when the distance between the release site and the grouper model (i.e., the native foraging piscivore predicted to elicit the strongest predator-avoidance response) became shorter (Fig. B2). Each model was therefore placed at a constant absolute distance from the release site (i.e., 50 cm) for experimental translocations.

Analyses

To determine whether the presence of different fish models along the homing route affected the likelihood that damselfish returned to their territory, I used generalized linear mixed-effects (GLMM) models (lmer library in R with the restricted maximum likelihood methods) to examine the effects of model treatment (4 levels: control (no model), non-piscivore, native piscivore, invasive piscivore) on the homing probability of damselfish. I considered homing probability as a logistic response (0 = did not home; 1= homed), and constructed 16 candidate models (with binomial error structure and a log-link function), representing all possible combinations of three habitat-related explanatory variables (i.e., treatment type, translocation distance, and density of conspecifics on the home patch) and one intrinsic variable (i.e., focal fish size). I used site as a random factor in all models to account for replication of patches within sites. Visual examination of the residuals plot confirmed that the assumption of homogeneity of residual variance was met, and there was no significant correlation between explanatory variables. The candidate models corresponded to the following *a priori* hypotheses: (1) the effects of model treatment type on homing should be related to damselfish's ability to recognize predators and accurately assess the level of threat associated with each model (Helfman 1989; Sih et al. 2010), (2) homing probability should decrease as the distance fish need to travel across sand increases (e.g., Turgeon et al. 2010; Chapter 2), (3) homing probability should increase as the density of conspecifics on the home patch increases, since conspecifics might offer predator protection via a dilution effect if a predator is unable to consume all prey in a group (Stamps 1988; Sieving et al. 2004; Schmidt et al. 2008) and (4) larger individuals should be more likely to home because risk of predation is often lower for larger fish (Rice et al. 2011; Hamilton et al. 2014). Using a model selection approach corrected for small sample size (i.e., Akaike Information Criterion, AICc; Burnham and Anderson 2002), I identified the best-supported GLMM model as that with the lowest AICc value (Burnham and Anderson 2002), although models that differed in AICc values by less than two units were considered equally well supported by the data (Burnham and Anderson 2002). I computed the AICc model-averaged coefficients for each parameter in the top model(s), and depicted them using the control (no model) treatment as a baseline. I plotted the binomial logistic regression (with a logit link function) from model-average coefficients for each treatment.

For the fish that successfully homed (n = 50 individuals), I compared total homing time, time spent at the release site (i.e., shelter time), detour distance swum, and swimming speed in the absence and presence of fish models. I calculated the 'detour' distance for every fish that homed by subtracting the distance between the release site and home patch from the length of the actual homing route of the focal fish. The detour distance therefore represents the additional distance swum beyond a straight path home. I calculated swimming speed as the total distance swum between the release site and home patch divided by the time spent swimming by each fish. I used separate linear models to test how each of the four responses co-varied with translocation distance in the absence of any fish model. I then used the line-of-best-fit of each linear model to predict the values of each of the four responses for each translocation distance tested with the different fish models. I subtracted the predicted from the observed values to obtain deviations in fish responses in the presence of each of the fish models and compared these values among fish model treatments using one-way analyses of variance (ANOVAs).

Results

The 154 translocated damselfish ranged in total length (TL) from 3.5 cm to 9.7 cm (mean ± SD: 5.51 ± 1.27 cm). There were no significant differences in mean damselfish size or in mean density of conspecifics at each territory across fish model treatments (one-way ANOVAs; TL: $F_{3,150} = 1.35$, $p = 0.26$; conspecific density: $F_{3,150} =$

0.37, p = 0.78). Following release, damselfish typically hid on or within the release site for variable amounts of time. Across all treatments, 62% of translocated damselfish (ranging from 53% in the no-model treatment to ~80% in the native piscivore treatment) did not return to their home territory within 30 min. The proportion of fish homing was highest in the first 4 minutes after release, and declined nearly exponentially thereafter (Fig. B3). To reduce the potential effect of variation in threat assessment time by damselfish, I limited my analyses to fish that homed within the first eight minutes of observation. This time window captured 80% of homing damselfish (Fig. B3).

Two models of homing probability were strongly supported (i.e., Δ AICc < 2; Table 2) and explained 62% of the variation in homing probability. They both included the presence/absence of a fish model along the homing route, as well as translocation distance and fish size. The second top model also included conspecific density (Table 2). The simpler top model obtained twice as much support as the second-ranked model (Table 2).

In the absence of a fish model, damselfish homing probability declined significantly (Fig. 4) but non-linearly (Fig. 5) with translocation distance, and damselfish stopped homing when released more than 5.6 m away from their territory (Fig. 5). Of all three fish models presented, only the native piscivore significantly decreased the probability that a damselfish would home compared to when no model was present (Figs 5 & B4). The presence of the native piscivore model reduced the threshold translocation distance, at which homing probability is 50%, from 3.4 m (in the absence of a fish model), on average, to 2.1 m (Fig. 5). In contrast, these threshold translocation distances in the presence of a non-piscivore model (3.8 m, on average) and of an invasive piscivore model (2.9 m, on average) were similar to that observed in the absence of any model (Fig. B4). The maximum homing distances were similar in the presence of the non-piscivorous grunt (4.8 m) and the invasive lionfish models (4.2 m; Fig. B4), but dropped to 3.4 m in the native piscivore treatment (Fig. 5).

Homing probability increased non-linearly with damselfish size (Fig. 6), such that the largest translocated damselfish (7.9 cm) was, on average, 70% more likely to return home than the smallest one (3.6 cm), in the absence of a fish model. Damselfish became more likely to home than not to home (i.e., homing probability = 50%) at 6 cm TL, on average (Fig. 6). Fish smaller than 4.1 cm, however, were never observed homing. The density of conspecifics at the home territory was not a determinant of damselfish homing (Fig. 4).

As expected, total homing time and the time spent in shelter upon release increased linearly with translocation distance in the absence of a fish model (homing time: adjusted r^2 = 0.29, $F_{1,17}$ = 8.53, p = 0.009; time in shelter: adjusted r^2 = 0.25, $F_{1,17}$ = 7.14, p = 0.016; Fig. B5a, b). Damselfish also took larger detours as translocation distance increased (adjusted r^2 = 0.55, $F_{1,17}$ = 7.54, p = 0.014; Fig. B5c), but swimming speed did not co-vary with translocation distance (adjusted r^2 = 0.07, $F_{1,17}$ = 2.46, p = 0.13) when fish models were absent. The presence of a fish model on the homing route significantly affected damselfish total homing time (one-way ANOVA; $F_{2,38}$ = 3.58, p = 0.038) and time in shelter (one-way ANOVA; $F_{2,38}$ = 2.80, p = 0.043). On average, damselfish released in the presence of the native grouper model took 3.3 min longer to home (Fig. 7a) and remained in shelter 2.6 min longer (Fig. 7b) than damselfish in the absence of any fish model. Damselfish confronted with models of a non-piscivorous grunt and an invasive lionfish had similar homing times and times in shelter as damselfish in the absence of a fish model (Fig. 7a, b). In contrast, detour distances in the presence of fish models did not significantly deviate from that in the absence of a fish model (one-way ANOVA; $F_{2,38}$ = 0.73, p = 0.49). Since swimming speed did not co-vary with translocation distance in the absence of a fish model, I simply compared absolute speed of translocated damselfish among treatments and found no significant differences (one-way ANOVA; $F_{3,55}$ = 1.51, p = 0.22)

Discussion

In this study, I asked whether the homing patterns of experimentally translocated bicolor damselfish could be used to infer recognition of invasive lionfish by native prey fish. In general, damselfish were more likely to home when they were larger and when they were released closer to their territory. As expected, a native grouper model elicited a strong predator avoidance response by bicolor damselfish: translocated fish were less likely to home, took longer to do so and stayed in the release shelter longer in the presence of the grouper model than in the presence of any other model. In contrast, damselfish facing a lionfish model exhibited similar homing behaviours to those of damselfish in the presence of a non-piscivorous grunt and in the absence of any model. My results suggest that bicolor damselfish were naïve to the threat of predation presented by invasive lionfish. Translocations offer a novel experimental approach to evaluate predator recognition and behavioural responses of native prey species under realistic field conditions.

Fish aversion to crossing sand gaps appears to be strongly related to perceived risk of predation. Translocation distance over open sand and fish size were the determinants of fish homing probability in the absence of a fish model. Given the low shelter availability presented by featureless sand habitat, and the likelihood of heightened encounter rates of predatory fishes (Shulman 1985; Sweatman and Robertson 1994; Turgeon et al. 2010), I expected that damselfish would be increasingly reluctant to return to their home territory as translocation distance over sand increased. This prediction was confirmed. In the absence of a model, the negative sigmoidal shape of the overall relationship between fish homing and translocation distance mirrors that documented by Turgeon et al. (2010) for another species of highly territorial Caribbean damselfish, the longfin damselfish (*Stegastes diencaeus*). The homing probability of translocated longfin damselfish decreased steeply and non-linearly with increasing sand gap widths, and individuals were unlikely to cross sand gaps wider than 3.9 m (Turgeon et al. 2010). The same threshold distance (i.e., translocation distance at which homing probability is 50%) was ~3.3 m in bicolor damselfish. This difference is consistent with the slightly smaller size of bicolor damselfish (Froese and Pauly 2016). Indeed, I demonstrated that smaller bicolor damselfish were less likely to home following experimental translocation than larger conspecifics. This pattern was expected, given the size-structured nature of predator–prey relationships in marine environments: smaller fish should be under greater risk of predation than larger fish away from areas of refuge (Boaden and Kingsford 2015).

