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Diver Fear Effects and Other Human Alterations of Predation Risk in Marine Systems

A dissertation submitted in partial satisfaction of the requirements for the

degree of Doctor of Philosophy

in Ecology, Evolution & Marine Biology

by

April Danielle Ridlon

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Diver Fear Effects and Other Human Alterations of Predation Risk in Marine Systems

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by

April D. Ridlon

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DEDICATION

This dissertation is dedicated first to my mother, Diane L. Turner Ridlon, whose love of learning was contagious, and who never doubted for a moment that I could dream as big and go as far as I wanted to in life. I also dedicate it to my father, Kenneth S. Ridlon, whose love of the ocean inspired mine, and whose own aspirations of being a marine biologist probably shaped my life path more than either of us realize. Lastly, I

dedicate this thesis to my son Riley, for all the hours he patiently spent sharing his
mama with the fishes.

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ABSTRACT

Diver Fear Effects and Other Human Alterations of Predation Risk in Marine Systems

by
April D. Ridlon

Humans have altered the ocean on a global scale. From large-scale extractive activities such as fishing, to the unintentional introduction and spread of invasive species via shipping vessels, human activities shape marine communities worldwide, having myriad effects on ecosystem functions and resilience. Even recreational activities that are assumed to have lesser impacts, such as SCUBA diving, are intensifying and becoming increasingly concentrated inside marine protected areas. Research into a wide range of direct and obvious human impacts has informed the effective management of marine systems for both conservation goals and human uses. However, understanding the more nuanced pathways for the effects of human disturbance is critical, especially in systems facing multiple stressors, as they may serve to tip the balance between healthy ecosystems and degraded ones. In particular, there is recent and growing evidence that human activities are altering predation risk in marine systems. When humans change the abundance, distribution, or behavior of marine predators, whether through fishing or other forms of disturbance, those changes can ripple through marine ecosystems due to the comparatively large effects that predators have on other trophic levels. Predators exert both consumptive and non-consumptive

effects on prey populations, and can thus influence other species interactions and trigger cascades that can result in the fundamental restructuring of marine systems. However, although risk effects have been well studied in terrestrial systems, these effects have been largely neglected in marine systems. In this thesis, I explore two different pathways for the effects of human alteration of predation risk. My first two chapters examine the non-consumptive, or fear effects of recreational spearfishing, diving, and snorkeling to marine fish. My third chapter examines the consumptive effects of an introduced predator on both a native and an invasive prey population, and the dynamics between them.

Chapters One and Two: Diver fear effects

The ecology of fear is based on evidence demonstrating that predation risk is a strong motivating factor in individual prey behavior, and has consequences at the population, community and ecosystem level. While predator escape theory was developed with natural predators in mind, humans can act as predators (e.g. while fishing) or mimic predators (e.g. while diving). The recent testing of predator escape theory by the measurement of flight initiation distance (FID) - the distance at which a fish flees from approaching diver - represents a promising new avenue for future research on diver fear effects to marine fish and in marine ecosystems. My synthesized review of the available empirical evidence suggested that fish react to divers with increases in vigilance and flight where they are exposed to spearfishers as compared to areas where they are protected from fishing. In contrast, I found that the effects of recreational diving on the flight and vigilance behavior of fish have not been well studied or effectively measured to date. In order to explore the effects of long-term

recreational diving on the behavior of a common reef fish, I conducted a series of experiments on reefs in the Cayman Islands where recreational diving activity has been consistent and spearfishing has been banned for decades. By measuring the FID and vigilance behavior of over 250 individual Stoplight Parrotfish (*Sparisoma viride*), I found evidence for habituation to divers by this species in areas where recreational diving is most concentrated. The near lack of a flight response in fish exposed to chronic diving activity represents the lowest FID recorded for the species in either protected or fished areas elsewhere in the world. The significant decrease in flight and vigilance in individuals in the highly dived area in comparison to those in less frequently dived areas also suggests that the frequency of diving activity drives this response. However, significant declines in the bite rates and frequency of cleaning interactions of individuals in the immediate presence of a diver also suggested that there may be fitness costs associated with recreational diver encounters, even for habituated fish. I therefore used these decreased bite rates to estimate a cumulative cost of daily diver encounters to an individual fish in terms of lost feeding. Where habituation to divers was extreme at my study site, estimated feeding loss for an individual fish was low. For scenarios in which I simulated lower levels of fish habituation and different diver behavior, estimated feeding loss due to diver encounters were much higher. This suggests that the cumulative costs of recreational diver encounters may be significant if, for example, larger flight distances must be maintained due to the occasional or nearby presence of spearfishers. Based on my findings, I make recommendations for future research into the behavioral effects of spearfishing, recreational diving, and the potential interaction of these two activities on the behavior of marine fish. I also

recommend the incorporation of these behavioral effects into marine spatial planning and management for multiple human uses, particularly where spearfishing and recreational diving co-occur.

Chapter Three: Predation effects of an introduced predator

As multiple invasions accumulate in marine systems, identifying the species traits and interactions that affect invasion success is critical for predicting the outcomes of multiple species introductions. Facilitation is a major mechanism for invasion success that can increase the magnitude of impact of an existing invasion. Marine predators can facilitate invasions and may be more likely to tip the balance of dynamics between species in an invaded system via top-down effects. I examined the effect of predation by an introduced crab, *Carcinus maenas*, on the native snail *Cerithidea californica* and the invasive snail *Ilyanassa obsoleta*. These two common snail species co-occur in the San Francisco Bay estuary, where there is evidence for the competitive displacement of the native snail by the invasive. Laboratory experiments revealed that *Carcinus maenas* predation was strongly and significantly greater on the native species as compared to the invasive. While the frequency of crab attacks was not significantly different between snail species, the predator was 5.45 times more successful at killing the native *C. californica* than the invasive *I. obsoleta* given an attack. This differential predation success drives the higher overall mortality in native snails. In light of the competitive displacement of the native snail by the invasive in this system, these results demonstrate that the introduced predator *C. maenas* can have both direct negative impacts on native species and indirect positive impacts on other invaders via facilitation. My results provide unique information about a predator's potential to

indirectly influence the success of an invasion, and contribute to our understanding of the role of introduced predators in influencing the dynamics of multiple invasions in marine systems.

Diver Fear Effects: Spearfishing, Recreational SCUBA Diving, and Snorkeling Alter the Behavior of Marine Fish

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Abstract

The number of recreational divers is on the rise globally, and their activities are becoming increasingly concentrated inside marine protected areas (Dowling, 2008; Gonson et al., 2015). Little is currently known about the effects of spearfishing or recreational diving, two of the most common marine recreational activities, on the behavior of fish or the ecosystems that are shaped by their behavior. There is growing evidence that as human activities alter risk landscapes in marine systems, resulting behavioral effects are occurring (Larson et al., 2016; Madin et al., 2016) potentially at a greater magnitude than consumptive effects (Preisser et al., 2005), and with the strong potential to trigger cascades in marine ecosystems (Madin et al., 2010; Mumby et al., 2012). The testing of optimal predator escape theory by the measurement of flight initiation distance (FID)- the distance at which fish flee from approaching divers - under different scenarios represents a promising new avenue for future research that informs an understanding of fear effects to marine species and their potential to affect marine

ecosystems. In this article, we provide an overview of the current status, opportunities, and future directions of research into diver fear effects. Using FID theory as the basis for testing the impacts of human activity on fish, we draw upon the current available evidence, and make predictions driven by both theory and existing empirical data. We provide specific recommendations for using standardized methods in future research to address chronic timescales of diver effects and to inform improvements in the current theory. We also discuss the need to move beyond the current understanding of various forms of diver fear effects, and particularly their interactions, by linking the effects of diver encounters to fitness and ecosystem-level consequences. Specifically, future studies should include the simultaneous measurement of FID and relevant fitness components (e.g. increased metabolic rate, reduced growth rate) to quantify the cumulative fitness costs of diver encounters to fish. Finally, future research into diver fear effects should include encounter rate with divers as a mechanism for changes in FID to account for the discrepancies between current theory and empirical findings, which may result in part from the unique nature of human predators.

Introduction

Humans are unique as marine predators in the breadth and magnitude of the predation pressure we exert, the selective forces we apply on prey populations, and the changes we cause to natural predation risk via fishing (Darimont et al., 2015, 2009; Diaz Pauli and Sih, 2017; Madin et al., 2016). Likewise, as SCUBA diving and snorkeling continue to gain popularity, physical disturbances unique to these human activities are intensifying (Hasler and Ott, 2008; Zakai and Chadwick-Furman, 2002), particularly

inside marine protected areas (MPAs; Gonson et al. 2015). While comparatively less is known about the behavioral effects of human activities in marine systems, both spearfishing and recreational SCUBA diving and snorkeling (hereafter recreational diving) have the potential to cause widespread ecological changes via fear effects analogous to those operating in terrestrial systems (Brown et al., 1999; Brown and Kotler, 2004; Ciuti et al., 2012a; Ripple and Beschta, 2004) by triggering anti-predator reactions in fish, including increased wariness and flight (Frid and Dill, 2002). In fact, as humans alter risk landscapes in marine systems at a rapid pace and on a broad scale, there is growing evidence that resulting behavioral effects are occurring (Larson et al., 2016; Madin et al., 2016), potentially at a greater magnitude than consumptive effects (Preisser et al. 2005) and with the strong potential to trigger cascades in marine ecosystems (Madin et al. 2010, Mumby et al. 2012). The impacts of the behavioral effects of divers on marine systems may even undermine conservation efforts to protect species by altering the spatial distribution of herbivore grazing, thereby affecting coral settlement and recruitment (Mumby, 2006), and/or the distribution of natural marine predators within an MPA (Jiao et al., 2016).

The predicted behavioral effects of consumptive and non-consumptive human activities share a common theoretical framework, based on the idea that animals respond to encounters with people according to the risk they associate with humans. Assessing this risk, and adjusting their anti-predator responses accordingly, enables animals to trade off the ultimate cost of being preyed upon against the energy spent on predator defense and the loss of opportunities to engage in other fitness-enhancing activities, including feeding, mating, and territorial defense (Cooper and Frederick,

2007; Helfman, 1989; Lima, 1998; Lima and Bednekoff, 1999). The distance at which an animal flees from the approach of a potential predator, the flight initiation distance (FID), is a standard metric commonly used to indicate an animal's perception of risk and to predict the energetic costs of responding to both lethal and non-lethal human activities (Côté et al., 2014; Gotanda et al., 2009; Taylor and Knight, 2003). According to optimal FID theory (Cooper and Frederick, 2010a, 2007) animals flee from predators at the distance that maximizes their lifetime fitness after an encounter, trading off between the probability of death based on the lethality of the predator encountered and the energetic costs of flight and lost opportunities due to fleeing. The predictions of optimal FID have been well supported in terrestrial systems (Blumstein, 2016, 2010; McLeod et al., 2013; Stankowich, 2008; Stankowich and Blumstein, 2005), and marine ecologists have recently undertaken experiments to understand how fear effects may alter FID in marine fish.

The testing of predator escape theory via the measurement of optimal FID in marine systems, particularly via the emergent research into the behavioral effects of spearfishing (e.g. Januchowski-Hartley et al. 2011; Feary et al. 2011; Côté et al. 2014; Alós et al. 2015; Goetze et al. 2017), represents a promising new avenue for future research that informs a fundamental understanding of risk effects to marine species and the ecosystems that are affected by their behavior. However, we lack a parallel understanding of behavioral effects of recreational activities in marine systems, which, like other non-consumptive human impacts, may alter marine ecosystems in important ways. While some important advances in the understanding of both natural and human induced risk effects have recently been made in marine systems (Long and Hay, 2012;

Madin et al., 2016), the mechanisms for, and consequences of, these effects are not well understood. Recreational divers in particular are generally assumed to have no negative effects on fish, especially where fish do not show obvious avoidance of divers, but this remains largely untested. With more people engaging in recreational marine activities than ever before, particularly inside protected areas (Gonson et al., 2015; Monz et al., 2010), we need to understand and consider the potential behavioral effects of recreational diving on fish populations, as well as the interactions between various human activities (e.g. spearfishing and recreational diving).

Moving beyond immediate behaviors to understand the magnitude and potential consequences of diver-induced risk effects requires that the fitness costs of encounters with divers be considered. Empirical evidence for persistent fitness effects and their population-level consequences for marine species that routinely encounter tourists is limited (French et al., 2011), but highlights the potential for these effects to be operating in similar ways as they are in terrestrial systems. Predator escape theory incorporates changes in individual fitness of prey over repeated encounters with a natural predator to both predict flight responses and account for the energetic and lost opportunity costs associated with them (Lima and Bednekoff 1999). However, the conceptual literature on predator avoidance is developed for and primarily tested on the effects of natural predators that have co-evolved with their prey, and humans are comparatively “new” and fundamentally different predators in some key ways. Spear guns increase the individual lethality and reach of humans, whose disproportionate targeting of large, adult, and predatory fish, have unique implications not only for their mortality effects (Conover et al., 2009; Dulvy et al., 2004; Mumby et al., 2012; Sutter et al., 2012), but

potentially for their behavioral effects as well (Diaz Pauli and Sih, 2017). In addition, where spearfishers and recreational divers make up a population of potential predators for fish to respond to, they present similar visual cues connected to vastly different levels of individual lethality. How fish assess predation risk during diver encounters in the dynamic scenarios created by human predation and recreation is untested, and the broader consequences of their responses are unknown. This highlights a clear and urgent need to consider encounter rate as a mechanism for fish responses to divers, and link flight and vigilance behaviors to their fitness effects on the individual and population-level, to better understand the magnitude of behavioral effects of divers on marine ecosystems.

In this article, we provide an overview of the current status, opportunities, and future directions of research into understanding human fear effects in marine systems. Using FID theory as the basis for testing the impacts of human activity on fish, we draw upon the current available evidence and make predictions driven by both theory and existing empirical data. We discuss the need to move beyond the current understanding of various forms of diver fear effects, and particularly their interaction, by linking the effects of divers on FID to fitness and ecosystem consequences. To that end, we: 1) review how optimal FID theory can be used to understand and disentangle the effects of consumptive and non-consumptive human activities on fish. We summarize and draw upon the empirical evidence for the effects of spear fishing, recreational diving, and their potential interaction on FID of marine fish; 2) predict the potential fitness effects of diver encounters and their consequences to marine fish, as well as the potential for diver-induced behavioral cascades by drawing upon relevant examples of similar

research, and 3) provide specific recommendations for future research into these effects, including suggestions for standardizing the methods, and for improving the current theory. We highlight the importance of including encounter rate with divers as a mechanism for changes in FID to account for the discrepancies between current theory and empirical findings.

Using Flight Initiation Distance to Understand Diver Fear Effects

Optimal FID theory can be used to understand and disentangle the role of humans as predators (e.g. spearfishers) from humans as observers (e.g. recreational divers) in the marine environment. Spearfishers are lethal predators, and encountering them carries a true risk of death, while encounters with recreational divers do not. FID theory is predicated on an individual fish having perfect information about the level of predation risk posed by an approaching potential predator, in this case, being able to distinguish a spearfisher from a recreational diver. Of course, prey rely not only on immediate cues, but also on recent previous exposure to predators to assess their current predation risk (Lima and Bednekoff, 1999). The observed FID should best match the predictions of optimal FID when prey receive consistent, reliable cues with which to update their assessment of predation risk.