In contrast to my prediction, conspecific density on the home territory was not a determinant of damselfish homing probability. Since the presence and/or abundance of conspecifics might indicate patch safety (Stamps 1988; Sieving et al. 2004; Schmidt et al. 2008), I had anticipated that damselfish removed from high-density patches would be strongly motivated to home to avoid the costs associated with loss of good or safe territories. However, bicolor damselfish colonies are organized in dominance hierarchies that are strongly size-dependent (Myrberg1972; Sadovy 1985), with aggressive behaviour most frequently occurring between individuals similar in size (Sadovy 1985). The size distribution of individuals on a home territory, and particularly where a translocated fish falls in this distribution, might therefore play a more important role in motivating focal fish to home than conspecific density.

The explicit predation risk presented by a native piscivore model triggered several changes in homing behaviour of bicolor damselfish. In the presence of a grouper model, the likelihood of damselfish homing was depressed across all translocation distances. Damselfish spent more time in the release shelter, an anti-predator response frequently recorded when perceived risk of predation is high (Shulman 1985; Sweatman and Robertson 1994; Madin et al. 2016; Turgeon et al. 2010). As a result, average homing times of damselfish were longer than when no fish model was present. In contrast, the behaviours of translocated damselfish in the invasive lionfish and native non-piscivore treatments mirrored those recorded in the no-model control, providing strong evidence that damselfish are naïve to the threat of lionfish.

The absence of recognition of invasive lionfish as a predator demonstrated by translocated bicolor damselfish is consistent with previous studies that used very different methods. In field experiments, native prey fish usually display the same lack of fear or aggression towards lionfish in cages or bottles as they do towards constrained native non-predators or empty containers (Black et al. 2014; Kindinger, 2015; Anton et al. 2016). In the laboratory, native prey fish sometimes show responses that are consistent with the perception of risk, such as foraging less (Eaton et al. 2016; see also Kindinger and Albins 2017 for a similar result in the field), spending more time under cover (Marsh-Hunkin et al. 2013), forming larger groups (Eaton et al. 2016) and moving less (Marsh-Hunkin et al. 2013), but these responses are inconsistent across studies. At any rate, one might wonder whether we should even expect predator recognition to evolve at all in lionfish prey in the invaded range since damselfish (*Chromis viridis* and *Pomacentrus chrysurus*) from the native range of lionfish showed no behavioural evidence of predator recognition, and were readily preyed upon by lionfish in captivity (Lönnsted and McCormick 2013; McCormick and Allan 2016). The cryptic body shape, scent and colouration of lionfish might allow it to circumvent prey risk assessment abilities, perhaps contributing to its successful invasion of Caribbean marine ecosystems (Lönnsted and McCormick 2013).

In conclusion, I found no evidence of recognition of invasive lionfish by bicolor damselfish at a Caribbean location invaded nearly a decade ago (de Léon et al. 2013).

Perhaps more importantly, I combined two traditional approaches in behavioural studies, namely translocations and the presentation of models, to provide a novel, well-controlled and highly replicable method to evaluate threat recognition by native species in invaded communities in a natural setting. Repeating these naiveté trials over space and time might offer a powerful means to detect invader-induced changes in the behaviour of native species.

Figures

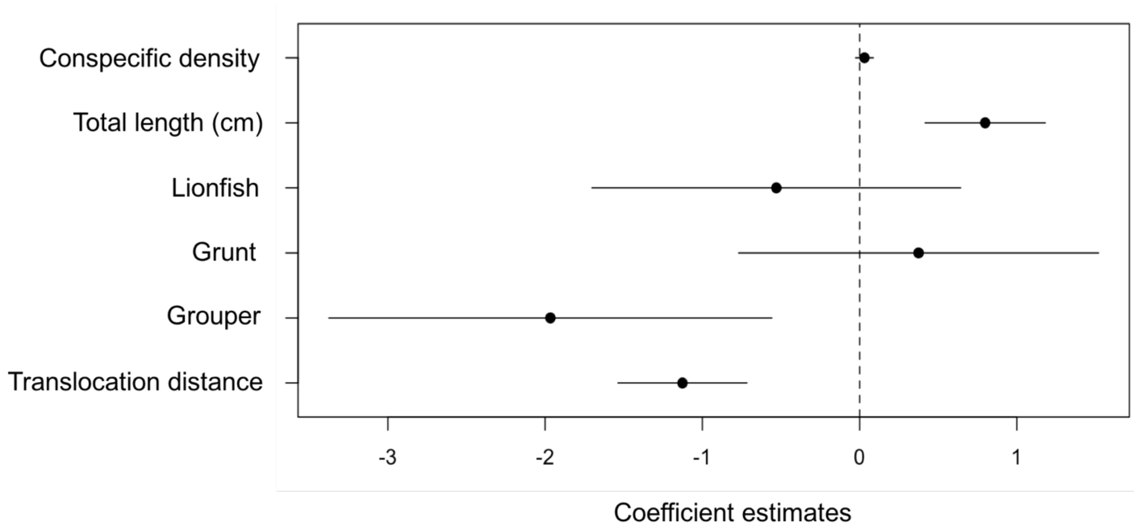


Figure 4 Coefficients of the effects of various factors on the homing probability of translocated bicolor damselfish in Curaçao, Netherlands Antilles. Points were averaged across two top generalized mixed-effects models, and are shown bounded by 95% confidence intervals. Positive value (to the right of the dashed vertical line) indicate an increase in homing probability, while negative values indicate a decrease. The levels ‘Lionfish’, ‘Grunt’, and ‘Grouper’ refer to the type of preserved fish model placed along the homing route, and are compared against the baseline level of no fish model

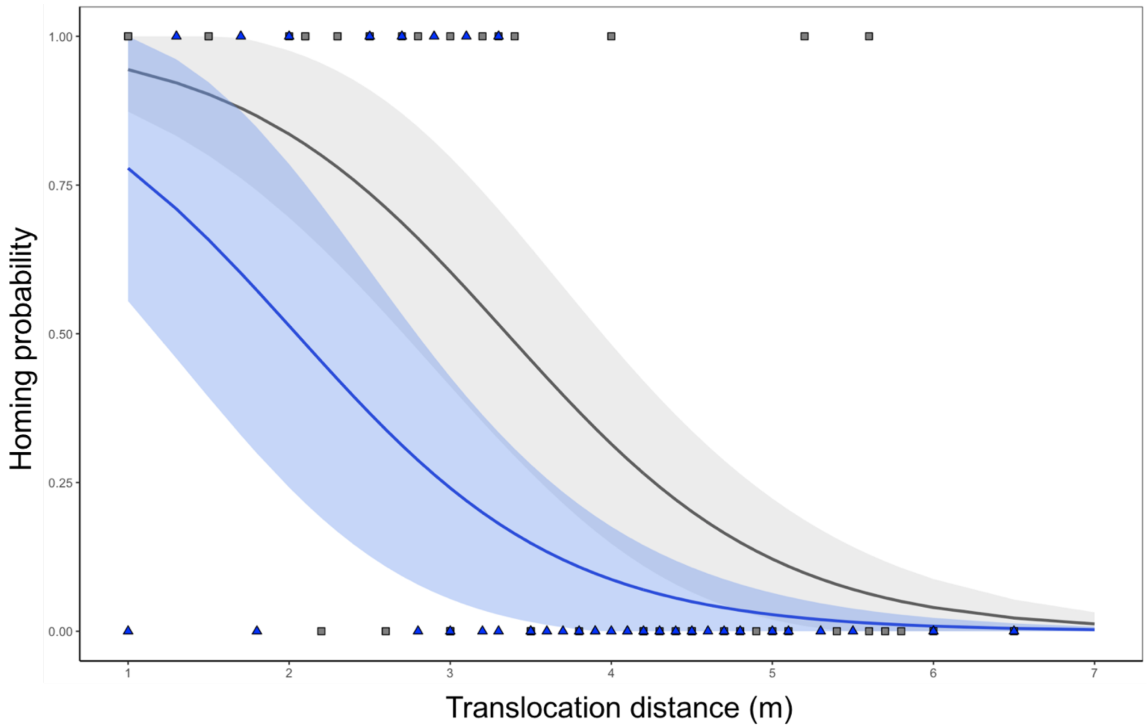


Figure 5 Relationships between the homing probability of translocated bicolor damselfish and the distance (in m) between the release site and the home patch, in the absence of a fish model (grey symbols and lines) and presence (blue symbols and lines) of a native piscivore (i.e., a black grouper) model along the homing route. The solid lines are the lines of best fit for the averaged, best-supported generalized linear mixed-effects model identified by AICc (equation: homing probability = exp(-1.31*translocation distance) * exp(-1.68*Grouper) * exp(0.59*Grunt) * exp(-0.32*Lionfish) * exp(0.83*Fish length) * exp(0.01*Conspecific density) * exp(6.23)). The shaded areas represent 95% confidence intervals

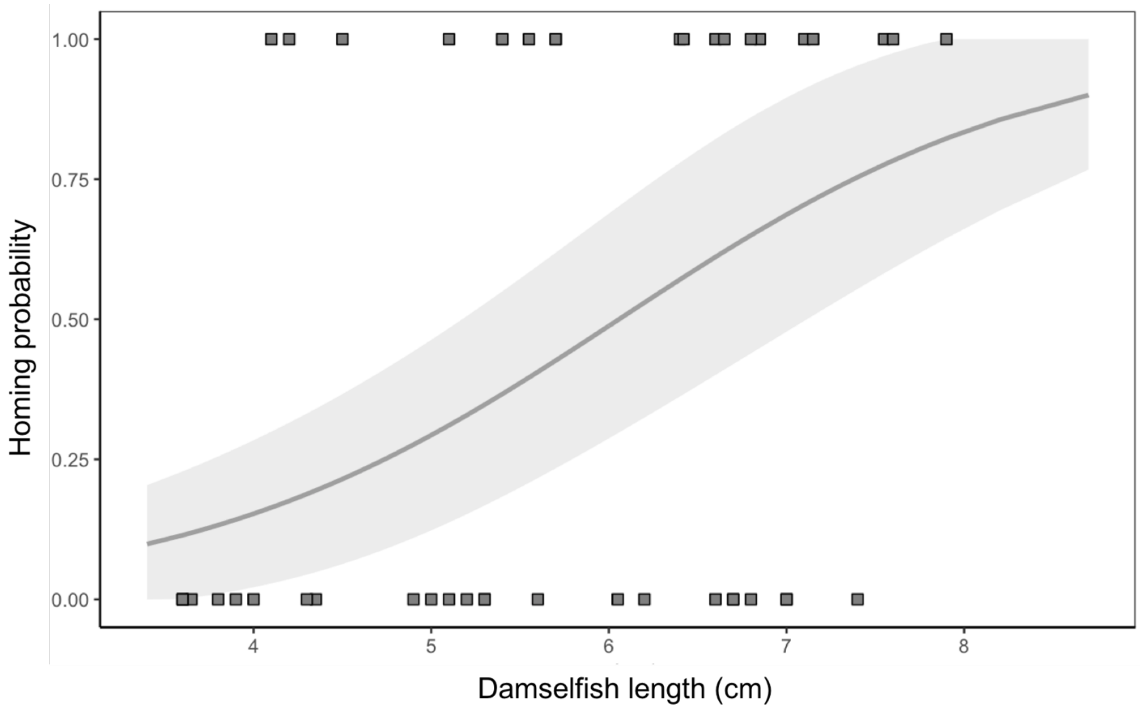
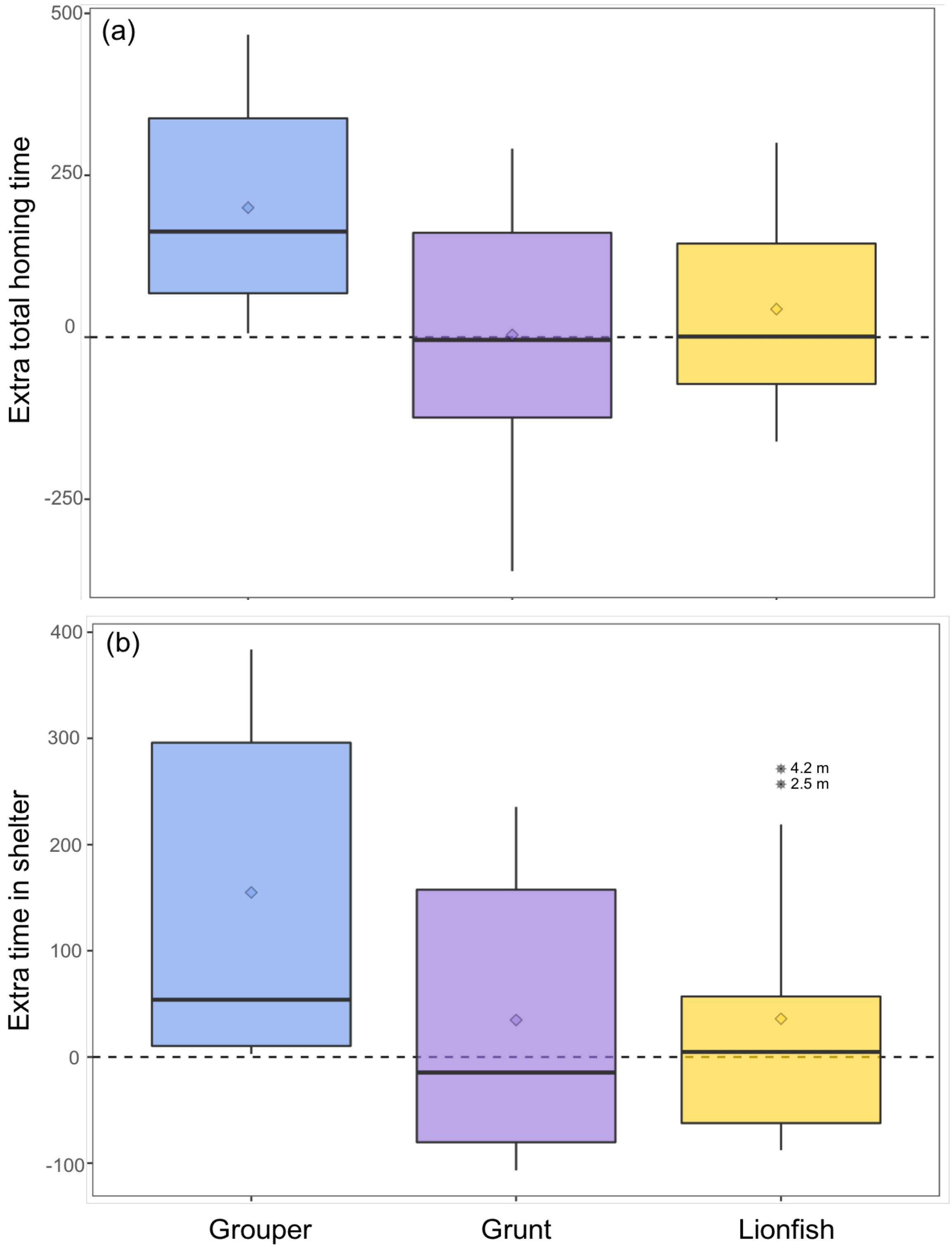


Figure 6 Relationship between the homing probability of translocated bicolor damselfish and damselfish length (TL in cm) in the absence of a fish model on the homing route. The solid line is the line of best fit for the averaged best-supported generalized linear mixed-effects model identified by AICc (equation as shown in Fig. 2). The shaded areas represent 95% confidence intervals



(a)
Extra total homing time
500
250
0
-250
(b)
Extra time in shelter
400
300
200
100
0
-100
4.2 m
2.5 m
Grouper
Grunt
Lionfish

Figure 7 Homing responses of translocated bicolor damselfish to the presence of various fish models along the homing route. (a) Extra time taken to home (s) and (b) extra time spent in shelter before homing (s) in the presence of models of a native piscivore (i.e., black grouper), native non-piscivore (i.e., French grunt) and a non-native piscivore (i.e., lionfish). Extra homing time and extra time in shelter were calculated relative to these responses in the absence of any fish model (see Methods). Positive values mean that times were longer than in the absence of a fish model. The thick horizontal lines are medians, diamonds are means, the top and bottom of the boxes are the 25th and 75th percentiles, and the top and bottom of whiskers are the 90th and 10th percentiles, respectively. Grey dots represent outliers and the translocation distances at which they occurred

Tables

Table 2 Results of AIC model selection analysis of logistic models describing homing probability of translocated bicolor damselfish in terms of translocation distance, fish size (total length, cm), density of conspecifics on the home patch, and fish treatment (i.e., no fish model, native non-piscivore model (grunt), native piscivore model (grouper), non-native piscivore model (lionfish)). Site was included as a random factor in all models. K is the number of parameters in each model; ΔAICc is the difference in AICc value between the focal model and the model with the lowest AICc; Akaike weight wi is interpreted as the probability that model is the best model of the candidate set given the data at hand. Models shaded in grey differ in ΔAICc values by less than two and are considered equally well supported by the data

Model	k	-Log likelihood	AIC_c	Δ AIC	W_i	pseudo-R^2
Model + Translocation distance + Fish length	5	62.39	139.6	0.00	0.60	0.59
Model + Translocation distance + Fish length + Conspecific density	6	61.89	140.8	1.22	0.33	0.60
Translocation distance + Fish length	4	68.24	144.8	5.21	0.044	0.54
Translocation distance + Fish length + Conspecific density	5	67.68	145.8	6.20	0.03	0.54
Model + Distance	3	72.98	158.8	18.98	0.00	0.47

References

Almada-Villela PC, Sale PF, Gold-Bouchot G, Kjerfve B (2003) Manual of methods for the MBRS synoptic monitoring system: Selected methods for monitoring physical and biological parameters for use in the Mesoamerican Region. Mesoamerican Barrier Reef Systems Project (MBRS): 158 pp

Albins MA, Hixon MA (2008) Invasive Indo-Pacific lionfish (*Pterois volitans*) reduce recruitment of Atlantic coral-reef fishes. Mar Ecol Prog Ser 367:233–238.