Thus, while repeated exposure to only spearfishing cues should reinforce anti-predator behavior and increase FID, repeated exposure to only non-consumptive human recreational activities, such as recreational diving, may cause an animal's perception of predation risk, and thus their FID, to progressively decrease (Burger & Gochfeld 1990), a learning process called habituation (Bejder et al., 2009). Habituating to the non-lethal

presence of humans can benefit animals, particularly when the level of encounters is high, by cutting the energetic costs associated with flight and vigilance (Blumstein, 2016; Lima and Bednekoff, 1999; Rodriguez-Prieto et al., 2010) and providing more frequent opportunities to increase fitness (via mating, feeding, etc.). However, habituating to recreational divers with lower FIDs may make animals more vulnerable to a natural predator via a mistake in risk assessment when they encounter one, so that the degree of optimal habituation depends on the level of exposure to true predation risk from both humans and natural predators in the system. Most marine recreational areas worldwide allow for multiple human uses, creating a varied landscape of human-induced predation risk for fish, and the costs and benefits associated with fleeing from them. The ratio of encounters between fish and spearfishers and recreational divers may be particularly important in assessing the risk posed by human predators, which are unique in presenting similar visual cues connected to vastly different levels of lethality. In order to understand how various human activities may interact to impact fish behavior, we review what is known about the impacts of spearfishing and recreational diving on marine fish species. In this section we summarize the empirical evidence for the effects of spearfishing, recreational diving, and their potential interaction on the FID of marine fish. By examining these findings in light of the predictions of optimal FID and predator escape theory, we highlight the unique role of humans as predators in marine systems, and gaps in the current understanding of diver fear effects that must be addressed to inform and improve fisheries management and the conservation of marine species.

2.1. Spearfishing

Insights into the anti-predator responses of marine fish under different human-induced risk regimes can be gleaned by measuring FIDs of the same species outside and inside of a no-take MPA (e.g. Gotanda et al. 2009; Januchowski-Hartley et al. 2011; Feary et al. 2011; Benevides et al. 2016) or by comparing the responses of targeted species to non-targeted species in the same location (e.g. Feary et al. 2011; Januchowski-Hartley et al. 2014; Bergseth et al. 2016). Existing studies on the impacts of spearfishing on fish behavior confirm the main prediction of optimal FID theory: that marine fish set their FID according to the lethality of the predator(s) they encounter, increasing their FIDs in response to the predation risk posed by spearfishers (Fig 1; Gotanda et al. 2009; Januchowski-Hartley et al. 2011; Feary et al. 2011; Januchowski-Hartley et al. 2012; Januchowski-Hartley et al. 2014; Nunes et al. 2016; Bergseth et al. 2016). Significantly elevated average FIDs of individuals in fished areas relative to protected areas are reported for a wide range of targeted species, and the average FIDs of targeted species are significantly higher than those of non-targeted species in the same location (Fig 1), indicating that fish set their FID at a higher average distance than that dictated by natural predation risk in response to human predators. Individual body size is positively correlated with FID for reef fish (Gotanda et al., 2009; Januchowski-Hartley et al., 2014; Miller et al., 2011), an effect that has also been found in hunted terrestrial species (Stankowich, 2008). This is in contrast to the negative relationship between body size and response to natural predators in marine fish. Natural predation risk is higher for small-bodied fish due to the gape limitation of their predators (Scharf et al., 2000), causing smaller prey to be more vulnerable to both a greater number of

predators in a given population, and a wider range of natural predatory species. In contrast, the significantly higher FIDs in larger fish exposed to spearfishing are likely driven by the unique nature of human predation, specifically that larger individuals and larger bodied species are often preferentially targeted by fishers (Dulvy et al., 2004).

Within species targeted by spearfishers, there is variability in the magnitude of the flight response to fishing, and in the species' ability to effectively escape human predators by increasing this distance (Gotanda et al. 2009; Nunes et al. 2016; Fig 1) For example, the average FIDs for both *S. trispinosus* and *S. vetula* in fished areas, while significantly higher than in protected areas, are still well below the average effective range of spear guns (310 cm: Feary et al. 2011; Fig 1). In addition, while the two families of predatory fishes for which there are data show a trend of increasing FID in fished areas, this is only significant for one species (*P. leopardus*), and only individuals in the Lutjanidae family increased their average FID beyond the range of spear guns (Januchowski-Hartley et al. 2011; Bergseth et al. 2016; Fig 1).

Studies that compare changes in FID over space and time in response to varying intensity in fishing pressure provide additional insights into the mechanisms controlling optimal FID in response to the risk of predation from spearfishers. Specifically, flight responses of fish that vary over spatial and temporal gradients in fishing pressure reveal the importance of the encounter rate with the predator in determining an optimal FID (Fraser A Januchowski-Hartley et al., 2011; Januchowski-Hartley et al., 2014). For example, Januchowski-Hartley et al. (2011) compared FIDs from areas of differential fishing pressure (i.e. areas with different rates of encounter with a potentially lethal human predator) and found that as the intensity of fishing pressure

increased, average FID significantly and incrementally increased for species in the Scaridae and Mullidae families, a trend that is apparent for a range of other fish species as well (Figs 3a; Fig 1 within Januchowski-Hartley et al. 2011a). Since spearfishers presumably maintain a relatively constant average level of lethality, the incremental nature of the increase in FID in areas of different overall fishing pressure provides support for the idea that the encounter rate with the predator is an important mechanism for this response. Theory predicts that fish are also experiencing higher cumulative costs associated with repeated flight in high-encounter scenarios, and yet the rise in FID suggests that the ultimate risk of death via predation outweighs the costs of fleeing, at least at the observed levels of fishing pressure.

It is important to note that these empirical results reflect population-level responses to spearfishing in the form of average FIDs, and not changes in the FID of an individual fish over time. This mismatch between the predictions from theory, which were developed to describe an individual animal's response to predation risk, and interpretations of empirical data makes it necessary to use caution in inferring the mechanisms of changing FIDs from empirical results. However, the evidence suggests two likely mechanisms by which average FID of a fish population increases in response to spearfishing: direct mortality effects and adaptive learning. As the encounter rate between spearfishers and fish increases, the cumulative risk of predation and the rate at which individuals are culled from the population increases. Since individual fish with lower FIDs are more easily caught by spearfishers, they are likely culled from the population first (Conrad 2011), leaving more individuals with higher FIDs - which enable them to more effectively escape fishers - in the population. At the same time,

increased encounter rate facilitates more frequent opportunities for individual fish to learn about the lethality of the predator and increase their FID accordingly. In higher encounter scenarios, fish can more rapidly gather information about current predation risk from sensory cues in the system (e.g. olfactory cues from speared conspecifics; Brown 2003; Brown et al. 2011), through social learning by seeing the reactions of nearby conspecifics to approaching threats (Brown and Laland, 2003; Manassa and McCormick, 2012), and by assessing the lethality of a predator from injury and escape from non-lethal encounters (Kelley and Magurran, 2003; Kieffer and Colgan, 1992). Though it is difficult to disentangle the role of each as separate mechanisms from these results, previous studies on the behavioral effects of spearfishing using other methods confirm that, in addition to the loss of individuals via mortality, some individuals respond behaviorally by moving out of an area that is opened to fishing (Jupiter, 2012).

Finally, like most fishers, spearfishers exert a fundamentally different predation risk than natural marine predators for two reasons. First, spearfishers often preferentially target predatory fish species, and second, they do so with the help of gear that enables them to outpace the capabilities and success rates (i.e. lethality) of natural predators (Darimont et al., 2015). Although not yet tested within the spearfishing literature, it is possible that the comparatively low level of natural predation risk experienced by marine predators predisposes them to a lower magnitude of response to spearfishers, just as a variety of natural history characteristics including high site fidelity, low motility, and boldness have been shown to increase the vulnerability of fish to other fishing methods (e.g. Alos et al. 2012, Sutter et al. 2012). The combination of certain natural history characteristics and selective pressures unique to human predation may

result in some species - like the large-bodied, slow moving, predatory species of the Serranidae family, for example - being more vulnerable to spearfishing predation than others. Further research into the effect of natural history characteristics on the anti-predator responses of marine fish to spearfishing is needed.

2.2. Recreational diving

Studies specifically designed to test the behavioral effects of recreational diving and snorkeling on marine fish are rare, and the majority of these do not measure the FID of fish (but see Miller et al. 2011; Bergseth et al. 2016; Ridlon, chapter 2). Instead, response variables such as presence, abundance, and/or community composition, or the interruption of other daily behaviors such as feeding are used to infer anti-predator behavior in fish, and thus avoidance or tolerance to divers. Existing research has also primarily been conducted in places where multiple human recreational activities occur, without isolation of diver effects from the effects of spearfishers or fish feeding by humans, both of which are known to strongly affect fish behavior (reviewed in Burgin and Hardiman 2015; Gallagher et al. 2015). In addition, the nature of long-term or previous contact with divers is not considered, making it difficult to interpret immediate responses of fish in the context of chronic exposure to humans. Even data from long-established MPAs are limited in their ability to lend insight into persistent behavioral effects to fish without measuring the frequency of recreational diving occurring within the protected area, which has not yet been incorporated into any research into these effects to date.

The conflicting empirical data on diving effects to date suggest two competing

hypotheses for the way that marine fish respond to divers: that recreational divers, like spearfishers and natural predators, elicit anti-predator behavior in marine fish, or that they can be recognized as a non-lethal disturbance to which fish can habituate (Fig 2). The first clear tests of these hypotheses provide evidence for habituation of marine fish to divers in the form of significantly decreased FIDs in areas of high recreational use that have been strictly protected from spearfishing for decades (Bergseth et al. 2016, Ridlon chapter 2; Figs 3b& 4). Although the measurement of FID requires an approaching observer, and thus cannot be measured in the complete absence of divers, the inclusion of “diver-free” areas in the methods of these studies is an important advancement, because it enables the comparison of the behavior of fish who have been exposed to divers to places where they have not, something that is missing from the FID data taken inside MPAs in spearfishing studies.

In isolating recreational diving from spearfishing and including observations of locations where fish have not been exposed (or are rarely exposed) to divers, Bergseth et al. (2016) and Ridlon (chapter 2) uniquely capture the cumulative effect of repeated encounters with divers over time, and compare it to a baseline anti-predator response in the long-term absence of human disturbance. Ridlon (chapter 2) explicitly measured FID over a gradient in chronic visitation of divers and found evidence for habituation to divers in the stoplight parrotfish, *S. viride*: the average FID of fish in a frequently dived area was significantly lower than those in less dived and “undived” areas (Fig 3b, 4). In addition, the median FID of habituated fish in the highly dived areas was 0, suggesting that long-term, consistent exposure to recreational diving in an area strictly protected from fishing can result in the nearly complete loss of flight response in at least one

species of marine fish. Likewise, Bergseth *et al.* (2016) found significantly lower average FIDs of the coral trout *Plectropomus leopardus* in dived zones with “higher numbers of recreational divers and tourists” compared with no-entry zones, suggesting that frequent contact with non-lethal divers also leads to habituation in this mesopredator. This collective evidence for habituation to recreational divers confirms the main prediction of optimal FID: when the lethality of the predator is zero, the ultimate benefit of flight is eliminated while the costs associated with it and the benefits offered by engaging in other activities remain, resulting in a lower optimal FID. Where divers pose no predation risk, the average FID instead presumably reflects the level of natural predation risk in the system, since natural predators still impose a cost to total loss of a flight response. The level of natural predation risk in these systems was not reported, and future studies will benefit from including this information.

The flight responses of fish to divers in the long-term absence of spearfishing also suggest that the degree to which fish habituate is driven not only by the lethality of the diver, but by the encounter rates between divers and fish, confirming the role of repeated encounters in the process of habituation (Bejder *et al.*, 2009; Burger and Gochfeld, 1990). The lowest average FIDs are those recorded in areas where the encounter rate with, and thus cumulative costs of repeated flight from recreational divers is highest, while fish retain higher FIDs where they rarely encounter divers (Fig 3a, 4; Bergseth *et al.* 2016; Ridlon, chapter 2). In high encounter scenarios, fish maximize their fitness by reducing costly flight from non-lethal divers, while in low encounter scenarios, the potential benefit of avoiding natural predation presumably outweighs the cost of occasional unnecessary flight from non-lethal divers. These

findings provide more support for the idea that individual fish are learning about the risk posed by divers through repeated and frequent encounters with them, and are adjusting their FIDs accordingly, due to the absence of the simultaneous mortality effects and learning opportunities posed by encounters with spearfishers. In places where fish encounter only recreational divers, the importance of learning via repeated encounters as a mechanism for the changes in FIDs is reflected by not only the lower FIDs in places of high diver encounters, but also the higher FIDs in places of low encounter rate, where fish have fewer opportunities to learn about the lethality of divers (Bergseth et al. 2016; Ridlon, chapter 2).

As with spearfishers, the responses of marine species to recreational divers are likely to be influenced by their natural history and trophic level (Fig 1 b and c). Although FID is not a metric that can be used with highly mobile predatory fish species, there is evidence to suggest that many marine predators and large bodied fish do not respond to recreational divers with flight or increased wariness. For example, reef sharks do not avoid areas of regular SCUBA diver visitation in comparison to places where divers are absent.: Bradley et al. (2017) found no significant differences in abundance, behavior, or residency patterns between heavily dived and undived locations. This result is in contrast to other evidence of shark avoidance of divers (Cubero-Pardo et al., 2011; Quiros, 2007), gleaned from the immediate responses of sharks to divers, and highlights the importance of examining these effects in the context of chronic diver exposure. Grouper, snapper, and jacks also do not significantly interrupt spawning behavior in response to approaches by recreational divers, although whale sharks in these aggregations do (Heyman et al., 2011). Of course, measuring the reactions of species at

a time when the cost of fleeing is potentially much larger than normal (i.e. due to a lost mating opportunity) is likely to affect their reactions to divers relative to times when they are engaged in other behaviors. Future experiments with better standardization of body condition, and done under more neutral conditions with respect to the relative costs of fleeing, are needed to further determine predator responses to recreational divers.

2.3. Interactions between spear fishing and recreational diving effects

Most marine recreational areas worldwide allow for both consumptive and non-consumptive diving, creating a varied spatial and temporal landscape of human-induced predation risk for fish. How fish respond to human encounters under these dynamic risk scenarios is unknown. The empirical data from places where consistent, frequent spearfishing or recreational diving activities take place in isolation from one another show that these two activities have opposing effects on the FID of marine fish, supporting the main prediction of optimal FID theory (e.g. Miller et al. 2011; Januchowski-Hartley et al. 2012; Januchowski-Hartley et al. 2014, Benevides et al. 2016; Fig. 1 & 3 and references therein). In those scenarios, spearfishers are similar to natural predators in that their lethality remains relatively constant, although potentially higher than that of natural predators based on the range of their spears (J. Cinner et al., 2005; Feary et al., 2011). However, where spearfishing and recreational diving co-occur, fish encounter a population of divers that, unlike most natural predators, are unique in presenting nearly identical visual cues connected to vastly different levels of individual lethality, introducing a higher level of uncertainty about the probability of death given

any one encounter with a diver. These fundamental differences in the predation risk created by spearfishers, and the high uncertainty associated with potential predator populations created by the mixture of spearfishers and recreational divers, may be driving important differences between the response predicted by optimal FID theory and the seemingly high sensitivity of average FID values to any level of contact with spearfishers reflected by the empirical data (e.g. Januchowski-Hartley et al. 2015; Fig 5).

Spatially explicit observations of FIDs inside versus outside of MPAs, for example, provide evidence for the bidirectional “spill over” of fear effects across MPA boundaries: both increased wariness from fished areas and naivete to fishers from protected areas (Januchowski-Hartley et al., 2015, 2013). Fish living within and around MPAs experience spatial differences in fishing pressure that remain relatively constant over time, assuming no poaching occurs inside the areas closed to fishing. There is evidence that where fishing occurs outside of protected areas, the effects of even a small level of exposure to this human predation can be transmitted inside via the movement of fish, and that as fishing pressure outside increases, the average FIDs of some targeted species inside the protected area also significantly increase (Januchowski-Hartley et al. 2015; Fig 5b).