Betancur-R R, Hines A, Acero PA, Ortí G, Wilbur AE, et al. (2011) Reconstructing the lionfish invasion: insights into Greater Caribbean biogeography. J Biogeogr 38:1281–1293.

Black AN, Weimann SR, Imhoff VE, Richter ML, Itzkowitz M (2014) A differential prey response to invasive lionfish, *Pterois volitans*: prey naiveté and risk-sensitive courtship. J Exp Mar Biol Ecol 460:1−7.

Boaden AE, Kingsford MJ (2015) Predators drive community structure in coral reef fish assemblages. Ecosphere 6:1–33.

Brock RE, Norris JE (1989) An analysis of the efficacy of four artificial reef designs in tropical waters. Bull Mar Sci 44:934–941.

Burnham K, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, NY, p 488

Cox JG, Lima SL (2006) Naiveté and an aquatic-terrestrial dichotomy in the effects of introduced predators. Trends Ecol Evol 21:674−680.

Côté IM, Smith NS (2018) The lionfish *Pterois* sp invasion: Has the worst-case scenario come to pass? J Fish Biol 92:660–689.

de Léon R, Vane K, Bertuol P, Chamberland V, Simal F, Imms E, Vermeij MJA (2013) Effectiveness of lionfish removal efforts in the southern Caribbean. Endanger Species Res 22:175–182.

Diamond J, Case TJ (eds) (1986) Community ecology. Harper Collins, New York, NY

Eaton L, Sloman KA, Wilson RW, Gill AB, Harborne AR (2016) Non-consumptive effects of native and invasive predators on juvenile Caribbean parrotfish. Env Biol Fishes 99:499–508.

Froese R, Pauly D (2016) Fishbase: World Wide Web. https://www.fishbase.org. Accessed 10 September 2016

Green SJ, Akins JL, Maljković A, Côté IM (2012) Invasive lionfish drive Atlantic coral reef fish declines. PLOS ONE 7:e32596.

Hamilton SL, Newsome SD, Caselle JE (2014) Dietary niche expansion of kelp forest predator recovery from intense commercial exploitation. Ecology 95:164–172.

Helfman GS (1989) Threat-sensitive predator avoidance in damselfish trumpetfish interactions. Behav Ecol Sociobiol 24:47–58.

Helfman GS, Winkelman DL (2010) Threat sensitivity in bicolor damselfish: effects of sociality and body size. Ethology 103:369–383.

Kindinger TL (2015) Behavioral response of native Atlantic territorial three spot damselfish (*Stegastes planifrons*) toward invasive Pacific red lionfish (*Pterois volitans*). Environ Biol Fish 98:487−498.

Kindinger TL, Albins MA (2017) Consumptive and non-consumptive effects of an invasive marine predator on native coral-reef herbivores. Biol Inv 19:131–146.

Knapp RA, Matthews KR (2001) Non-native fish introductions and the decline of the mountain yellow-legged frog from within protected areas. Conserv Biol 14: 428–438.

Lewis SM, Wainwright PC (1985) Herbivore abundance and grazing intensity on a Caribbean coral reef. J Exp Mar Biol Ecol 87:215–228.

Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool 68:619 – 640.

Lönnstedt OM, McCormick MI (2013) Ultimate predators: lionfish have evolved to circumvent prey risk assessment abilities. PLOS ONE 8: e75781.

Madin EMP, Dill LM, Ridlon AD, Heithaus MR, Warner RR (2016) Human activities change marine ecosystems by altering predation risk. Glob Change Biol 22:44–60.

Marsh-Hunkin KE, Gochfeld DJ, Slattery M (2013) Anti-predator responses to invasive lionfish, *Pterois volitans*: interspecific differences in cue utilization by two coral reef gobies. Mar Biol 160:1029−1040.

McCormick MI, Allan BJM (2016) Lionfish misidentification circumvents an optimized escape response by prey. Conserv Physiol 4:cow064.

Meyer JL, Schultz ET, Helfman GS (1983) Fish schools: an asset to corals. Science 220:1047–1049.

Mittelbach GG, Persson L (1998) The ontogeny of piscivory and its ecological consequences. Can J Fish Aquat Sci 55:1454–1465.

Myrberg AA (1972) Ethology of the bicolor damselfish, *Eupomacentrus partitus* (Pisces: Pomacentridae): a comparative analysis of laboratory and field behaviour. Anim Behav Monogr 5:197–283.

Rice JA, Crowder LB, Rose KA (2011) Interactions between size-structured predator and prey populations: experimental test and model comparison. Trans Amer Fish Soc 122:481–491.

Sadovy Y (1985) Field analysis of the dominance hierarchy of the bicolor damselfish, *Stegastes partitus* (Poey) (Pisces: Pomacentridae). NOAA Symposia Series for Undersea Research 3:129–138.

Salo P, Korpimaki E, Banks PB, Nordström M, Dickman, CR (2007) Alien predators are more dangerous than native predators to prey populations. Proc R Soc London B 274:1237−1243.

Scharf FS, Juanes F, Rountree RA (2000) Predator size–prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. Mar Ecol Prog Ser 208:229–248.

Schmidt KA, Lee e, Ostfeld RS, Sieving K (2008) Eastern chipmunks increase their perception of predation in risk response to titmouse alarm calls. Behav Ecol 19:759–763.

Schofield PJ (2010) Update on geographic spread of invasive lionfishes (*Pterois volitans* [Linnaeus, 1758] and *P. miles* [Bennett, 1828]) in the western North Atlantic Ocean, Caribbean Sea and Gulf of Mexico. Aquat Invasions 5: S117−S122

Sieving KE, Contreras TA, Muate KL (2004) Heterospecific facilitation of forest-boundary crossing by mobbing understory birds in north-central Florida. Auk 121:738–751.

Sih A, Bolnick DI, Luttbeg B, Orrock JL and others (2010) Predator-prey naïveté, antipredator behavior, and the ecology of predator invasions. Oikos 119:610−621.

Shulman MJ (1985) Recruitment of coral reef fishes: effects of distribution of predators and shelter. Ecology 66:1056–1066.

Stamps JA (1988) Conspecific attraction and aggregation in territorial species. Am Nat 131:329-347.

Sweatman HPA, Robertson DR (1994) Grazing halos and predation on juvenile Caribbean surgeonfishes. Mar Ecol Prog Ser 111:1–6.

Syms C, Jones GP (2000) Disturbance, habitat structure, and the dynamics of a coral-reef fish community. Ecology 81:2714-2729.

Turgeon K, Robillard A, Grégoire J, Duclos V, Kramer DL (2010) Functional connectivity from a reef fish perspective: behavioral tactics for moving in a fragmented landscape. Ecology 91:3332–3342.

Whitfield PE, Hare JA, David AW, Harter SL, Muñoz RC, Addison CM (2007) Abundance estimates of the Indo-Pacific lionfish *Pterois volitans/miles* complex in the western North Atlantic. Biol Inv 9:53−64.

Chapter 4.

Discussion

How coral reef fishes perceive risk of predation, and tailor their movement decisions in response, may determine the fate of individuals, as well as drive key ecosystem processes on fragmented coral reefs (Nathan et al. 2008; Turgeon et al. 2010). My research shows that fish aversion to crossing sand gaps – which is widely considered a predator avoidance response – is tied to the degree to which sand acts as a barrier to movement (i.e., the width of the sand gap; Chapter 2 and Chapter 3) and the risk of predation associated with specific predators (Chapter 3). Specifically, I demonstrate that: (1) the rate at which fishes are observed moving over sand declines non-linearly with increasing distance to the nearest coral reef (Chapter 2), and (2) study designs that harness the natural reluctance of reef fish to cross sand gaps can be used to reveal recognition of novel predators (Chapter 3). Indeed, through the novel use of experimental translocations over sand, I show that one species of Caribbean damselfish, *Stegastes partitus*, is naïve to invasive predatory lionfish (*Pterois* sp.) (Chapter 3). Taken together, my research has implications for the design of studies of reef fishes on coral patches, and may help managers more easily define marine protected areas boundaries.

Implications for the design of studies in fragmented coral reef habitats

How far apart should reefs be to be considered to have separate fish populations? My results from Chapter 2 suggest there might be significant movement of fishes among coral patches separated by less than 50 m of sand. If units of replication (i.e., reef patches) are not independent, then the exchange of adult fishes among neighbouring patches may attenuate differences in community estimates (i.e., fish abundance, diversity, biomass, etc.). In fact, previous study designs have operated on the assumption that patch reefs separated by just a few metres of sand are relatively isolated “island” systems, in which fishes live sedentary lifestyles after larval settlement (Smith and Tyler 1975; Sale and Steel 1989; Turgeon et al. 2010). In this context, the results of my literature review of studies on patch reefs are particularly concerning.

Nearly half of the studies examined fish populations on patches separated by less than 50 m of sand, and over one-third of the studies did not report inter-patch distances at all. At a minimum, I recommend inter-patch distances be reported in future studies on patch reefs. Better still, minimum distances between nearest-neighbour patches should be selected and justified using published empirical estimates of movement (Chapter 2; Table 1), and body size of the focal species(s). Indeed, my research suggests that body size is an important determinant of the distance fish will move away from shelter (Chapter 2 and 3), and potentially among patch reefs (Chapter 2). If distant patch reefs are connected by the movement of larger individuals, and near patches are connected by both small and large individuals, then body size in conjunction with inter-patch distances should be a key consideration in the effective design of future studies.

A novel way to study predator recognition

In Chapter 3, I demonstrated how a novel study design, developed on the basis of the reluctance of coral reef fishes to cross open expanses of sand, could be harnessed to evaluate predator recognition in the field. Using experimental translocations over sand, I showed that the presence of fish models significantly affected the homing decisions of bicolor damselfish: prey exhibited strong predator-avoidance responses (i.e., the probability of crossing a sand gap to home was significantly reduced) when confronted with a native-piscivore model, while damselfish were seemingly indifferent to the presence of an invasive piscivorous lionfish model. In previous studies of naïveté to lionfish, variation in the behaviour of living predators constrained in translucent bottles and/or containers has been difficult to control (Anton et al. 2016, Black et al 2014, Kindinger 2015). Also, at times the body sizes of captive lionfish may not have been sufficiently large to pose a credible threat to focal prey (e.g., Kindinger 2015). Future studies can alleviate these issues through the use of experimental translocations and standardized invasive fish models in the field. My design could also be used to examine the threat-sensitivity of small-bodied coral reef fishes to either camouflaged or partially hidden native predator models and in turn, evaluate the effectiveness of such unique hunting tactics (e.g., *Synodus* sp. typically stay partially covered in sand surrounding coral patches before ambushing exposed prey). Lastly, the use of different-sized models of the same species, or same-species models oriented in differing poses (i.e., foraging vs. non-foraging orientations), may help future researchers determine what threshold sizes and/or body positions elicit significant predator avoidance responses in prey inhabiting mosaic coral reefs.

On a smaller scale, my results mirror what translocation and gap-crossing studies on terrestrial taxa, particularly forest-dwelling birds, have already shown us: open habitat some tens of metres wide provides at least a partial barrier to movement (Bakker and Van Vuren 2004; Bosschieter and Goedhart 2005; Roberston and Radford 2009; Lees and Peres 2010). Indeed, predator-playback experiments suggest risk of predation tied to distance from safety hinders bird movement over open habitat (Creegan and Osborne 2005; Robertson and Radford 2009), but how specific predators mediate movements away from cover is still poorly understood. The use of standardized predator models, together with playback calls in gap-crossing studies, could provide empirical evidence on how predator recognition facilitates or impedes movement between terrestrial patches. Understanding how terrestrial animals move in response to specific predators, and within increasingly fragmented habitats, could help managers select reserve boundaries that confer adequate protection to vulnerable species or populations.

Implications for the design of marine reserves

An important issue in marine reserve design is the likelihood that adult fishes will stray beyond reserve boundaries. The degree to which sand acts as a barrier to movement can influence whether individuals settled in marine reserves will be exposed to adjacent fisheries. There is a growing body of evidence that marine reserves foster larger fish sizes, enhance larval dispersal and accumulate biomass (Côté et al. 2001; Gell and Roberts 2003; Bortholomew et al. 2007; Lester et al. 2009). However, highly mobile reef fishes, for example jacks (Carangidae sp.), may not receive adequate protection from small-scale reserves if they frequently move over non-reef habitat and are exposed to fishing (Hixon and Carr 1997; Kramer and Chapman 1999; Chapman and Kramer 2000).

My video-generated estimates of the distances 55 different species of reef fishes are willing to venture away from reefs (Chapter 2; Table 1) may help illustrate the minimum extent of habitat discontinuities that are needed to reduce movement over sand, and in turn help define strategic and/or species-specific marine protected area boundaries (Abesamis and Russ 2005; Bartholomew et al. 2007; Mumby and Steneck 2008). No-take zones established over sufficiently large expanses of sand can minimize the rates of coral reef fish straying into unprotected habitat: in my model, for example, distances greater than 140 m away from the nearest reef structure were enough to minimize movements of the largest of fishes to less than 1 individual per hour. Growing concerns over coastal habitat loss and increased fragmentation, typically related to destructive fishing practices and severe weather, have motivated a strong interest in how fishes respond to sand patches adjacent to coral reefs (Sambrook et al. 2016). In the future, defining reserve boundaries with reference to distance estimates of fish movement over open sand (Chapter 2; Table 1) may help protect stocks within reserves, and/or maximize potential yields of commercially important fish (e.g., Serranidae and Lutjanidae) via adult fish dispersal into adjacent fisheries.

Future directions

The implications for future study designs and marine management listed above lead to several methodological issues that should be addressed in future work on fish movement among fragmented coral reefs. In Chapter 2, I was successfully able to generate minimum distance estimates for a wide range of species traveling over open sand, away from shelter. However, I recommend future studies combine video-generated estimates of fish movements with comprehensive mapping of the seascape between coral patches. This may highlight the potential for alternate habitat types (i.e., seagrass, macroalgae, isolated coral head or rock) to act as protective stepping stones for coral reef fish, and in turn influence movement patterns over sand. In addition, to my knowledge, there are currently no estimates of fish traffic between coral patches. While my results imply there might be extensive, size-structured exchange of adult fishes between close coral patches (i.e, inter-patch distances < 50 m; Chapter 2), I was unable to ascertain the direction and/or destination towards which focal individuals were moving. Placing additional cameras at varying distances from patch reefs (i.e., not just mid-way between patches) may help alleviate this issue, and in turn, may facilitate habitat mapping between patches.

Lastly, in Chapter 3, I showed that translocation distance over sand, body size and predator recognition are important determinants of damselfish homing. However, I found no evidence that home patch conspecific density was a significant predictor of fish homing, despite recent research that shows the presence and/or abundance of conspecifics might indicate patch safety. Thus, in theory, damselfish removed from high-density patches should have been strongly motivated to home to avoid losing high quality territories (Stamps 1988; Sieving et al. 2004; Schmidt et al. 2008). Since intraspecific aggression typically occurs over territorial disputes between individuals of similar sizes, it is possible that the interactive effects of the size distribution and the density of conspecifics plays a more important role in fish homing than conspecific density alone. Therefore, I recommend future authors measure the body lengths of conspecifics on the focal patch, and include an interactive effect of the conspecific density and the conspecific size distribution in their homing models. If conspecific population dynamics are, in fact, a determinant of fish homing, then the distribution of dominant fishes on some patches may block adult fish dispersal, and more broadly, reduce connectivity even between close clusters of patches (Hilty et al. 2006; Turgeon et al. 2010).

References

Abesamis RA, Russ GR (2005) Density-dependent spillover from a marine reserve: long-term evidence. Ecol Appl 15: 1798 – 1812.

Anton A, Cure K, Layman CA, Puntila R, Simpson MS, Bruno JF (2016) Prey naïveté to invasive lionfish *Pterois volitans* on Caribbean coral reefs. Mar Ecol Prog Ser 544: 257 – 269.

Bakker VJ, Van Vuren DH (2004) Gap-crossing decisions by the red squirrel, a forest-dependent small mammal. Conserv Biol 18:689–697.

Bartholomew A, Bohnsack JA, Smith SG, Ault JS, Harper DE (2007) Influence of marine reserve size and boundary length on initial response of exploited reef fishes in the Florida Keys National Marine Sanctuary, USA. Landscape Ecol 23: 55-65

Black AN, Weimann SR, Imhoff VE, Richter ML, Itzkowitz M (2014) A differential prey response to invasive lionfish, Pterois volitans: Prey naïveté and risk-sensitive survivorship courtship. J Exp Mar Biol Ecol 460: 1-7.

Bosschieter L, Goedhart PW (2005) Gap crossing decisions by reed warblers (*Acrocephalus scirpaceus*) in agricultural lanscapes. Landscape Ecol 20: 455 - 468

Creegan HP, Osborne PE (2005) Gap-crossing decisions of woodland songbirds in Scotland: an experimental approach J Appl Ecol 42:678–687.

Hitly JA, Lidicker WZ, Merenlender AM (2006) Chapter 6: Potential pitfalls of linking landscape. Pages 146 – 173 in Corridor ecology: The science and practice of linking landscapes for biodiversity and conservation. Island Press: Washington, DC.

Kindinger TL (2015) Behavioral response of native Atlantic territorial three spot damselfish (*Stegastes planifrons*) toward invasive Pacific red lionfish (*Pterois volitans*). Env Biol Fishes 98: 487−498.

Lees AC, Peres CA (2008) Gap-crossing movements predict species occupancy in Amazonian forest fragments. OIKOS 118: 280-290.

Mumby PJ, Steneck RS (2008) Coral reef management and conservation in light of rapidly evolving ecological paradigms. Trends Ecol Evol 23: 555 – 563.