Likewise, changes in the FID of fish experiencing pulse fishing events offer insights into the timing and nature of anti-predator responses to spearfishers. Customary and periodically harvested closures (PHCs) are temporal fisheries management techniques in which an area is closed to fishing for a known period of time, often for the explicit purpose of restoring naïve behavior in, and thus increased catchability of reef fish (J. E. Cinner et al., 2005; Feary et al., 2011; Januchowski-Hartley et al., 2014; Macintyre and

Foale, 2007). Measuring the effect of pulse fishing events in PHCs demonstrates how quickly population-level changes in behavior take place in response to spear-fishing, which may serve as evidence for the comparative strength of exposure to human predation in setting FID, versus the benefits of habituation to recreational divers. Average FIDs significantly increased in within three days of an area being opened to fishing (Goetze et al., 2016; Januchowski-Hartley et al., 2014), confirming relatively rapid population-level shifts in behavior towards predatory divers. In contrast, the FID of marine fish can take much longer to be “restored” to pre-fishing levels (e.g. six months after the area was closed to fishing again, Januchowski-Hartley et al. 2014), and this retention of “wariness” in fish due to pulse fishing has led to recommendations to keep periodic closures in place for a minimum of three years to provide adequate time for flight responses to decrease (Goetze et al., 2016). It is possible that this discrepancy in the speed with which average FIDs change indicates that fish retain a higher FID based on long-ago encounters with predators (fishers) even in the absence of current fishing. Alternatively, the observed finding could be the result of fish having had very few total human encounters once the area was closed, preventing an opportunity for learning about the lethality of divers or an incentive for reducing FID.

In these dynamic risk scenarios, the ratio of lethal divers to non-lethal divers that a fish encounters represents the true level of predation risk that a fish is under from the population of “predators”; as the proportion of lethal divers increases, theory predicts that optimal FID should also increase (Fig 5a). Thus, the encounter rate of fish with divers may be a particularly important in these mixed diver populations as a mechanism with which fish learn about both the lethality of divers as a potential predator and the

cumulative costs and benefits associated with fleeing from them. If fish could perfectly distinguish between lethal and non-lethal divers, they could adjust their FID accordingly with each encounter. However, the visual cues associated with spearfishers and recreational divers are similar, given that fishers also use both snorkeling and SCUBA gear. The few studies that test the effects of different types of gear on the FID of marine fish do not provide support for the idea that fish can distinguish between spearfishers and recreational divers, showing no significant difference in the FIDs of fish approached by a SCUBA diver or snorkeler, or between those with or without a spear in hand (Januchowski-Hartley et al. 2012; Bergseth et al. 2016; but see Tran et al. 2016). To the degree that fish are unable to assess lethality of an individual diver, either because humans present identical visual cues or because they can kill fish from further distances than visual cues are useful via spear guns, we predict that they a) rely more heavily on information gained from their past encounters with that predator and/or b) potentially retain a higher FID to conservatively avoid the ultimate loss of lifetime fitness (i.e. death). This should especially hold true in places where the encounter rate with all divers is low, due to both the limited information the fish has and the low costs associated with occasional flight.

What is completely untested empirically is how the FID of fish changes as both the ratio of spearfishers to recreational divers changes, and as a fish's encounter rate with divers changes. Consider, for example, that a fish encounters twenty divers a day, and that ten of them are spear fishers, creating a 50% probability of death given encounter, assuming spearfishers are completely efficient predators. At that level, one would predict that the risk of predation is sufficient, and the cost of flight low enough, for fish

to flee from all encounters with divers. Conversely, if fish encounter 200 divers a day, and only ten of them are spear fishers, the probability of death given encounter is reduced to 5%, and FID theory would predict that they reduce their FID considerably to cut the high costs of frequent flight from non-lethal divers. These are examples of the effect of the lethality of the predator (via the ratio of lethal divers to non-lethal divers) on the FID of fish. However, given the same probability of death from our first example but a higher rate of encounter with all divers – e.g. fish meet 200 divers a day, and 100 of them are spear fishers -- the costs of fleeing will increase enormously, and a fish is expected to reduce its FID only once the cost of fleeing outweighs the risk of not fleeing (i.e. >50% probability of dying). For example, we would expect FID to decrease when the frequency of flight prevents a fish from eating and engaging in other fitness-enhancing activities to such an extent that overall body condition is so low that they are forced to take greater risks (as predicted by risk allocation hypothesis; Lima and Bednekoff 1999, and seen with marine fish and other species responding to natural predators; reviewed in Ferrari et al. 2009). How the ratio of lethal to non-lethal divers and the encounter rates with each influence the FID of marine fish is currently untested. However, empirical evidence from the Scaridae family (Januchowski-Hartley et al. 2011; Ridlon, chapter 2; Fig 4) suggests that at low levels of encounter rate with spearfishers or recreational divers in isolation, the change in FID does not appear to be different: all diver encounters are met with essentially the same flight response (Fig 4, middle panel). In addition, the level of encounters at which average FIDs significantly increase in response to spearfishers is lower than that required to drive a decrease in FID with exposure to only recreational divers. This is further evidence that encounter rate drives

relative changes in FID, and that fish FID may be more sensitive to the number of spearfishers they encounter in proportion to recreational divers. However, it is important to test these hypotheses explicitly with quantification of the ratio of lethal to non-lethal divers and the frequency with which fish encounter them, as it is relevant to understanding the ecological consequences of spearfishing and recreational diving where these activities co-occur and how management interventions can address these impacts.

Existing empirical results provide support for the idea that exposure to predation risk from spearfishers may have a stronger influence on the average FID of fish populations than repeated encounters with non-lethal divers. However, the evidence for habituation to solely recreational diver encounters illustrates that the cumulative costs of unnecessary flight are sufficient enough to drive reductions in FID where the frequency of incurring that cost is high (high diver encounters). Thus, the retention of higher FIDs within MPAs may be driven by either the comparatively higher cost associated with mistaking a spear-fisher for a recreational diver (death) given a spear fisher's reach and the uncertainty of diver lethality, or an overall low encounter rate with divers inside the MPA. How we interpret existing empirical findings relies on quantification of the ratio of lethal versus non-lethal divers and the encounter rate between divers and fish. Future studies need to distinguish between these possibilities in order to understand the interaction between the two activities where they co-occur.

Beyond Behavior: Linking Diver Fear Effects to Fitness and Ecosystems

The emergent research into diver fear effects has not yet developed to include

direct measurements of the potential consequences (e.g. fitness consequences and ecosystem level impacts) of changes in the FID or other anti-predator behaviors of marine fish. However, empirical evidence from marine systems suggests that the magnitude of fear effects can exceed that of mortality effects on the population level, because fear of predation can be transmitted simultaneously to all members of the population and persist over time (Preisser et al., 2005). Natural predators thus set risk regimes that affect not only the individual fitness of prey species and their populations, but also trigger behaviorally-mediated cascades that have broader impacts on marine ecosystems (Heithaus et al., 2008; Preisser et al., 2005; Werner and Peacor, 2003; Wirsing et al., 2008). Based on the compelling evidence herein that diver fear effects are operating in marine systems, we predict that spearfishing and recreational diving have the potential to similarly affect the fitness of marine fish, resulting in population effects, and to trigger behaviorally-mediated cascades. The behavioral effects of spearfishing in particular may operate on a broader scale and at a faster rate than those induced by natural predators, due to the use of gear that enables human predators to outpace the capabilities and success of natural predators (Darimont et al., 2015, 2009). These effects may also be differentially distributed to predatory fish species, which fishers often preferentially target (Estes et al., 2011), and whose behavior is likely to impact entire food webs via their influence on lower trophic levels (Dulvy et al., 2004; Mumby et al., 2006).

In order to better understand ecosystem-level impacts of interactions with divers, a first step will be to quantify the fitness consequences of changes in FID from both spearfishing and recreational diving to marine fish. Although FID was not

measured, Barnett et al. (2016) showed that sharks attracted to recreational diver groups (via provisioning) experienced a significant increase in their metabolic rate and daily energy expenditure through increases in their daily activity level on days when they interacted with divers. Likewise, California Sea Lions with frequent exposure to tourists did not avoid them, but exposure to humans resulted in lower reproductive rates, from which authors predicted reduced long-term population growth rates that could lead to population declines for the species (French 2011). In addition, boat noise has been shown to impact fitness via increased cortisol levels, decreased rates of post-larval settlement, and suppressed feeding rates in a range of marine and freshwater fish (Wysocki et al. 2006; Bracciali et al. 2012; Holles et al. 2013; Berthe and Lecchini 2016), and has been directly linked to decreased survival of young due to reduced parental care in a species of reef fish (Nedelec et al., 2017). These studies illustrate the potential pathways for and consequences of diver-induced behavioral effects. However, in order to determine the prevalence and magnitude of these effects to marine fish, it is necessary to simultaneously measure FID and relevant fitness components (e.g. increased metabolic rate, reduced growth rate) to quantify the cumulative fitness costs of their flight behavior. Directly measuring the accumulation of an effect on components of individual fitness through repeated encounters with divers will identify any persistent effects, and give a basis of data from which to predict their consequences to fish populations.

The potential for cascades due to diver-fish encounters has also yet to be studied in marine systems. However, multiple lines of evidence suggest that cascades from diver impacts are likely to occur where encounters with humans change the behavior of

predators and herbivores, in particular. Marine herbivores respond to natural predation by changing the spatial distribution and intensity of grazing activities (Rizzari 2014) or by switching diets (e.g. dugongs with sharks; Wirsing et al., 2007). For example, bottlenose dolphins (*Tursiops cf. aduncus*), dugongs (*Dugong dugon*), green sea turtles (*Chelonia mydas*), and pied cormorants (*Phalacrocorax varius*) all modify their behavior in response to variation in chronic predation risk from tiger sharks (*Galeocerdo cuvier*), in Shark Bay, Australia. Subsequent changes in the distribution and intensity of foraging behavior of some of these species appear to drive the spatial pattern of seagrass abundance and community composition, and thus alter the abundance and composition of teleost communities (Burkholder et al., 2013; Heithaus et al., 2012, 2007). Similarly, where humans alter natural predation risk via fishing, there is evidence for risk-induced behavioral cascades (Byrnes et al., 2006; Madin et al., 2016, 2011). For example, Madin et al. (2010) found the removal of or avoidance of fishers by marine predators created differences in natural predation risk that altered herbivore foraging behavior, and led to changes in macroalgal distribution on a coral reef.

Given the evidence for changes in the feeding behavior of marine fish in response to fear effects, it stands to reason that diving could similarly trigger ecosystem cascades via this behavioral pathway. Although habituated fish may not experience large feeding losses due to encounters with recreational divers, (Ridlon, chapter 2), the effects of spearfishers on the feeding behavior of fish are unknown. Fear effects from spearfishers are likely to mimic natural predation risk in re-distributing herbivore effort, and deserve further attention. Further, the effects of any reduction in feeding due to diver encounters may be especially crucial in ecosystems that are already at a

“tipping point” (Mumby, 2006; Mumby et al., 2007). If there are limited fish in an area, or algae have reached a critical abundance in proportion to coral, for example, then a reduction in the feeding rate or spatial distribution of herbivores could have large negative impacts on an already imperiled system. Additionally, where shifts in behavior due to diver encounters impact species interactions - as with cleaning, competition, and predation - there is the strong potential for secondary ecosystem-level effects. While these have not often been demonstrated in marine systems, changes in the nature and duration of species interactions of the kind that are known to have knock-on effects have been recorded in marine fish. For example, cleaning rates of fish were suppressed by 50% in the immediate presence of a diver, even on reefs that have been visited regularly by divers for decades in a protected recreational area, showing a community-level response and the potential for diver presence to interfere with an important ecosystem function in marine systems (Titus et al., 2015). In addition, diver encounters can increase natural predation risk for some marine fish (Di Franco et al., 2013), and significantly alter the diel behavior/ time budget of fish (Côté et al. 2014; Ridlon chapter 2) . This collective evidence suggests that diver risk effects may be influencing marine fish through a number of behavioral pathways, each with potentially unique fitness consequences, and highlights the need to determine both the direct and persistent fitness effects of diver-induced changes in FID, and to explore the effects of diver encounters on other behaviors in marine fish that could have community-level and ecosystem consequences.

Management Implications of Diver-Induced Fear in Fish

As the number of recreational divers within marine reserves increases worldwide (Gonson et al., 2015), the ability of some marine fish to habituate to divers is an important consideration to incorporate into our understanding of both the ecological dynamics and management of marine reserves. Specifically, where habituation to recreational divers and snorkelers occurs in isolation to spearfishing, it represents a potential win-win scenario for marine fish and recreational divers. Habituated fish reduce the time and energy spent on vigilance and flight, and experience less disruption in opportunities to feed or mate due to diver encounters. Divers likewise benefit from engaging in close range observation and photography of habituated fish, which likely increases diver satisfaction (e.g. as found with whale watching (Valentine et al., 2004)). While the generalizable nature of these results is limited by a current lack of data from a range of species, similar habituation to chronic encounters with divers has been suggested for some marine species (Ayling and Choat, 2008; Titus et al., 2015), and there is evidence that marine fish can habituate to other recreational disturbances through repeated exposure over time, including boat noise (Nedelec et al., 2016; Radford et al., 2016). This evidence for habituation suggests that these findings may be more broadly applicable both to a range of marine species and to a number of other human recreational activities, particularly in MPAs. If the result of habituation under increased levels of recreational diving holds true for many marine species, it suggests that concentrating diver activity into one area on the reef, and keeping another area as a complete no-entry zone would minimize behavioral effects of diving both to the populations of reef fish (who have a true refuge elsewhere) and the reef itself (left

untouched by divers except in the highly dived area).

However, the lack of data on these effects may be hindering the effective management and zonation of marine systems, many of which are simultaneously being identified as needing protection from consumptive human activities, and attracting increasing levels of recreational users. For example, Reed et al (2008) found that hiking, an activity similar to recreational diving in many ways, led to a five-fold decline in the density of native carnivores and a substantial shift in community composition from native to nonnative species inside a terrestrial protected area. This comparatively large gap in our understanding of the role of human-induced behavioral effects in ecosystem-level consequences, or in affecting the resilience of marine ecosystems, is stark in comparison with what is known about the effects of similar recreational activities in terrestrial systems.

There are several unique management implications of the spatially-explicit responses of average FID to spearfishing. First, fish not exposed to spearfishing cues reduce their FIDs, and the empirical evidence for the “spillover” of naïve fish with shorter FIDs from protected areas into fished areas or after a period of closure (Jupiter et al. 2012; Januchowski-Hartley et al. 2013; Januchowski-Hartley et al. 2015) illustrate how an understanding of behavioral effects of spearfishing and recreational diving can be used to leverage fisheries benefits, including higher catchability of fish. The behavioral effects of spearing can likewise “spill in” to protected areas, to the detriment of both the fish and recreational users. The sensitivity of average FID to even low levels of exposure to nearby spearfishing highlights the importance of the effective enforcement of no take areas for the management of diver fear effects. In contrast to the

mortality effects of poaching, this evidence suggests that fear effects from non-lethal exposure to spearing can be transmitted to many more individuals in the population (Januchowski-Hartley et al., 2015), having a comparatively larger effect than the removal of fish, especially at low levels of poaching. In addition to strict enforcement of no take areas, buffer zones between areas that allow for spearing and those that allow for recreational diving could serve to dampen the spatial extent to which behavioral effects of spearing are transmitted into protected areas. Buffer zones prohibiting diving activities, but allowing for hook-and-line fishing and boating recreation, for example, offer fish a refuge from all diver encounters in places directly adjacent to fished areas. Similar buffer zones have had success in reducing behavioral effects of human disturbances on land, particularly for birds (Beale and Monaghan, 2004; Blumstein et al., 2003; Carney and Sydeman, 1999). Finally, areas free from all human disturbance within marine protected areas, where no diving or other recreational activities are allowed, may provide a more complete refuge for fish from the behavioral effects of divers. This type of zonation- “no go” zones, buffered from fishing effects by surrounding recreational diving areas- is already employed in the Great Barrier Reef MPA. The broader implementation of such zonation could help further reduce the extent to which diver fear effects are transmitted inside protected areas.