Robertson OJ, Radford JQ (2009O Gap-crossing decisions of forest birds in a fragmented landscape. Austral Ecol 34:435–446.

Sambrook K, Jones GP, Bonin MC (2016) Life on the edge: Coral reef fishes exhibit strong responses to habitat boundary. Mar Ecol Prog Ser 561: 203 – 215.

Schmidt KA, Lee e, Ostfeld RS, Sieving K (2008) Eastern chipmunks increase their perception of predation in risk response to titmouse alarm calls. Behav Ecol 19: 759-763.

Sieving KE, Contreras TA, Muate KL (2004) Heterspecific facilitation of forest-boundary crossing by mobbing understory birds in north-central Florida. Auk 121: 738-751.

Stamps JA (1988) Conspecific attraction and aggregation in territorial species. Amer Natur 131: 329-347.

Turgeon K, Robillard A, Grégoire J, Duclos V, Kramer DL (2010) Functional connectivity from a reef fish perspective: behavioral tactics for moving in a fragmented landscape. Ecology 91:3332–3342.

Appendix A.

Supplementary tables and figures for Chapter 2

Table A1. Full results of a systematic search for studies of fish behaviour and ecology conducted on patch reefs published between 1996 and 2016. The table is available as a supplemental EXCEL file to this thesis. The table includes 11 spreadsheets that follow the steps outlined in Fig. S1. The final spreadsheet contains the 43 studies included in the synthesis and the minimum inter-patch distances reported, the species and family studied, as well as maximum lengths (from FishBase). DNR means that no inter-patch distance was reported. The frequency distribution of reported distances is shown in Figure 1.

Table A2. Body sizes (total length, cm) of strongly reef-associated species observed over sand in my videos. Maximum lengths were obtained from Fishbase; mean lengths were obtained from a database of fish surveys conducted between 2011 and 2015 on coral reef patches near the Cape Eleuthera Institute. The numbers of adult individuals contributing to mean lengths are given in parentheses.

Family	Species	Maximum length (Fishbase)	Mean length (CEI patches)
Acanthuridae (surgeonfishes)	*Acanthurus bahianus*	38	18.2 (14)
	A. coeruleus	39	17.9 (493)
	A. chirurgus	39	23.3 (63)
Haemulidae (grunts)	*Haemulon album*	79	27.5 (453)
	H. carbonarium	36	18.3 (3)
	H. flavolineatum	30	20.3 (218)
	H. macrostomum	43	15.0 (4)
	H. plumierii	53	21.8 (1090)
	H. sciurus	46	22.0 (769)
Labridae (wrasses)	*H. garnoti*	19.3	12.0 (473)
	H. maculipinna	18	12.3 (4)
	H. radiatus	51	13.2 (47)
	Lachnolaimus maximus	91	25.0 (26)
	Thalassoma bifasciatus	25	11.7 (890)
Lutjanidae (snappers)	*Lutjanus analis*	94	41.1 (77)
	L. griseus	89	26.3 (69)
	L. synagris	60	23.3 (448)
	Ocyurus chrysurus	86.3	27.5 (20)
Ostraciidae (box/trunkfishes)	*Acanthostracion polygonius*	50	19.7 (1)
	A. quadricornis	55	29.3 (9)
	Lactophrys bicaudalis	48	19.3 (1)
Pomacanthidae (angelfishes)	*Holacanthus ciliaris*	45	21.0 (170)
	Pomacanthus arcuatus	60	23.4 (509)
	P. paru	41	25.2 (13)
Pomacentridae (damselfishes)	*Abudefduf saxatilis*	22.9	9.3 (276)
	Chromis cyanea	15	4.7 (716)
	Stegastes leucostictus	10	6.0 (948)
	S. variabilis	12.5	7.3 (713)
Scaridae (parrotfishes)	*Scarus taeniopterus*	35	17.3 (6)
	Sc. vetula	61	19.7 (32)
	Sparisoma aurofrenatum	28	18.6 (24)
	Sp. chrysopterum	46	18.0 (1)
	Sp. rubripinne	47.8	20.0 (10)

	Sp. viride	64	23.3 (183)
Serranidae (groupers)	*Epinephelus striatus*	122	29.1 (412)
	Mycteroperca bonaci	150	29.4 (85)
Tetraodontidae (pufferfishes)	*Canthigaster rostrata*	12	5.7 (1801)
Urotrygonidae (round stingrays)	*Urobatis jamaicensis*	76	26.6 (307)

Table A3. Mean species-specific hourly observation frequency of eight strongly-reef associated species, at sites where the cameras were < 25 m from the nearest patch. The number of sites at which reef fish species were recorded are given in parentheses. The last column lists the distances (m) at which reef fish species were observed from a patch reef.

Family	Species	Mean hourly observation frequency	Distance to the nearest patch
Haemulidae	*Haemulon album*	33.3 (4)	2.7, 2.8, 7.2, 16
(grunts)	*H. plumierii*	68.4 (5)	2.7, 2.8, 4.1, 7.2, 16
Pomacanthidae (angelfishes)	*Pomacanthus arcuatus*	14.6 (5)	2.7, 2.8, 4.1, 5.5, 7.2
Scaridae	*Scarus taeniopterus*	17.8 (4)	2.7, 2.8, 4.1, 7.2
(parrotfishes)	*Sp. chrysopterum*	8.7 (3)	2.8, 4.1, 7.2
	Sp. viride	4.3 (4)	2.7, 2.8, 4.1,7.2
Serranidae	*Epinephelus striatus*	5 (4)	2.7, 2.8, 4.1, 7.2
(groupers)	*Mycteroperca bonaci*	12.7 (3)	2.7, 4.1, 7.2

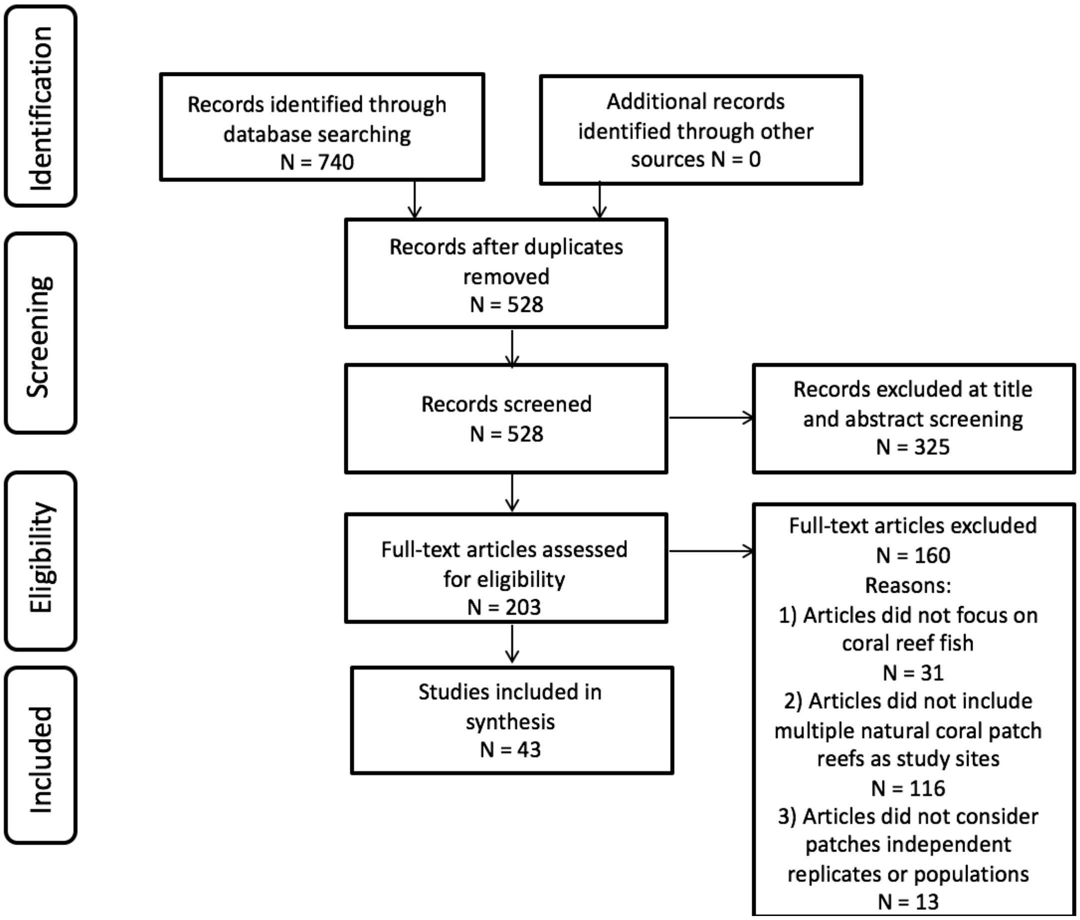


Figure A1. Flow diagram of the method and selection criteria used in the systematic review of studies of fish ecology and behaviour on coral reef patches from 1996 to 2016.

Appendix B.