The incorporation of an understanding of diver fear effects into the management of marine systems may prove critical in advancing the multiple goals of MPAs, where consumptive and non-consumptive diving often take place in tandem. Collectively, the evidence for diver-induced behavioral changes in fish suggests that reducing the behavioral effects of fishing on targeted species may result in the spillover of both

increased biomass and more easily caught fish to fished areas, and provide opportunities for closer encounters between fish and recreational divers within protected areas. However, a better understanding of the effect of the ratio between spearfishers and recreational divers that fish encounter on their flight behavior is needed. The empirical evidence presented here suggests that the FID of marine fish may be more sensitive to human predation than natural predation, and that fish are not entirely protected from the behavioral effects of fishing activity, even where they are protected from mortality effects via MPAs. To the degree that any level of exposure to spearfishers can be transmitted inside protected areas, the behavioral effects of fishing can be magnified via encounters with non-predatory divers, and elevated anti-predator responses of fish within protected areas has the strong potential to undermine both fisheries and recreational goals. In particular, exposure to spearfishers may cause fish to incur higher energetic costs than they would if they habituated to recreational divers alone. At the same time, “wary” behavior in response to divers will likely make them both more difficult to catch outside the MPA, and more likely to flee or stay away from recreational divers inside the MPA. Recommendations for the simultaneous management of spearfishing and recreational diving could be further improved by studying the influence of species motility and home range, MPA size, the degree of poaching, and the ratio of recreational diver versus spear fisher encounter rates on these behavior spillover effects and optimal FID.

Conclusion & Recommendations for Future Research

The testing of optimal FID theory in marine systems, in the context of diver

effects on fish, provides the most complete and comparable data on the behavioral effects of human recreational activities in marine systems to date. From existing studies, patterns are emerging to suggest the influences of divers on the behavior of marine fish: in isolation, spearfishing and recreational activities have clear and opposing effects on the flight behavior of marine fish, as is predicted by optimal FID theory. However, we provide evidence that the encounter rate between fish and divers drives relative increases and decreases in FID, and may be a particularly important mechanism for fish to assess the predation risk posed by humans. Further, in order to understand the broader implications of the effects of divers on the FID of marine fish, future research is needed to determine both the cumulative fitness effects and potential ecosystem-level consequences of diving activities in marine systems. The recent research into the effects of both spearfishers and recreational divers on the FID of marine fish therefore represents a promising area of future research into behavioral effects of human recreation in marine systems on which to build. Here, we make specific recommendations for moving the field forward to ensure that studies are comparable, findings are generalizable, and results can be used to directly test fitness and ecosystem-level effects.

5.1 Standardizing the methods

The lack of standardized data collection methods and response variables used to test recreational diving effects makes direct comparisons between studies difficult, and broader patterns in these effects hard to detect. Thus, while these data provide some useful insights into the anti-predator responses of a broad range of marine fish to

recreational divers, it is difficult to draw generalizable conclusions from them. The measurement of FID in marine fish is both simple and informative, and its usefulness in testing and improving upon predator escape theory by quantifying a behavioral response to divers is already clear. It is important that future research employs standard empirical methods from which to build, ensuring that comparisons among and between the effects of consumptive and non-consumptive diving can be made across species and locations.

The measurement of FID in marine systems is straight forward: a focal fish is approached at a steady swimming speed by an observer, who drops a marker when the fish begins to flee, and then places a second marker at the location from which the fish fled. The distance (cm) between markers is then measured to obtain FID (e.g. Gotanda et al. 2009; Januchowski-Hartley et al. 2011). Agreement on the method for measuring FID is generally good within spearfishing studies but there remains a need to further standardize the collection of FID data. For example, methods in spearfishing studies vary in whether fishing behavior is mimicked or spears are carried during approaches, what gear types are used by observers (SCUBA or snorkel cf. Gotanda et al. 2009; Benevides et al. 2016; Bergseth et al. 2016), and even the end points from which FID is measured (e.g. from the tip of spear sensu Nunes et al. 2016 vs. head of the observer sensu Gotanda et al. 2009; Januchowski-Hartley et al. 2011). Each of these implications for accurate and comparable data. In addition, the distance from which an observer begins a trial, start distance, has been shown to influence FID in animals reacting to humans (Blumstein, 2010; Chamaillé-Jammes and Blumstein, 2012) including reef fish (Tran et al., 2016), and should also be standardized or controlled for. The type of spears

used in the study area (and by the observer if appropriate) and their range should be reported as well, because this directly influences the optimal distance at which a fish should flee from humans. As alternative methods and metrics of anti-predator behavior, minimum approach distances (MAD) taken by diver-operated video seem promising in offering automated and potentially more precise FID data (e.g. Lindfield et al. 2014; Goetze et al. 2017) but there is a need to confirm their comparability to human observers taking these data, both for future comparisons and because these methods require expensive equipment. In the absence of the use of these technologies, measuring FIDs by divers is relatively easy to do with minimal training and at low cost, making it accessible to managers and scientists in remote areas alike, so it is likely that diver-generated data will continue to be an important source of our understanding of these effects.

Next, future research will benefit from experimental designs including “control” treatments that more accurately reflect or simulate the absence of human presence with which to compare the effects of both consumptive and non-consumptive diving activities. For example, while the behavioral responses of fish to divers inside protected areas is often used as a “no spearing” control treatment, the level of recreational diving happening inside the MPA is rarely quantified, or even given consideration. Given the evidence for spearing effects to be transmitted via fish movement and recreational diver encounters inside protected areas, these areas likely do not offer a true baseline for fish behavior where humans are not present. In lieu of a “diver free” area, which may be absent from many protected areas, sites that experience temporal variation in diving activities (as in the “off” season for diving tourists, or as has been done with temporary

fisheries closures) can be used. In all cases, quantification of recreational use inside MPAs and the duration of time an MPA has been in place will allow for a more accurate interpretation of the behavioral responses of fish to divers within and outside of MPAs. In addition, experimental designs should ensure the isolation of confounding factors, especially fishing and fish feeding, from the measurement of effects of recreational divers to fish behavior.

5.2 Determining the mechanisms: the inclusion of encounter rate

Further investigation is needed into whether fish can distinguish between spearfishers and recreational divers and the threats they pose. Spearfishers report anecdotally that fish act differently when they carry a spear versus when they snorkel or dive without one, suggesting that the fish use the spear as a visual cue for human predation (personal interviews, Ridlon) but initial data comparing the reaction of fish to the presence of spears in diver approaches does not support this (Januchowski-Hartley et al. 2012; Bergseth et al. 2016 but see Tran et al. 2016). Since fish respond to the body size, approach angle, and speed of natural predators (Domenici, 2002), they may also use the swimming behavior of divers to assess their risk, but this is untested. In lieu of direct mechanistic experiments, measurements of the FID of a species across separate gradients in consumptive and non-consumptive recreational activities where consistent levels of diver visitation occurs (*sensu* Januchowski-Hartley et al. 2011; Bergseth et al. 2016; Ridlon chapter 2) will help to further explain the role of diver-fish encounter rate on the sensitization and habituation of fish to divers. Empirical tests of the interaction between consumptive and non-consumptive diving with spatially explicit FID data that

includes the quantification of the ratio of spear fishers to recreational divers that fish encounter will explore the relative importance of the lethality of the predator and the encounter rate with divers in driving the FID of marine fish. This is a priority particularly for species targeted by fishers and with the potential to drive cascades or other secondary effects in the system, such as predators and herbivores. These empirical data can then be used to update optimal FID theory to explicitly include the encounter rate between fish and divers and incorporate the nuances of humans as predators, namely their increased lethality compared with natural predators and their wide variability in individual lethality (spearfishers vs. recreational divers).

5.3 Beyond Behavior: Fitness and Ecosystem effects

It is essential to gain a more thorough understanding of how the consumptive and non-consumptive recreational activity of humans is affecting marine ecosystems through changes in fish behavior. While the quantification of immediate, anti-predator responses of fish to divers is a good basis for understanding these effects, there is also a need to quantify individual fitness effects to marine fish and look for evidence of cascades triggered by these very common human activities to better understand the magnitude and breadth of these effects in marine systems.

In order to determine whether persistent fitness effects result from diver encounters for fish, it will be necessary to link the measurement of FID to the cumulative fitness costs of their flight behavior. The clearest way to determine the fitness costs associated with diver encounters is through direct individual measures of fitness such as body condition, growth rate, and reproductive output in relationship to

different levels of exposure to divers. The inclusion of direct fitness measures into future studies could be especially useful in revealing whether fitness effects accumulate with higher recreational diver encounters, even for habituated fish. These individual measurements could then be used to predict the population-level consequences of diver risk effects (e.g. *sensu* sea lion population declines, French et al. 2011; increased energy expenditures and reduced breeding success in penguins exposed to tourists, Ellenberg et al. 2006). The inclusion of alert distance (AD, the distance at which an animal becomes vigilant to a potential predator) and other pre-flight behaviors of fish into future research would add further insights into risk assessment in and the costs associated with vigilance for marine fish. The consideration of vigilance costs is critical to include in future studies, because it allows for more thorough cost-benefit analyses and optimality approaches to understanding the fitness effects of diver encounters for fish. Standardized measurements of fitness enhancing behaviors in the presence of divers including feeding (bite rates), cleaning, mating, and territory defense will also increase our understanding of the broader behavioral effects of recreational diving, especially when considered in the context of the long-term frequency of diver encounters for fish populations. The potential effects of the natural history of a fish species on their response to the risks posed by divers, particularly divers acting as predators, are still very limited. Predators and herbivores are promising focal species on which to focus future research due to their strong potential to trigger cascades.

In comparison to what is known in terrestrial systems, and for natural predators, evidence for and research into the ecosystem-level effects of recreational activities of

humans in marine systems is sorely lacking. Currently, we can only draw inferences about the broader implications of diver-induced behavioral effects on fish to marine communities and ecosystems based on findings from related areas of research (e.g. human effects in terrestrial systems, natural predation studies). This is problematic, because marine systems are different from terrestrial systems in many fundamental and important ways, and behavioral effects may therefore operate differently in each system. Likewise, humans represent unique predators, and therefore may influence fish behavior differently than natural predators in ways that must be directly assessed. In particular, the isolation of different human activities in space, especially in highly dived areas, may be more critical to managing the behavioral effects of fishing than its mortality effects. The measurement of FID in marine fish is an exciting and important new avenue for research into behavioral effects in marine systems that has the potential to advance our understanding of the impacts humans have on the function, structure, and resilience of marine ecosystems through non-consumptive effects of common recreational activities, and to inform their effective management.

Figures

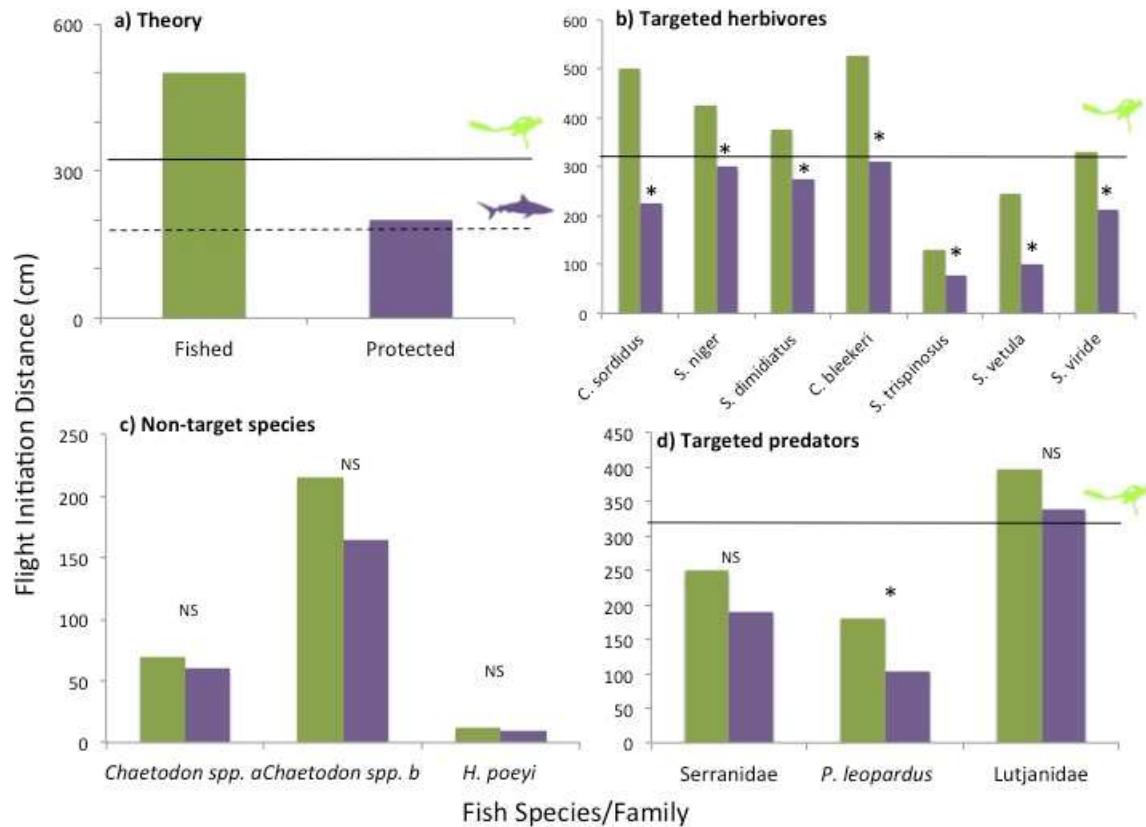


Fig 1. a) Optimal FID theory predicts that targeted marine fish will set their FID higher in areas where they are exposed to spear-fishers (green bars in all panels) than in places protected from them (purple bars in all panels), and base that distance on the lethality of the predators they encounter (top line represents recorded spear gun range, dotted line is a hypothetical FID set by the lethality of natural predators in the system). Empirical data (Gotanda et al. 2009; Feary et al. 2011; Januchowski-Hartley et al., 2011; Bergseth et al. 2016; Nunes et al. 2016) confirm that protection from fishing results in significantly lower FIDs for a number of targeted species of marine fish within reserves (b and d), as compared to non-target species (c). Recorded FIDs are species-specific, and predatory species in particular may not significantly adjust their FIDs in response to human predation (d). *Chaetodon spp. a* are those reported in Bergseth et al. 2016, *Chaetodon spp. b* are those reported in Januchowski-Hartley et al., 2011. Species are ordered by maximum body size (FishBase, Froese, R. and D. Pauly eds., 2017). Note difference in x-axis scales.

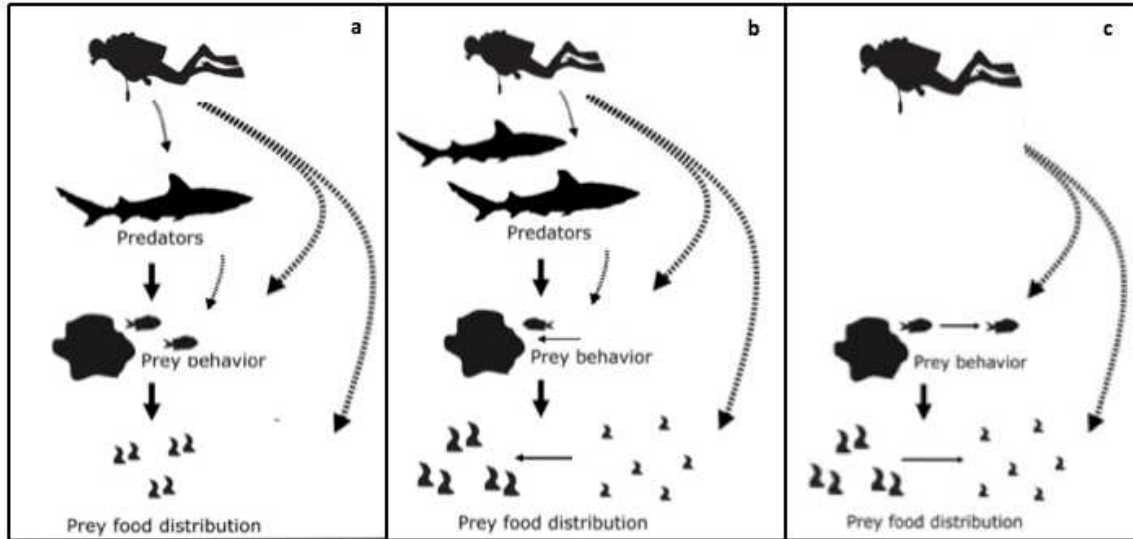


Fig 2: Potential pathways for behavioral effects (dashed arrows) of recreational divers to marine fish. Fish of different species and at different trophic levels may respond to diver stimuli with neutral (a), attractive (b), or repellent behavior (c), as shown here with predatory fish, potentially creating cascading effects in marine systems. Existing studies report mostly neutral (a) and aversive (c) responses to divers, but little is known about the prevalence or magnitude of recreational diver effects due to a current lack of empirical data. Figure modified from Fig 1, in Madin et al., 2010.

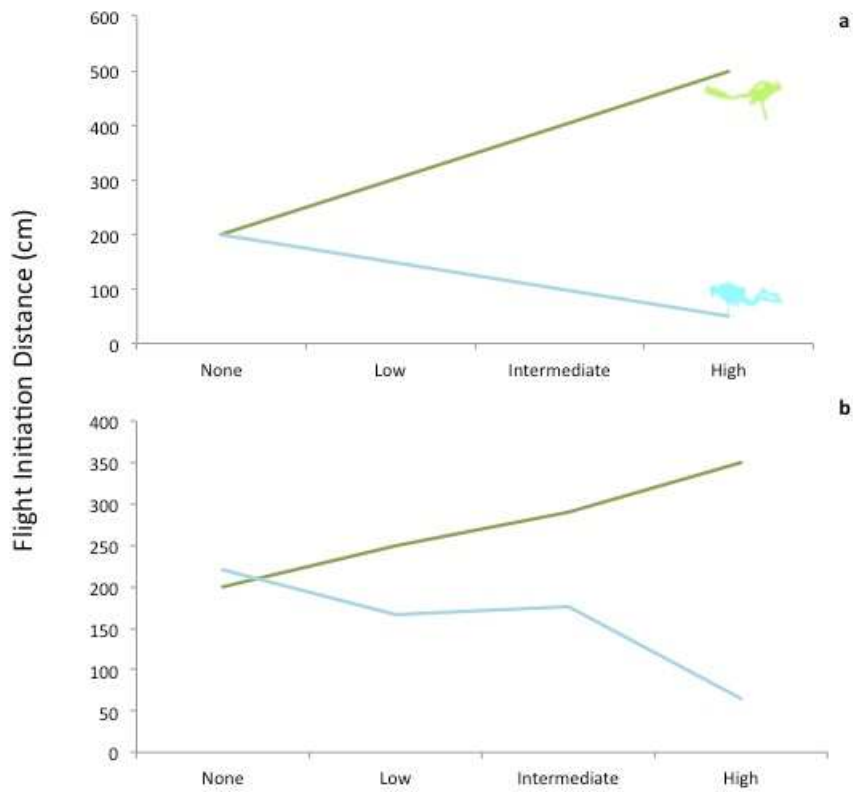


Fig 3. (a) Spearfishing (green) and recreational diving (blue) are predicted by theory to have opposing effects on FID in marine fish. (b) Empirical FID data from the Scaridae family (Ridlon et al in prep; Januchowski-Hartley, 2011) show that when each activity is consistently done in isolation, FID increases in response to spear fishers and decreases in response to recreational divers as the encounter rate between divers and fish increases.

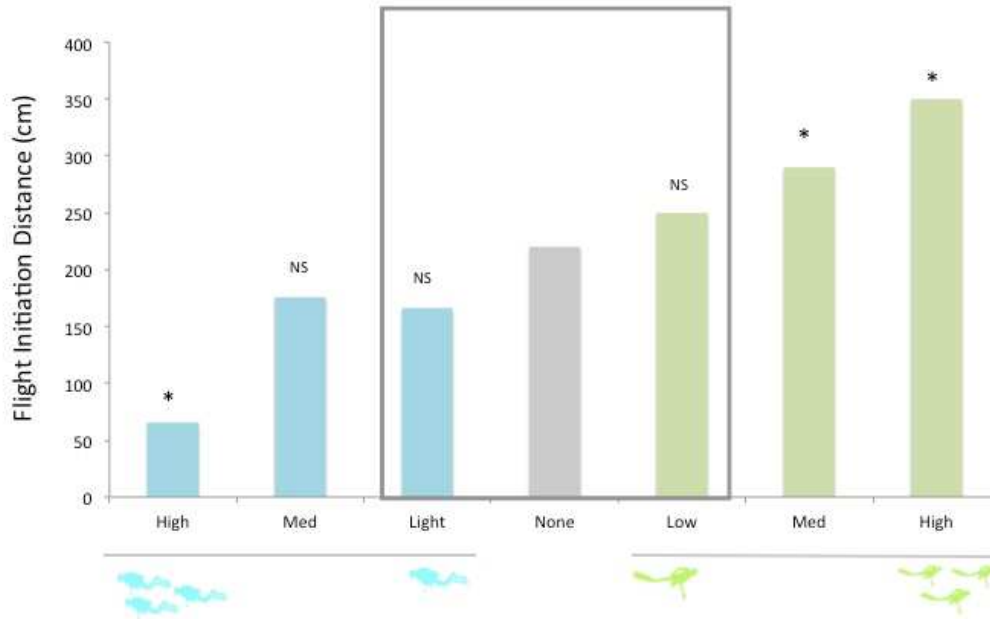


Fig 4. Scarid FIDs across separate gradients in intensity of recreational diving (left, blue) and spear fishing (right, green) show habituation to recreational divers and sensitization to spear fishers at high levels of encounter, but average FIDs at low levels of exposure to either activity are similar to one another. Data are average *S. viride* response to diver approaches in places of recreational diving only (first 4 bars from Ridlon et al., in prep); and for individuals from the Scaridae family in places where spearing takes place (Januchowski-Hartley, 2011). The center grey bar is the averaged value resulting from the average FID of *S. viride* from a reef that is protected from fishing and virtually undived (220 cm; Ridlon et al., in prep), and the average FID for Scaridae individuals inside a no-take area protected from fishing (200 cm; Januchowski-Hartley, 2011). Significance indicators refer to differences between recreational visitation frequency (Ridlon et al., in prep, blue bars) and fishing intensity levels (Januchowski-Hartley, 2011, green bars), and as compared to the “no exposure” FID within each respective study.

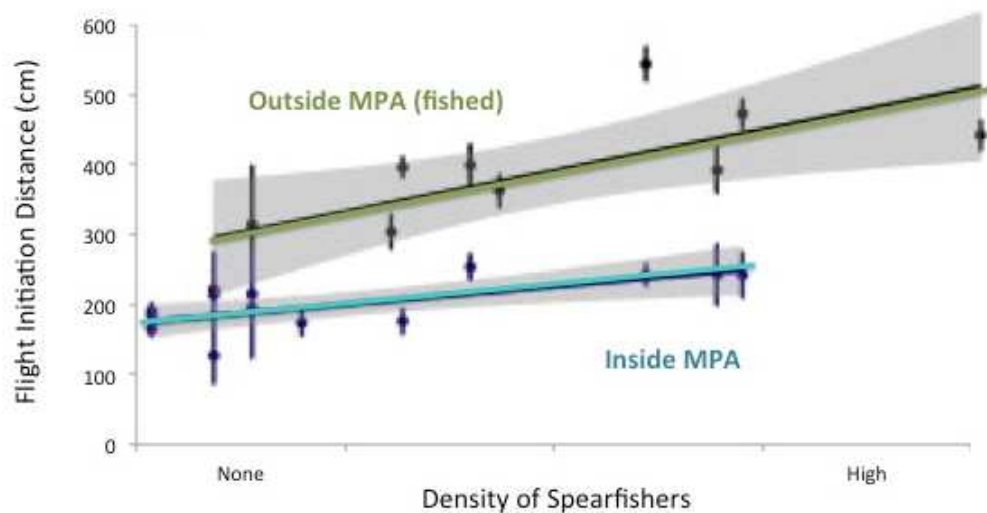


Fig 5. Empirical data from Scaridae species show significant increases in average FID inside protected areas (lower blue line) as both nearby fishing pressure, and average FID (upper green line), increases in adjacent fished areas (redrawn from Fig. 2, Januchowski-Hartley et al., 2015; x axis was originally given in fishers/km). This shows the effect of occasional exposure to spearfishing (via fish movement between areas) on the flight behavior of fish, and demonstrates the effect of the ratio of lethal versus non-lethal diver encounters on the FID of marine fish. The uncertainty of individual lethality involved with diver encounters could drive this increase, by causing fish to react to recreational divers as predators, where spearfishing and recreational diving are done in tandem or nearby one another.

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CHAPTER TWO

Habituation to chronic recreational diving by a coral reef fish

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Abstract

The number of SCUBA divers is on the rise globally (Dowling, 2008), and their activity is becoming especially concentrated inside marine protected areas (Gonson et al., 2015). While there is growing evidence that fish react to divers with increases in wariness and flight where they are exposed to spear fishers (Gotanda et al., 2009; Fraser A. Januchowski-Hartley et al., 2011; Januchowski-Hartley et al., 2015), the effects of recreational diving on the anti-predatory behavior of fish in the absence of spear fishing have not been well studied or effectively demonstrated. By measuring two important components of anti-predator behavior - flight initiation distance (FID) and alert distance (AD) - we found evidence in the Cayman Islands for habituation by a common Caribbean coral reef fish (Stoplight Parrotfish, *Sparisoma viride*) to divers where recreational activity has been concentrated for decades and reef-wide bans on spearfishing have been well-enforced. The near lack of a flight response found in fish exposed to higher levels of chronic diving activity not only contrasts with the responses of fish in less frequently visited areas on this protected reef, but represents the lowest FID recorded for the species in either protected or fished areas elsewhere in the world.

However, significant declines in the bite rates and frequency of cleaning interactions of individuals in the immediate presence of a diver suggest that there may be fitness costs associated with recreational diver encounters, even for habituated fish. We use feeding data to estimate the cumulative cost of daily diver encounters to an individual fish, and use these estimations as a framework to discuss the potential persistence of fitness effects of diver encounters on marine fish. We also discuss the management implications of our results for marine ecosystems, which are affected by the behavior of herbivorous fish, particularly where multiple human uses occur.

Introduction

As non-extractive, recreational activities such as SCUBA diving steadily gain popularity (Dowling, 2008), so too do the number of recreational users, especially inside marine protected areas (Gonson et al., 2015). Current design and management of marine protected areas on coral reefs and other marine ecosystems broadly assume negligible effects of this increased human activity in places that have been identified as needing protection from extractive activities, despite evidence that these areas may have a “carrying capacity” for recreational divers (Davis and Tisdell, 1995). In fact, while many physical effects of SCUBA divers and snorkelers on reefs have been documented (e.g., increased coral breakage, sedimentation, (Guzner et al., 2010; Hasler and Ott, 2008)), we know very little about the effects of SCUBA diving via altered behaviors of marine life, including fishes. This lack of knowledge is a critical gap in our ecological understanding of indirect effects on coral reef systems and may be

undermining the goals of current management of these systems for multiple human uses.

On land, similar, seemingly unobtrusive recreational activities such as hiking can reduce the effectiveness of protected areas (Reed and Merenlender, 2008) by triggering behaviorally-mediated cascades. These can result in a dramatic restructuring of the community by altering per capita foraging rates and/or the spatial distribution of herbivore effort (Creel and Christianson, 2009; Ripple and Beschta, 2004; Schmitz et al., 2004). Indeed, where people engaged in recreation elicit anti-predator responses by terrestrial species, the magnitude of human-induced fear effects can exceed those of natural predation (Beale and Monaghan, 2004; Ciuti et al., 2012b; Frid and Dill, 2002). Likewise, in marine systems the magnitude of behavioral effects on prey species and their resources have been shown to exceed the consumptive effects of natural predators (Preisser et al., 2005), and human alteration of predation risk is widespread (Madin et al., 2016). While fewer definitive examples of human-induced cascades in marine systems exist, human presence can alter foraging behavior in marine fish (Berthe and Lecchini, 2016; Bracciali et al., 2012), and recent studies of marine herbivores suggest the potential for human-induced behaviorally mediated cascades via analogous fear effects (Madin et al., 2010; Madin et al., 2011; Wirsing et al., 2007).

Although behavioral responses of marine species to divers have long been recognized by the recreational and scientific diving communities (Chapman et al., 1974; Kulbicki, 1998; Seifert, 2013), consistent patterns in the direction of these effects are not well established, and evidence for the mechanisms is lacking. Studies designed to test the accuracy of underwater data collection find a range of fish responses to the

immediate presence of a diver. This research provides evidence that behavioral effects of divers can bias monitoring data, affecting both our understanding of marine community dynamics and our assessments of management tools including marine protected areas (Bozec et al., 2011; Dickens et al., 2011; Lindfield et al., 2014; Watson and Harvey, 2007). The methods used in these studies limit their applicability to recreational diving effects for two reasons. First, recreational divers often behave differently than scientific divers (e.g., approach fish directly and at close range, hover over them for photographs). Second, these studies typically do not measure the frequency or intensity of diving, thus precluding any measure of the chronic effects of the disturbance. The few studies that have explicitly examined the effects of recreational divers and snorkelers on fish behavior provide evidence of increased avoidance, vigilance behaviors and evasion in many species in the presence of recreational divers (Albuquerque et al., 2015; Hawkins et al., 1999; Kulbicki, 1998). However, acute responses of fish to divers cannot be used to infer anything about the effects of chronic recreational diving activity without also considering the frequency or intensity of diving activities in these studies. In addition, nearly all studies that measure the responses of fish to divers fail to isolate the effects of different diver types, such as spear fishers or those engaged in fish feeding, and thus confound the cues to which the fish are responding. Fish respond to exposure to spear fishing with flight and increased anti-predator responses, even inside protected areas if fishing occurs nearby (Feary et al., 2011; Gotanda et al., 2009; Fraser A. Januchowski-Hartley et al., 2011; Januchowski-Hartley et al., 2015), and fish feeding is known to result in attraction in some species of marine fish (Corcoran et al., 2013; Di Franco et al., 2013; Feitosa et al., 2012).

This is the first study to quantify the behavioral effects of long-term recreational diving activity on a coral reef fish in a system where spear fishing and fish feeding are absent. To test the assumption that long-term SCUBA diving activity has no effect on the behavior of a coral reef fish, we conducted our experiments on a reef where recreational diving is popular, especially inside a well-enforced marine protected area, and spearfishing has been prohibited for decades. We chose a common grazer and an important bioeroder, *Sparisoma viride* (Stoplight Parrotfish), as our focal species. Widespread throughout the Caribbean, *S. viride* has the potential to trigger a trophic cascade via changes in its spatial foraging behavior (Adam et al., 2015; Bellwood et al., 2012) and is commonly targeted by spear fisherman in other areas. Human-induced changes to an animal's time budget can affect both the individual fitness of the animal and create secondary effects in the system, including cascades (Nevin and Gilbert, 2005; Ordiz et al., 2012; Stensland and Berggren, 2007; Symons et al., 2014). Thus, we measured two anti-predator responses of *S. viride* to diver approaches with standard measurements that indicate a fish's perception of threat and are often used to predict the energetic costs of animals responding to human disturbance (Côté et al., 2014; Gotanda et al., 2009; Taylor and Knight, 2003). We measured alert distance (AD), defined as the distance between a focal individual and a disturbance when the animal becomes visibly alert (Côté et al., 2014; Taylor and Knight, 2003), and flight initiation distance (FID), defined as the distance at which an animal begins to flee in response to an approaching threat [31,43,51]. We also tested for an effect of diver presence on fitness-enhancing activities, including feeding and cleaning interactions in vigilant fish. We use the behavioral responses to recreational diver activity to estimate a cost to

individual fish of diver encounters under different fish habituation levels and diver behavior scenarios, providing a framework to explore the potential effects of recreational SCUBA diving on other marine species. We also examine interactions between recreational diving and spear fishing by comparing our results in the absence of spear fishing to the behavioral responses of the same species from other studies on reefs where both consumptive and recreational diving are allowed. Finally, we consider the broader ecological and management implications of our findings.