Supplementary tables and figures for Chapter 3

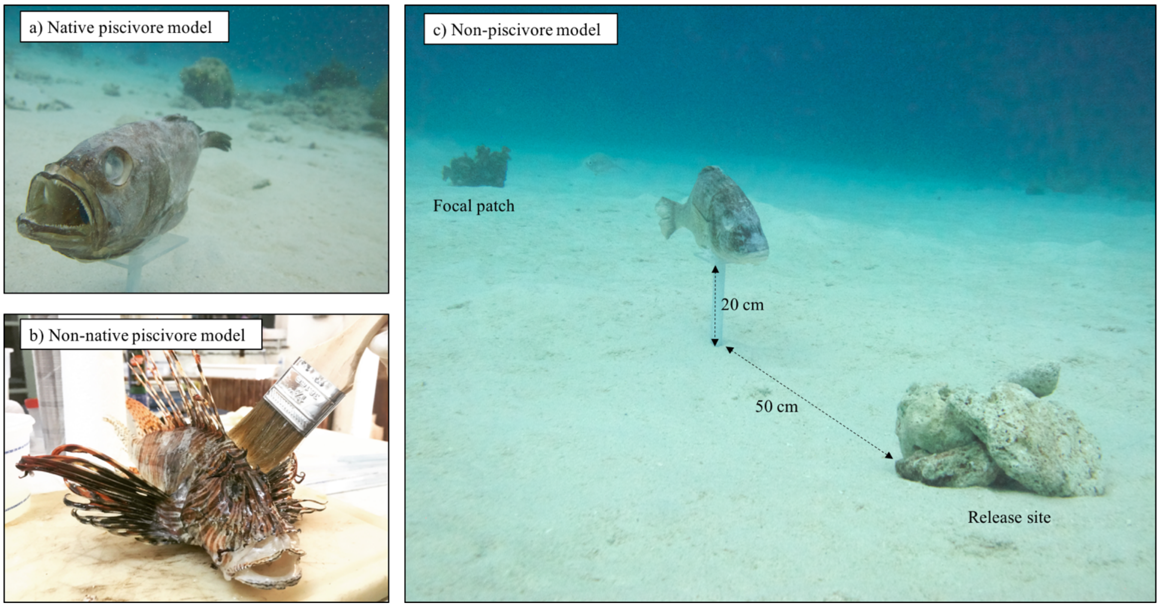


Figure B1. Formalin-preserved, resin-coated models of (a) a native piscivore (black grouper; *Mycteroperca bonaci*), (b) a non-native piscivore (lionfish; *Pterois* volitans) and (c) a non-piscivore (French grunt, *Haemulon flavolineatum*). Each model was placed 20 cm above the sand, at a constant absolute distance of 50 cm from the release site for experimental translocations.

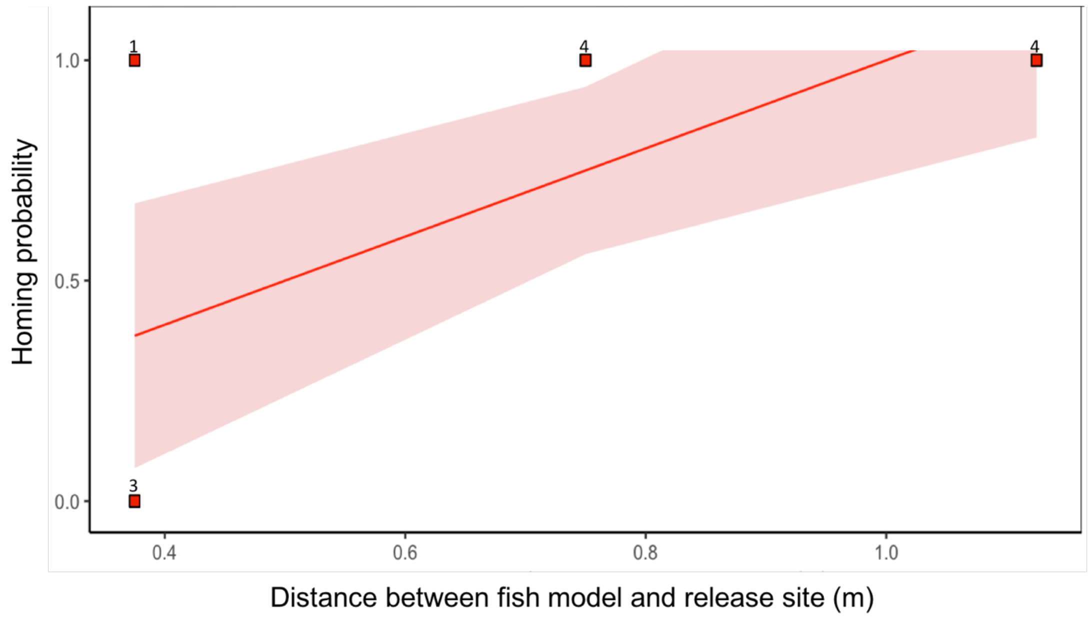


Figure B2. Relationship between the homing probability of translocated bicolor damselfish and the distance (in m) between the fish model (i.e., a native piscivore) and the release site in a pilot experiment. Each distance point (i.e., 0.375 m, 0.75 m, and 1.175 m) was tested four times, for a total of 12 translocations. The values above each data point represent the number of individuals contributing to that point. The release site was 1.5 m away from the home patch on all trials. The solid line is the line of best fit (equation: Homing probability = 1.00 * Distance between fish model and release site + 3.84e-16), and the shaded regions represent the 95% confidence interval.

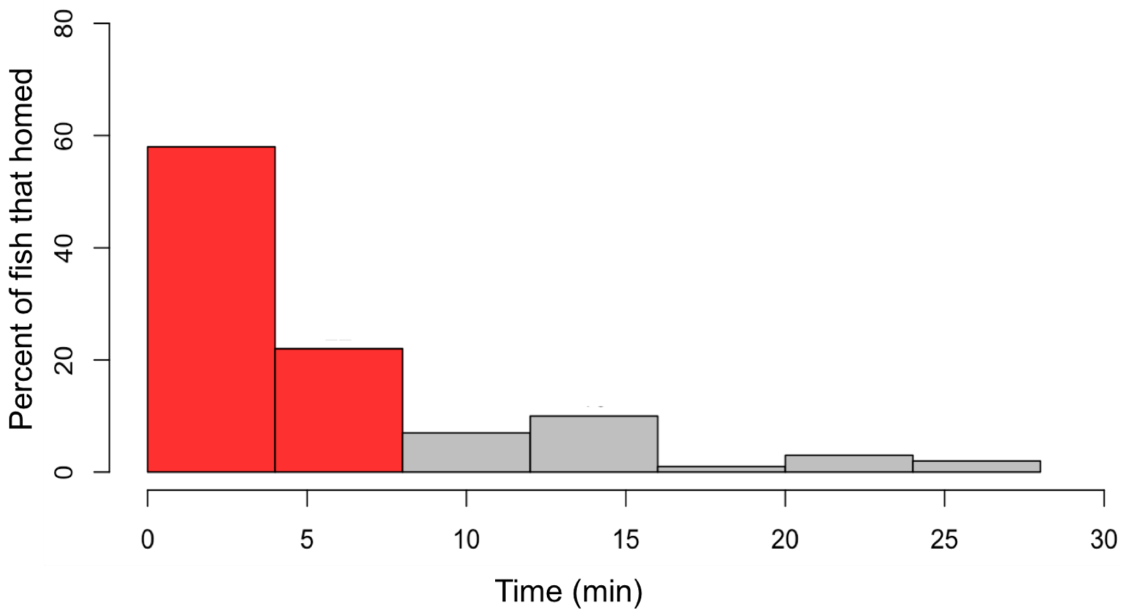


Figure B3. The percentage of translocated bicolor damselfish that homed in each 4 min period of the 30 min observation across all four treatments. Fifty individuals homed out of the 154 translocations carried out. The first eight minutes of observation (red bars) captured 80% of fish homing.