Methods

Location & Site Selection

Little Cayman is the smallest of the Cayman Islands (17 x 2 km), situated between Grand Cayman and Cayman Brac, 145 km southwest of Cuba. Little Cayman is an ideal site to isolate the effects of SCUBA activity from other consumptive human recreation on coral reef fish in the Caribbean due to the presence of a well-enforced no-take marine protected area created in the late 1980's, and island-wide regulations prohibiting spearfishingⁱ and hook-and-line fishing directly on the reef. The fishing regulations on Little Cayman are enforced with regular patrols of the reefs by Cayman Islands Department of the Environment (DOE) staff, and the small residential community (~200 year-round residents) has strong incentives for stewardship of the reef, because the economy of the island is almost solely dependent upon diver-centered tourism. Thus, voluntary compliance with fishing bans and other regulations is high (DOE staff, personal communication).

Little Cayman also provides a setting with consistent, long-term spatial variability in

recreational diving, due in part to the concentration of diving within Bloody Bay Marine Park which is the primary attraction for diving tourists. The decades of consistency in differences in diving frequency allowed us to quantify both the chronic effects of recreational diving activity on fish behavior and the extent of habituation of fish to divers. Overall diving activity on the reefs surrounding Little Cayman is low relative to many other tourist destinations worldwide. The maximum number of divers is constrained by the relatively low capacity on island (maximum capacity ~ 150 divers d^{-1} ; ~ 6300 y^{-1} ; versus $>30,000$ dives y^{-1} for example in the Red Sea)(Hasler and Ott, 2008). Even the most frequently visited site inside the marine park (~ 3600 dives y^{-1}) is still visited well below the limit recommended for sustainable recreational diving considering physical damage to corals incurred by recreational divers (5000-6000 per site per year (Hawkins, 1997)). SCUBA operators on Little Cayman also observe strict diving regulations and promote best diving practices for low impacts to the reefs (e.g. regulations limiting the number of divers at a site to 20, no fish feeding, no wearing of gloves, pre-dive briefings and supervision underwater). These factors have been linked to lower recreational diver impacts to coral reefs (Barker and Roberts, 2004; Krieger and Chadwick, 2013).

Chronic Diver Visitation Rates

Informal interviews with and diver visitation logs from the four tour operators on Little Cayman established both historical and current patterns of spatial use of reefs by recreational divers. We identified four areas of the reef that vary in their average visitation rate (divers per day for the period of May-July) from High = 273 to Medium =

52 to Light = 3 to Low = 0.3) on the northern side of the island (Fig. 1). At the extremes, Bloody Bay Marine Park is the most highly visited area on the reef, while sites in the northeast (our “Low” treatment) have not been visited by recreational divers for at least 3 years (based on dive records and personal communication with staff of the Central Caribbean Marine Institute and Cayman Islands Department of the Environment) and serve as our “no diver” control treatment. To minimize confounding effects other than diver densities, we used historical benthic habitat characterization, fish abundance, and community composition data taken over a ten year period via Atlantic and Gulf Rapid Reef Assessment (AGGRA) surveys to identify sites within each region with similar physical relief, algal and coral abundances, and abundance of focal species (unpublished data, Central Caribbean Marine Institute).

Focal Species

Sparisoma viride (Stoplight Parrotfish) is one of the most common, ecologically important herbivorous reef fish in the Caribbean. An excavating herbivore, *S. viride* targets endolithic algae associated with dead coral. It plays a crucial role in bioerosion, contributing to the removal of algae from reefs and providing new surfaces for settling coral recruits (Adam et al., 2015; Bruggemann et al., 1994). Changes in the amount of time *S. viride* invest in grazing relative to other activities, including anti-predator responses, have the potential to affect the degree to which this species serves its multiple functions on the reef.

S. viride are protogynous sequential hermaphrodites. All focal individuals included in this study were in the initial phase (IP), which includes both sexes but in which

females predominate (Robertson and Warner, 1978). Initial phase individuals were far more abundant at our study sites than terminal phase fish. They spent the majority of their time grazing, and generally inhabited the reef crest where divers also spend the majority of their dives. Terminal phase males were not included in our analysis, because they maintain territories at depth and ascend to shallower habitat primarily to chase IP conspecifics (Mumby and Wabnitz, 2002; van Rooij et al., 1996).

Body size is positively correlated with anti-predator behaviors in *S. viride* and other parrotfish species (Gotanda et al., 2009). Thus we chose only mature (>15 cm, (van Rooij et al., 1996)) individuals between 19 and 37 centimeters total length [TL]. Since individuals maintain relatively stable home ranges of typically less than 500 m² (Mumby and Wabnitz, 2002; van Rooij et al., 1996), we were confident that individuals were not traveling between study sites of differing diving visitation frequency.

Finally, *S. viride* are widely targeted by spear fishers throughout the Caribbean, and where they are fished, increase their flight initiation distances relative to areas in which they are being protected from fishing (Gotanda et al., 2009). This makes them an ideal species for this study and future related studies regarding the combined effects of recreational diving and spearfishing.

Flight and Vigilance

To quantify the anti-predator responses of *S. viride* to an approaching SCUBA diver, we measured AD and FID of over 300 focal individuals.

To find focal individuals, divers swam a few meters apart along the edge of the reef (on wall sites), in a search pattern over the middle of a spur (at spur-and-groove sites),

or in a haphazard fashion at sites with a combination of walls and patch reefs. Search patterns were always determined before entering the water, and careful notes and site maps were maintained to ensure that no part of a dive site was sampled more than once to avoid resampling individuals. Focal individuals that were foraging, resting, being cleaned, and otherwise not engaged in interactions with other species were chosen from approximately ten meters away based on methods used in behavioral studies of *S. viride* and other parrotfish species in fished areas (Feary et al., 2011; Gotanda et al., 2009). The first diver (always A. Ridlon) estimated the individual's size, took note of benthic features to identify the fish's start position. She then dropped a small flagged weight to mark her own start position, since start distance of the observer has been shown to affect fluctuations in FID in terrestrial studies (Cooper, Jr., 2005). Swimming at a steady speed, directly towards and at approximately the same depth as the focal individual, the first diver took note of the behavioral responses and positions of the fish, while the second diver observed the trial from a greater distance, sometimes recording it via video. At the first sign of alert behavior displayed (S2), the first diver dropped another flagged weight onto the seafloor, mentally noting the focal individual's location. When the fish fled (S2), the first diver likewise dropped a weight on the seafloor and estimated the fish's position. After the fish fled, its final position before fleeing, as well as all other locations of the fish during the trial (if applicable) were also marked with a flagged weight. The distances (in cm) between the approaching diver's body and the focal individual were then measured and recorded by the second diver using a tape measure to obtain AD and FID.

Feeding and Time Budget

To determine whether the immediate presence of divers influenced the time vigilant *S. viride* spent on other behaviors, we conducted bite rate and time budget experiments approximately one month after the end of our approach trials. We assumed that the acute effects of our prior scientific diver approaches were eliminated after this time period. Focal individuals were selected as described above. Using the average AD measured for fish at each diver visitation area as a guide, divers initially stayed outside of a focal individual's alert zone to record their behaviors in the absence of diver effects (our treatment control). Then the first diver (always A. Ridlon) moved just inside the alert zone, so that the fish became alert but did not flee. To quantify fish behaviors, the second diver recorded the bite rate of the focal fish for a three-minute period, while the first diver timed all other behaviors, including cleaning, aggressive interactions, and defecation (see S2 for descriptions of all behaviors). Paired estimates of bite rates and time budgets were thus recorded for the same fish first under baseline conditions (with both divers outside of the individual's AD) and then while the fish was vigilant due to the presence of a diver (one diver inside the AD, one outside). If at any point during these trials, the focal fish swam away from the diver in a manner similar to flight as described above, the trial was aborted.

Statistical Analysis

All data were analyzed using R version 3.3.3 (©2017 The R Foundation for Statistical Computing). Anti-predator behavior data (FID and AD, n= 252 trials) were

analyzed using a Poisson generalized linear model (GLM), and multiple pairwise comparisons between areas of different diver visitation frequency were examined using general linear hypotheses via the *multcomp* package. Explanatory variables included for model selection were: diver visitation frequency, observer start distance, habitat relief, depth, time of day, body size, and date. Model selection for the generalized linear models was based on minimization of corrected Akaike's Information Criterion (AICc), using the *MuMIn* package. All models within 2 delta AIC were examined, and the best fit model (lowest AIC value) was used.

Linear mixed effects models were used to examine the effect of diver visitation frequency and vigilance state (yes/no) of the fish on bite rates and all other time budget behavior data via the *lme4* package. Impact of fixed factors was compared using likelihood ratio tests conducted on models fit using maximum likelihood (Crawley 2007, Zurr 2009).

Results

Flight and Vigilance

For FID and AD, the model with the lowest AIC value, thus indicating best fit, included diver visitation frequency and observer start distance as explanatory variables but did not include habitat relief, depth, time of day, body size, or date (n= 252 trials). The effect of diver visitation frequency and observer start distance were significant in the main general linear models for both AD and FID (AD high diver density: SE= 24.32, t = -3.294, p < .001; observer start distance: SE = 0.054, t= 10.75, p < .001; FID high diver density SE = .184, t= -5.57, p < .001; observer start distance: SE = 0.0003, t = 4.394, p < .001). The

significant effect of diver visitation frequency was driven by significantly lower average AD and FID at the sites with the highest chronic diver visitation (mean AD = 212 cm, SE = 24.3, $t = -3.29$, $p < .001$; mean FID = 65 cm, SE = 22.8, $t = -5.46$, $p < .001$; Table 1; Figs. 2 and 3), with no significant differences among sites in other diving visitation categories. Notably, many fish within the highly dived area responded to the direct, relatively rapid approach of a SCUBA diver by failing to flee (median FID = 0). Although average ADs and FIDs decreased in response to increased diver visitation, some individuals maintained larger flight and alert distances, even in the highly dived area. In addition, the relatively higher average ADs in the less dived areas, and the high variability in individual responses in FID in the medium diver visitation area (Fig. 2) reveals that some individuals retained elevated anti-predator responses despite long-term exposure to non-predatory diver encounters. These conserved anti-predator responses were found in adult fish, indicating that these behaviors were not an artifact of juvenile fish still learning that divers do not pose a real predation risk.

Feeding

Data on the feeding behavior of fish are repeated measures from individuals over time ($n = 104$ trials, 208 paired), and included identity of the focal individual as a random effect. Baseline bite rates taken when divers stayed outside of the fish's AD were not significantly different among sites with different diver visitation rates. Vigilance had a significant effect on bite rates, which decreased by an average of 24% (mean baseline bite rate = 7.5 bm^{-1} , mean vigilant bite rate = 5.7 bm^{-1} , Fig. 4) with the presence of a diver within the fish's AD (SE = 0.803, $t = -6.73$, $\text{Chisq} = 41.164$, $df = 1$, $p < .001$). The

decrease in bite rates of vigilant fish did not differ significantly across areas of chronic variation in average diver visitation levels.

Time Budget

All behavior data taken as a part of the time budget are repeated measures from individuals over time (n= 104 trials, 208 paired), and included identity of the focal individual as a random effect. For all models, vigilance was a significant fixed effect, while dive intensity was not. Fish became significantly less active (all behaviors pooled) with the presence of a diver within their alert distance (SE= 1.723, t= -4.138, Chisq = 15.97, df = 1, p < 0.001) with a 33% decrease in all recorded activities.

The total amount of time spent engaged in all cleaning-related behaviors (pooled) significantly and greatly decreased in the immediate presence of a diver (SE= 1.774, t= -4.082, Chisq = 15.592, df = 1, p < 0.001), spending on average less than half the time on cleaning behaviors with divers present (vigilant mean= 5.3 seconds vs. non-vigilant mean = 12.6 sec; Table 3). Likewise, when analyzed separately, focal fish significantly reduced the time they spent asking to be cleaned by 32% (SE= 1.349, t = -3.566, Chisq = 12.13, df = 1 p < .001; Table 3, Fig. 5) reduced the the time they spent being cleaned by 54% with a diver within their AD (SE = 1.164 t = -2.09, Chisq = 4.318, df = 1, p < 0.05; Table 3).

In contrast, the incidence of defecation increased by 22.6% in the immediate presence of a diver (SE= 0.077, t = 2.962, Chisq = 8.515, df = 1, p < 0.01; Table 3). Finally, there were no significant differences in aggressive interactions, either initiated by the focal ("Chase": SE= 0.07, t = 0.693, Chisq = 0.484, df = 1, p = 0.487) or by another fish

("Chased by": SE= 0.186, t= -.878, Chisq = 0.777. df = 1, p = 0.378) in the presence of a diver (Table 3).

Discussion

Flight and Vigilance

Flight is a costly behavior, and should not be maintained in places where false cues repeatedly cause undue expenditures of energy (Frid and Dill, 2002; Stankowich and Blumstein, 2005), as is the case in areas where frequent encounters with recreational divers carry no predation risk for fish. Through repeated exposure to only non-consumptive human recreational activities, an animal's perception of predation risk, and thus their FID, can progressively decrease (Burger and Gochfeld, 1990), a learning process called habituation (Bejder et al., 2009). The near absence of a flight response (median FID= 0) to the direct, rapid approach of a SCUBA diver in so many *S. viride* individuals within Bloody Bay Marine Park, provides strong evidence that this reef fish can become habituated to the presence of recreational divers. In addition, the significant reduction in average FID in the park relative to less dived areas demonstrates that where SCUBA diving activity has been concentrated for decades, and in the long-term absence of fishing, fish can habituate much more fully to diver approaches than was previously assumed. Average FID at sites within the park are nearly 50% lower than the lowest average FID previously recorded for this species inside a protected area (65 cm vs. 116 cm, Gotanda et al., 2009).

Like fleeing, engaging in vigilant behavior precludes or reduces the time an animal spends engaged in other fitness-enhancing activities (Brown and Kotler, 2004; Lima and

Bednekoff, 1999), as demonstrated by the reductions in feeding and cleaning behaviors we measured in vigilant fish. By decreasing the distance at which they become alert to divers in places where they are more frequently encountering them, *S. viride* individuals reduce the time they spend, and thus the costs associated with, maintaining vigilance due to diver encounters in these areas. The significant reduction in both average AD and FID of fish in response to more frequent diver encounters provides new evidence that reef fish, like other marine species, weigh the costs and benefits of engaging in anti-predator behaviors depending upon differences in perceived predation risk (Semeniuk, 2004). Other studies have demonstrated that where the risk of predation by natural predators and humans is low, habituation reduces the costs incurred by fleeing or maintaining vigilance in response to a non-predatory cues (Lima, 1998; Lima and Bednekoff, 1999), but this evidence is very limited in marine systems, especially with fish. Our results demonstrate that not only can habituation to divers occur in the absence of fishing, but also that the degree to which fish habituate is dependent upon the frequency of encounters that they have with recreational divers.

The near lack of a flight response in fish in the most highly dived areas of our study, in contrast to the responses in less frequently dived areas, suggests that consistently concentrating recreational diving activity over long time periods in one place can drive habituation to divers in fish. Knowing more about the process of habituation in fish, for example how many divers a fish encounters before attenuating its flight response as *S. viride* has within the highly dived areas, could inform management strategies for recreational diving activities. For example, the significant decreases we observed in anti-predator behavior only in the most frequently dived areas on Little Cayman may

indicate a stepwise function in the response of fish to the frequency of false predation cues, where after a certain number of diver encounters, the risk of predation attributed to divers is low enough and the cost of vigilance and flight high enough that flight responses are reduced. This would suggest that concentrating divers in one area may be a practical management tool to drive habituation in fish, keeping the behavioral effects of recreational diving activity spatially constrained. At our study site, diving activity is highly concentrated within the marine park, and the diver visitation frequencies between the other sites are not evenly spread, so we are not able to determine the shape of the habituation curve as diver frequency increases using these data. Pairing accurate and more finely scaled data on diver visitation frequencies over time with data on the flight and vigilance behavior of fish in future studies would not only add insight into the nature of habituation to recreational divers over time, but provide managers with better information with which to make decisions about the spatial distribution of divers in protected areas.

Unlike our study sites, most marine protected areas worldwide allow both recreational diving and spear fishing to be done in tandem or nearby to one another. Our results underscore the importance of the absence of a predation risk associated with humans in driving habituation. Exposure to spear fishing, a clear and true predation cue, increases the FIDs and changes the types of anti-predator responses employed in a wide range of coral reef fish species, including *S. viride* (Gotanda et al., 2009; Guidetti et al., 2008; Januchowski-Hartley et al., 2015). The average FIDs that we measured in the absence of exposure to fishing are one third to one fifth the average distance of flight recorded for this and other scarid species in places where spearing

takes place in tandem with recreational diving or even on adjacent reefs (average FID ~350 cm in fished areas (Gotanda et al., 2009; Fraser A. Januchowski-Hartley et al., 2011)). The elevated wariness of coral reef fish inside protected areas where spear fishing intensity is high just outside the borders (Januchowski-Hartley et al., 2015) further supports the idea that even infrequent exposure to this predation cue (which can result from fish swimming between boundaries or with occasional poaching) can cause fish to respond to all divers with elevated anti-predator responses (Bregnballe et al., 2004; Lima and Bednekoff, 1999; Sirot, 2010). Where this happens, fish encountering recreational divers inside a protected area are not experiencing a true refuge from the behavioral effects of fishing. Based on this empirical evidence, the potential for any exposure to fishing cues to increase the costs and consequences of encounters with recreational divers within marine protected areas is clear. A synergistic interaction between consumptive and non-consumptive diving activities also has clear implications for the ecological understanding and management of marine areas. Taken with the evidence above, our results suggest that more fully separating extractive and recreational diving in space, with full-reef bans like the one in place on Little Cayman, by the use of buffer zones between areas of different uses (Blumstein et al., 2003), or with larger marine protected areas that allow for a more complete refuge from fishing effects, can result in a higher degree of habituation of reef fish to recreational divers.

Feeding and Costs of Diver Encounters

Maintaining vigilance to human presence can preclude or reduce the time marine animals spend feeding or engaged in other activities that enhance their individual

fitness and affect population growth (Berthe and Lecchini, 2016; Bracciali et al., 2012; French et al., 2011; Lima and Bednekoff, 1999). The significant decrease we found in overall activity in the immediate presence of a diver, including significant reductions in bite rates, indicate that vigilant fish alter a number of behaviors that can have a direct effect on the fitness of the individual. Any changes in the foraging behavior of herbivores are of particular importance, because in addition to reductions in daily intake of food being directly correlated to reduced fitness for the individual, vigilant animals have been shown to induce cascades and alter the structure and function of the surrounding ecosystem in response to real or perceived predation risk over time (Creel and Christianson, 2009; Schmitz et al., 2004). We found a nearly 24% reduction in average bite rates in vigilant fish, which was not significantly different across diver visitation frequency (Fig. 4), indicating that even where fish repeatedly encounter divers, they respond to each diver encounter by reducing their feeding by the same amount. The fact that these reductions in feeding were significant across all diver activity levels, including the area with decades of consistent exposure to diving activity, highlights the fixed nature of this trade-off (vigilance in place of another activity) during a diver encounter. However, evidence of a reduction in feeding or any other fitness-enhancing behavior in response to the immediate presence of a diver cannot, by itself, be accurately used to infer persistent fitness costs associated with human activity, although it sometimes is used in this context. In order to estimate the magnitude of these effects, one must consider the frequency with which animals incur the costs of vigilance or flight in response to encounters with humans. For example, the degree to which a reduction in feeding affects the fitness of an individual fish, or affects changes in its

resource base, depends upon how much time a fish spends being vigilant or fleeing instead of eating. By calculating the proportion of daily intake of food that is lost to vigilance, we can estimate both a fitness-related cost to an individual fish, and better understand a potential consequence of these encounters to the coral-algae balance on the reef. With this in mind, we used our data on reduced bite rates and diver visitation frequencies to estimate the proportion of total feeding loss for an individual in *S. viride* resulting from daily encounters with divers at the most popular dive site on Little Cayman. Using the methods outlined in the supplemental text, we developed this simple heuristic model to estimate the potential cost of encounters with respect to one behavior that impacts fitness, and to explore the factors that drive these costs, including diver-fish encounter rates, fish behavior, and diver behavior.

Using the 24% reduction in feeding we observed in vigilant fish, and diver-fish encounter rates based on average visitation at the most highly dived site, our estimations show a negligible cumulative loss of feeding to *S. viride* on Little Cayman: the average proportion of daily feeding lost to diver encounters is only 0.5% (S1). This result is driven by both the low frequency and short length of diver encounters even on the most dived site on the reef, and the comparatively high total time available for a fish to feed over the course of a day. Although we estimate an average of 87 divers visit the site per day, based on a random distribution of fish across the site and random swimming patterns for the divers, an individual fish has on average only 20 diver encounters a day. On average, six of these encounters cause the fish to flee, totaling just under 4 minutes of combined vigilance and flight per day. Since parrotfish graze nearly continuously over most daylight hours, this level of interruption in feeding is clearly

negligible as a loss from its total daily food intake. This result suggests that currently the population of *S. viride* is not accruing large feeding costs due to encounters with divers. Moreover, since we used diver visitation estimates from the high season (our sampling period), at the most popular dive site within the park, we predict the cumulative feeding losses to be even lower at slower times of the year and at less popular sites. Given the relatively limited maximum capacity on each dive site on Little Cayman under their current regulations, these effects are also not likely to increase on these reefs. In fact, based on these estimations, diver visitation at this site would have to increase to around 400 divers per day to incur an average daily loss of 10% of an individual fish's total feeding.

These estimations also give us a useful framework for considering the conditions under which the cumulative effect of diver encounters on fitness-enhancing behaviors, including feeding, may be of greater magnitude than those we found on the Little Cayman reefs. For example, a higher overall cost of diver encounters may occur for fish species that do not attenuate anti-predator behaviors in response to exposure to recreational divers, as is seen with so-called “shy” species (Conrad et al., 2011), or for the range of reef fish species that respond to divers with elevated FIDs due to exposure to spear fishing cues, including *S. viride* and other parrotfish (Feary et al., 2011; Gotanda et al., 2009; Fraser A Januchowski-Hartley et al., 2011). To estimate a cost of diver encounters to fish that have not habituated to diver presence, we used the average values for AD and FID from our sites of lowest diver visitation. To simulate a high influx of recreational divers into the undived area, we used the maximum capacity of divers currently possible on these reefs. Under these conditions, proportional feeding loss rose

to 2.3%. Although the overall loss is still relatively small, the increase in feeding loss relative to that in habituated fish demonstrates the benefit of habituating. Fish that do not habituate incur higher cumulative costs due to diver encounters. Finally, diver behaviors also determine the frequency and length of encounters with fish, and thus can influence the magnitude of their effects. When divers seek out and remain near species of interest, not only are encounters longer and more numerous, but also diver behavior is less careful, and contact with these species has been shown to result in increased damage to the surrounding reef (Uyarra and Côté, 2007). To simulate this scenario, we assumed that all divers encounter the fish (100% encounter rate, average diver density = 87 divers a day), and spend two-minutes within its alert distance. We estimated a 9.9% total daily feeding loss with these changes in diver behavior. This estimated feeding loss is equivalent to the effect of an increase in diver density to 400 divers (as above), highlighting the importance of encounter frequency and length in driving these costs. Particularly for sought-after species that are site-attached, and thus both easier to locate and less motile (e.g., seahorses, frogfish), our estimations suggest that a higher contact rate and more lengthy encounters with divers could result in the accumulation of high fitness costs even at relatively low diver densities. Indeed, these types of prolonged and close-range diver encounters are likely to occur for an increasingly broader range of species as underwater photography becomes commonplace among recreational divers (Barker and Roberts, 2004; Roupheal and Inglis, 2001).

Cleaning and Species Interactions

Although feeding loss is not large in the population of the reef fish species we

studied, the significant reductions in other behaviors warrant further investigation, as they also represent fitness costs in the immediate presence of a diver. Changes in time budgets due to vigilance in the presence of humans of the kind we recorded in *S. viride* have been correlated to persistent fitness effects via increased energy expenditures, reduced reproductive output, and slowed population growth in other marine species (French et al., 2011; Stensland and Berggren, 2007; Symons et al., 2014). Likewise, changes in the amount of time spent engaged in interactions with conspecifics (e.g., mating, competition) and other species (e.g., cleaning interactions) can have effects on community dynamics and transmit the costs and consequences of maintaining vigilance to other species (Cheney and Cote, 2003; French et al., 2011). In particular, cleaning interactions, due to their potential to influence the individual fitness of other species and alter an important ecosystem function, are a ripe area for future research into the nature and magnitude of diver effects (Grutter, 1999; Grutter et al., 2017; Titus et al., 2015). Cleaning significantly decreases parasite abundance on the host and provides food for the cleaner fish, contributing to the individual fitness of both (Grutter, 1999). Cleaning is a service that attracts fish to particular areas, and can drive increases in local fish diversity on coral reefs (Grutter et al., 2017). We found that *S. viride* spent 42% less time engaging in cleaning behaviors in the presence of divers, and this reduction was significant even in places where diver visitation had consistently been high (Fig. 5). Similar decreases in cleaning behavior due to diver presence were shown to significantly depress cleaning for all species at stations on another intensely dived coral reef (Titus et al., 2015), and these changes in cleaning were highlighted as a potential mechanism for lowered fitness for fish populations and an interruption of ecosystem

services due to chronic recreational diving activity. The potential for reduced cleaning to result in persistent fitness effects and community-level consequences highlights the need for future studies to include direct measures of fitness for marine fish responding to diver encounters. Metrics such as growth rate, body condition, and reproductive output, for example, when considered in the context of diver encounter frequency and length, can be used to estimate the cumulative costs of reductions in cleaning and other species interactions in the presence of divers.

Conclusion

As the number of recreational divers within marine reserves increases worldwide (Gonson et al., 2015), the ability of marine fish to habituate to divers is an important consideration to incorporate into our understanding of both the ecological dynamics and management of marine reserves. Where habituation to recreational divers and snorkelers occurs in isolation from spearfishing, it represents a potential win-win scenario for marine fish and recreational divers. Habituated fish reduce the time and energy spent on vigilance and flight, and experience less disruption in opportunities to feed or mate due to diver encounters. Divers likewise benefit from engaging in close-range observation and photography of habituated fish, which increases diver satisfaction (Valentine et al., 2004). Our data from within the park, where diver density is highest, and our estimations of a cumulative cost of those diver encounters illustrate the importance of considering encounter rate and length, as well as fish and diver behaviors, in understanding the nature and magnitude of these effects. While we did not directly measure fitness effects of diver encounters to *S. viride*, future research into

diver effects would greatly benefit from the inclusion of direct measures such as the body condition or reproductive output of fish, particularly for sought-after species that divers may spend more time interacting with. Future research should also incorporate both more precise quantifications of the encounter rates between divers and fish, and link those to direct measures of the fitness costs associated with diver encounters to better inform our understanding of the mechanisms, ecological consequences, and management implications of habituation to divers in marine fish.

Our evidence for habituation to encounters with recreational divers for Stoplight Parrotfish comes from reefs where spear fishing is almost completely absent, and where the long-term diving activity is well managed and low impact in comparison to many other diving destinations. Growing empirical evidence of the flight responses of marine fish suggest that habituation to divers can be constrained by the nature and frequency of human activities happening within and around MPAs, especially spear fishing. While the applicability of these results to other species of marine fish is limited by a current lack of data, evidence for neutral behavior in response to encounters with divers has been found a range of marine fish species (Bradley et al., 2017; Claudet et al., 2010; Dearden et al., 2010; Heyman et al., 2011). It is therefore critical to test these effects under different diver activity regimes and for different fish species.

Bloody Bay Wall Marine Park represents a case study in the potential consequences of increasing diving activity on coral reefs worldwide, and our findings underscore the importance of incorporating a more thorough understanding of the behavioral effects of diver presence on marine life in the design and management of marine protected areas in particular.

Figures

Main Figures

Fig. 1: Sites, Little Cayman

Fig. 2: FID

Fig. 3: AD

Fig. 4: Bite Rates

Fig. 5: Clean & Clean Ask (main effects)

Main Tables

T1: AD and FID pairwise comparisons by dive visitation

T2: Cleaning activity by dive intensity, detailed results

T3: Time budget behaviors for vigilant versus non-vigilant fish



Fig. 1: Study sites were located on the reef along north side of Little Cayman, where Bloody Bay Marine Park (black box) is located. Text indicates the four areas of chronic diver visitation frequency (diver density), based on average daily visitation data for the period of May-July as follows: High = 273 divers/day, Medium = 52, Light = 3, and Low = 0.33 divers/day. Multiple dive sites were sampled within each diver visitation area.

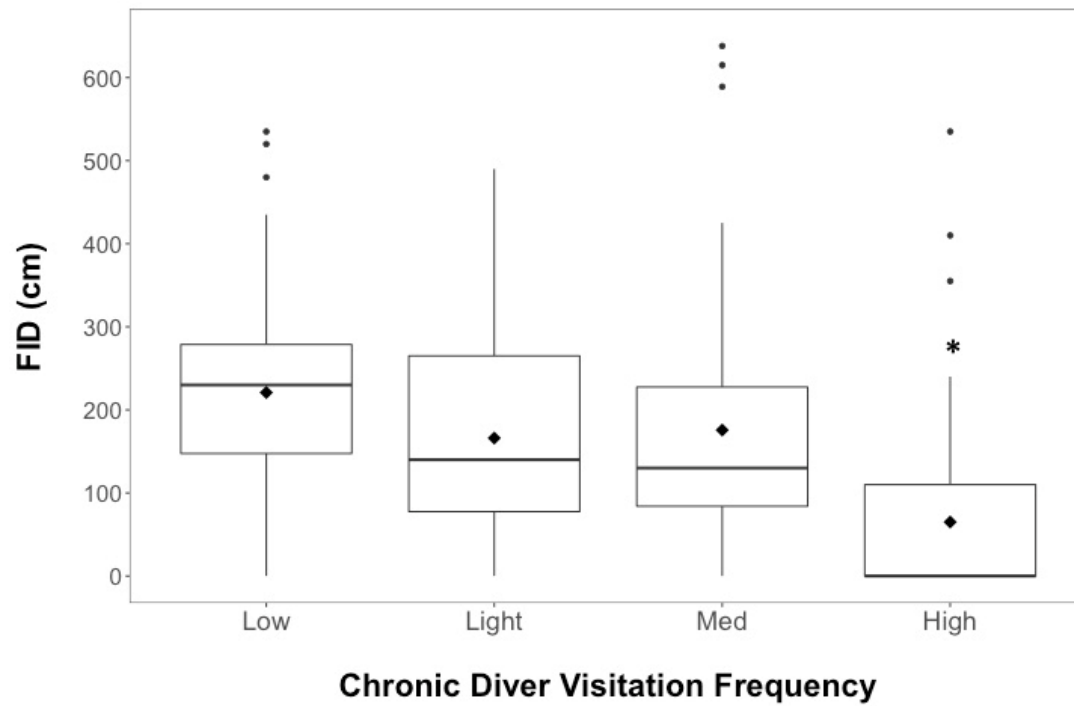


Fig. 2: Average (black diamonds) and median (bar) flight initiation distance (FID) in centimeters for *S. viride* at sites of differing frequency of recreational SCUBA activity. FID decreases significantly (*) at sites with most frequently visited by recreational divers (mean FID = 65 cm, $p < .001$). Boxplots display minimum and maximum “whiskers”, points are outliers.