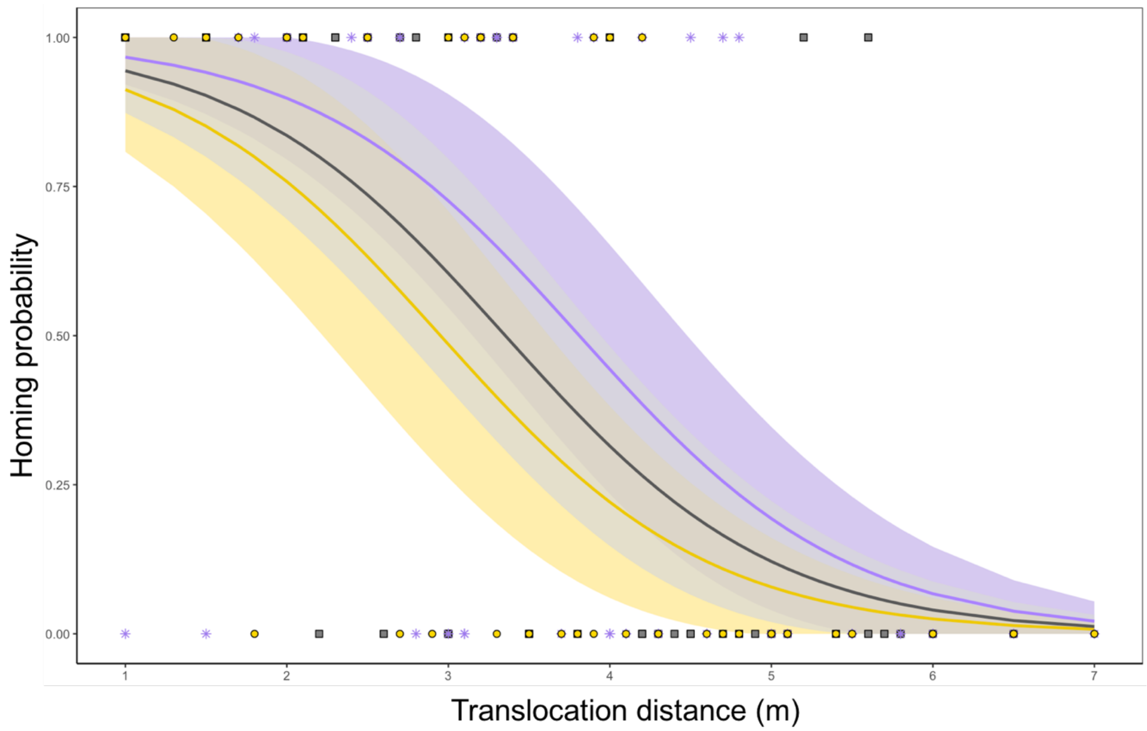
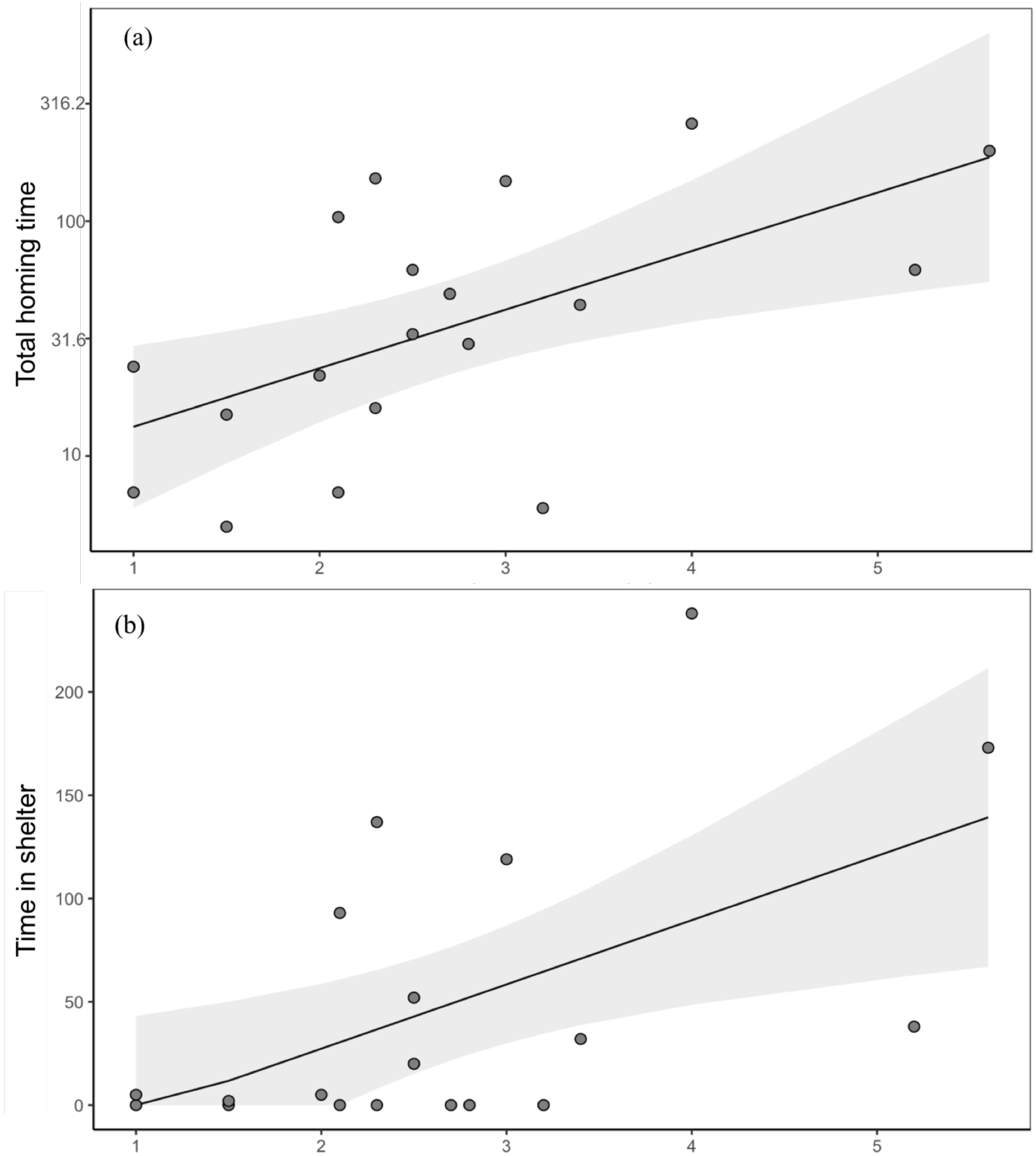


Figure B4. Relationships between the homing probability of translocated bicolor damselfish and the distance (in m) between the release site and the home patch, in the absence (grey symbols and lines) and presence of a non-piscivore (i.e. a French grunt) fish model (magenta symbols and lines) and an invasive piscivore (i.e. a lionfish) model (yellow symbols and lines). The solid lines are the lines of best fit for the averaged, best-supported generalized linear mixed-effects model identified by AICc (equation: homing probability = exp(-1.31*translocation distance) * exp(-1.68*Grouper) * exp(0.59*Grunt) * exp(-0.32*Lionfish) * exp(0.83*Fish length) * exp(0.01*Conspecific density) * exp(6.23)). The shaded areas represent 95 % confidence intervals.



(a)
Total homing time
316.2
100
31.6
10
1
2
3
4
5
(b)
Time in shelter
200
150
100
50
0
1
2
3
4
5

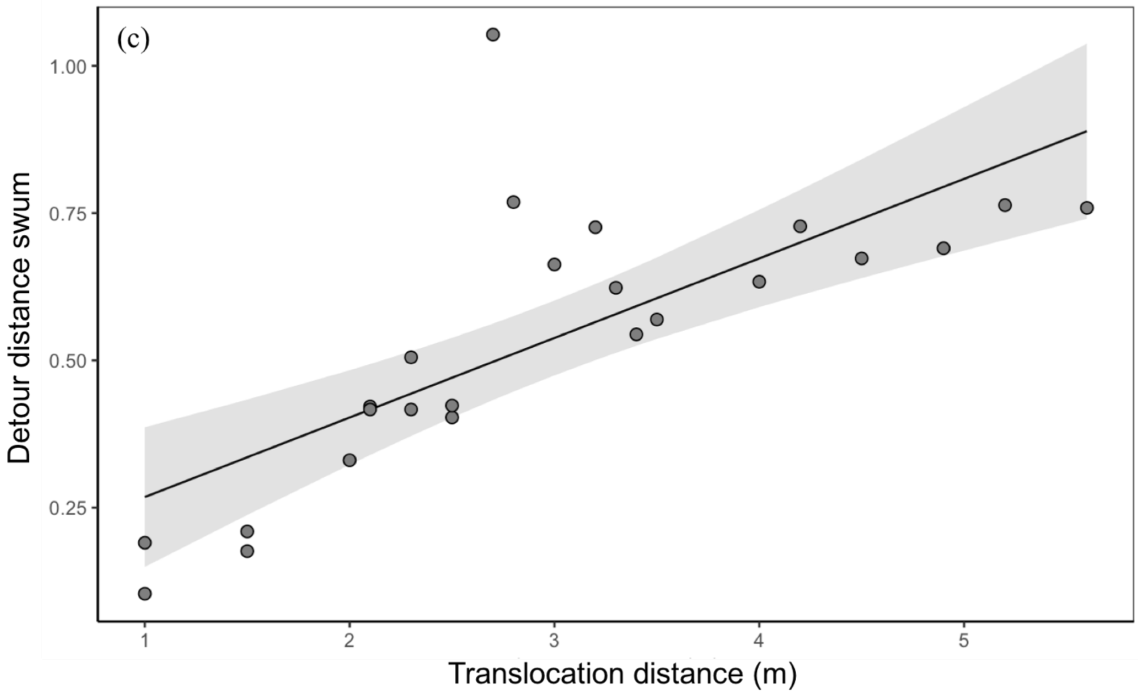


Figure B5. Relationships between (a) total homing time (seconds), (b) time in shelter (seconds), (c) detour distance swum (metres) and translocation distance (metres) from the home territory for bicolor damselfish (N =24) in the absence of a fish model near the release site. The detour distance swum is the additional distance swum beyond a straight path back to the home territory. The solid lines are the lines of best fit (equation: Homing time = 0.410 * Translocation distance + 0.627; Time in shelter = 31.109 * Translocation distance – 34.907), and the shaded regions represent the 95% confidence interval for each model.