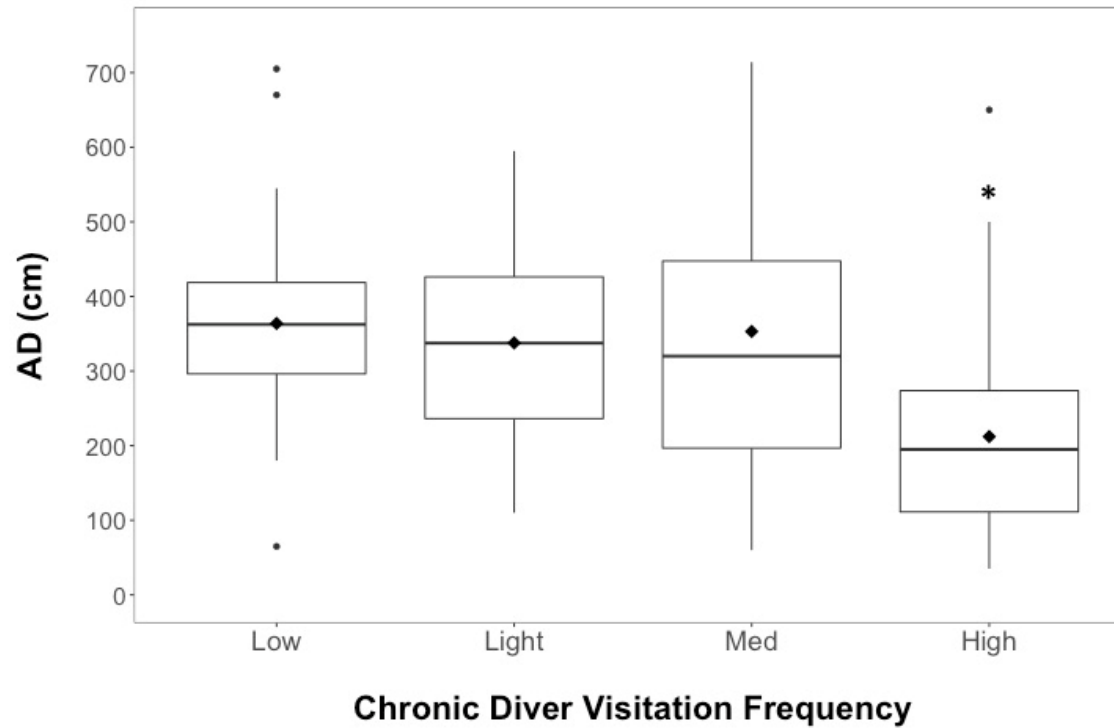


Fig. 3: Average (black diamonds) and median (bar) alert distance (AD) in centimeters for *S. viride* at sites of differing frequencies of recreational SCUBA activity. AD decreases significantly (*) at sites most frequently visited by recreational divers (mean AD = 212 cm, $p < .001$). Boxplots display minimum and maximum “whiskers”, points are outliers.

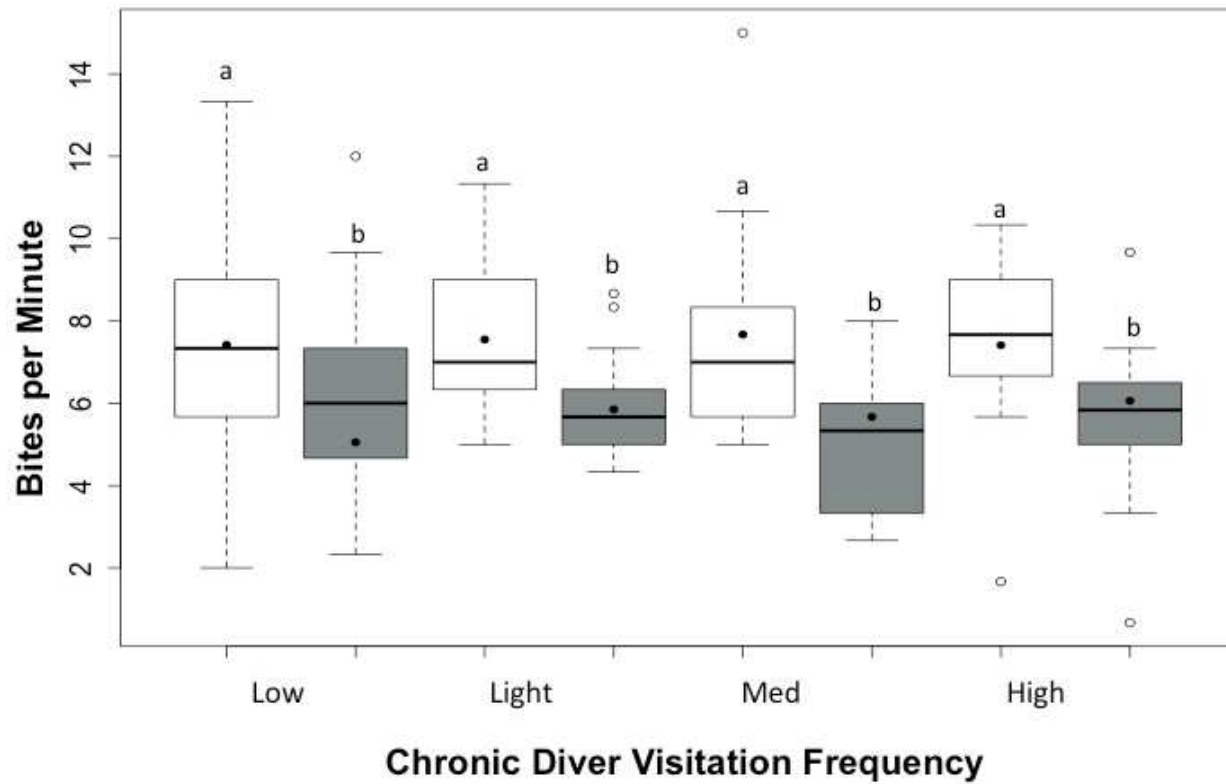


Fig. 4: Average (black dots) and median (bar) bite rates for *S. viride* at sites with differing frequencies of recreational SCUBA activity. Light bars represent baseline bite rate (bites/min), while darker bars represent bite rates of vigilant fish. Bite rate decreases significantly and uniformly at all sites in response to the immediate presence of a diver, regardless of chronic exposure to diving activity (mean baseline = 7.5 bites m^{-1} , mean vigilant = 5.7 bites m^{-1} , $p < .001$). Boxplots display minimum and maximum “whiskers”, points are outliers.

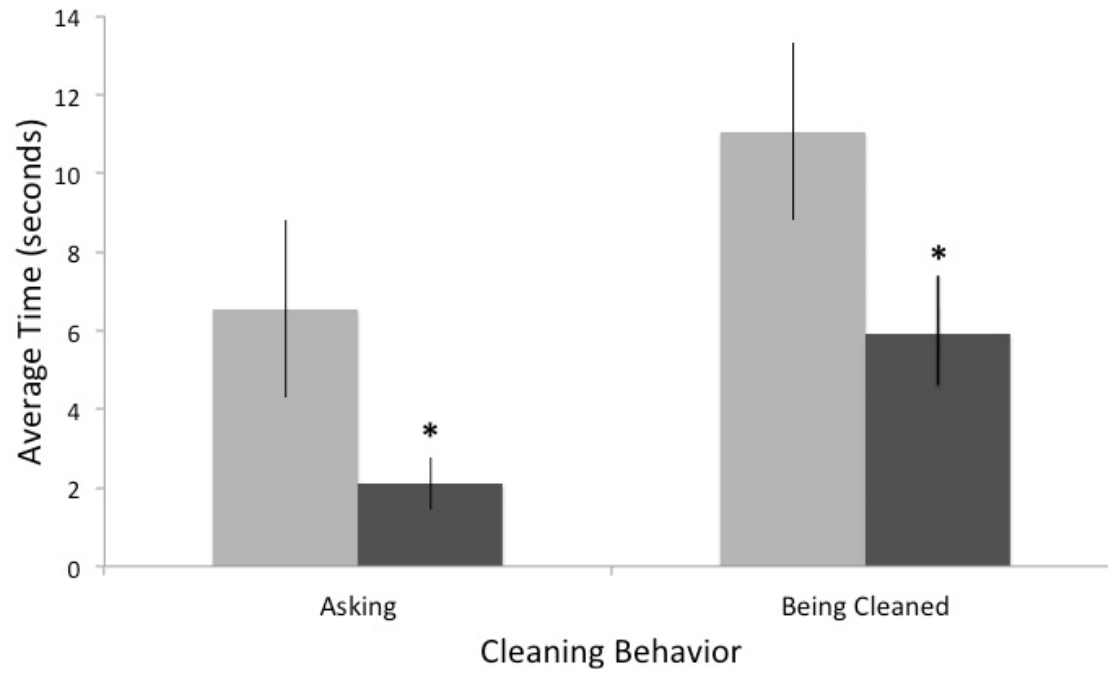


Fig. 5: Average (\pm SEM) time fish spent engaged in cleaning behaviors during observations of vigilant (dark bars) or non-vigilant (lighter bars) fish (diver areas pooled). *S. viride* spent 32% less time asking to be cleaned and ($p < .001$) and 54% less time being cleaned while in the presence of a diver ($p < .05$)

Dive Frequency	AD			FID		
	SE	<i>z</i>	<i>p</i>	SE	<i>z</i>	<i>p</i>
Low: Light	24.052	0.176	0.998	0.133	-1.409	0.488
Low: Med	25.614	-0.803	0.852	0.143	-1.401	0.493
Low: High	24.316	-3.294	< 0.01	0.184	-5.574	< .001
Light: Med	25.312	-0.980	0.760	0.144	-0.090	0.999
Light: High	23.090	-3.652	< 0.01	0.179	-4.681	< .001
Med: High	25.701	-2.316	0.094	0.191	-4.312	< .001

Table 1: Multiple pairwise comparisons (Tukey HSD) by diver visitation frequency areas for average alert distances (AD) and flight initiation distances (FID). Probabilities in bold indicate a significant difference.

Chronic Diver Visitation	Vigilant	Total Activity (sec)	<i>p</i>	Cleaned (sec)	<i>p</i>	Clean Ask (sec)	<i>p</i>
High	No	11.5		5.6		4.0	
	Yes	5.5	<0.05	1.2	<0.05	1.9	0.22
Med	No	15.9		4.8		9.4	
	Yes	9.1	0.17	4.9	0.98	2.4	0.1
Light	No	17.6		5.3		10.8	
	Yes	4.6	<0.001	0.9	<0.05	2.1	<0.01
Low	No	13.2		4.7		6.2	
	Yes	10.7	0.59	5.1	0.92	4.9	0.51
Total	No	14.3		5.2		7.3	
	Yes	7.20	<0.001	2.8	<0.05	2.5	<0.001

Table 2: Average time (sec) spent in each behavior while fish were vigilant (diver observing from within the alert distance of the fish) and not (diver well outside the alert distance). Total activity and time spent engaged in cleaning behaviors decreased significantly in the presence of a diver, but do not follow a consistent pattern based on chronic diver visitation. Probabilities in bold indicate a significant difference.

Behavior	Chi-squared value	d.f.	<i>p</i>
Clean Ask	12.3	7	<0.001
Clean	4.317	7	0.038
Chase	0.488	7	0.48
Chased by	0.789	7	0.374
Defecated	8.52	7	0.004

Table 3: Chi-squared results for time budget behaviors of *S. viride*. P- values in bold indicate a significant difference for the frequency of the behavior observed in vigilant fish (diver observing from within the AD) versus non-vigilant (diver outside the AD).

Supplemental Materials

Text: Estimating the Cost of Diver Encounters

S1: Diver encounter cost estimations

S2: Anti-predator behavior descriptions

S2: Time budget behavior descriptions

Supplemental Text

Estimating the cost of diver encounters

To estimate the expected number of daily encounters an individual fish has with divers at the most popular site within the park, we assumed a random distribution of fish on the reef and random movement of the diver independent of other divers. The diver swims at a constant speed (.05 m/s) without retracing her path for the duration of a 45 minute dive, giving a linear random path of movement of the diver, D_d . The average alert distance between the fish and the diver is then incorporated as one alert distance to either side of the diver ($2D_a$) which moves with the diver as she swims. The probability of encounter between a single fish and any diver during a dive, P_e , is then calculated by dividing the alert area of the diver by the total area of the reef at the dive site (A_s):

$$P_e = \frac{2 (D_d D_a)}{A_s} \quad (1)$$

and the expected number of daily encounters with a diver N_e is the average number of divers on that site per day, N_d , multiplied by the probability of a fish encountering any

given diver during a dive P_e :

$$N_e = (P_e N_d) \tag{2}$$

The distance between the fish and the diver during the encounter will either cause the fish to be vigilant, when the diver is moving within the alert distance of the fish, or result in the fish fleeing, when the diver moves within the flight initiation distance of the fish, notated here as the distance between the diver and the fish that triggers flight (D_f). The number of expected encounters that will result in the fish fleeing N_f , is a proportion of all expected encounters based on the alert and flight distances:

$$N_f = \left(\frac{D_f}{D_a} N_e \right) \tag{3}$$

and the remaining number of expected encounters that will result in fish vigilance N_v is:

$$N_v = 1 - \left(\frac{D_f}{D_a} N_e \right) \tag{4}$$

The total time a fish spends vigilant to divers during a single day (T_v) is a product of the number of expected encounters that result in vigilance (N_v) and the the average length of each diver encounter, which is estimated by using the average chord length of the alert distance circle surrounding a fish ($D_a \frac{\pi}{2}$) divided by the diver's average swimming speed (s) as she moves along that length:

$$T_v = \left(\frac{D_a \frac{\pi}{2}}{s} N_v \right) \tag{5}$$

Thus, to estimate the cumulative cost of vigilance to divers in a day, C_v , we calculated the proportion of total daily feeding lost due to vigilance in response to diver encounters:

$$C_v = \frac{[(b_b - b_v) T_v]}{B_d} \tag{6}$$

where the total bites lost during a day is the difference between the bite rate (bites per minute, bm^{-1}) in the absence of divers (*baseline bites*: b_b) and the number of bites taken while the fish are vigilant to diver presence (*vigilant bites*: b_v) multiplied by the

time spent vigilant during a day T_v . Dividing total daily bites lost by the average total daily bites an *S. viride* would take in the absence of divers (calculated with our site-specific bite rate data and species specific active daily feeding time from Hanley (1984)) gives us the proportion of daily feeding that a fish loses due to vigilance during diver encounters.

To further determine the cost of diver encounters in terms of the proportion of feeding time that fish lose due to fleeing from divers, we first calculate the total time per day that a fish spends fleeing divers (T_f), which is a product of the number of expected encounters that initiate flight (N_f) and the average time it takes for a fish to flee from the diver and then return to feeding behavior (T_r) (estimated via video observations of *S. viride* by A. Ridlon):

$$T_f = (N_f T_r) \tag{7}$$

The daily total cost of fleeing divers (C_f) in terms of lost feeding is then a product of the time spent fleeing (T_f) and the baseline bite rate (b_b) that the fish would have engaged in if it were not fleeing:

$$C_f = (T_f b_b) \tag{8}$$

Finally, to estimate the cumulative daily cost of diver encounters to an individual fish,

(C_d) in terms of the total proportion of bites lost during all diver encounters, we combine the daily costs of vigilance (C_v) and flight (C_f):

$$C_d = C_f + C_v \tag{9}$$

Simplifying Assumptions

We made a number of simplifying assumptions about diver and fish behavior in calculating feeding loss: 1) Fish distribution is random, 2) Diver movement is random, and 3) There is no compensation in feeding behavior or rate when divers are not present. We used site-specific area measurements and diver densities from the most popular dive site within the marine park (“Mixing Bowl”). We do not consider the energetic costs of flight or vigilance, and instead use solely the loss of feeding during these behaviors as one example of a fitness-related cost of diver encounters.

Extensions

We estimated the above current average cost of diver-fish encounters on the reef at average diver visitation frequency during the high season, using the average values from our empirical data where appropriate, as stated in the main text. We then estimated C_d for two other scenarios to explore how the cost of diver encounters would change under different fish behavior and diver encounter scenarios. First, we estimated the increase in cost that that would occur if divers suddenly dove at maximum capacity in the least-dived areas (“worst case scenario”) using the average AD from the least-

dived sites, and the maximum diver number possible at the most highly dived site within the park (“Mixing Bowl”). Next, we estimated C_d using all the original empirical values, but under a 100% probability of encounter with divers, and a 2 minute fixed encounter length with divers inside the alert distance of the fish to simulate longer and more frequent encounters due to changes in diver behavior (as happens towards rare fish or during photography).

Calculating the probability of encounter with any diver (P_e)

Total area of the reef at the most popular site = 24,000 m²

AD from the diver to the fish (2AD) = 4 m

Swimming at a fixed 0.5m/s for 45 minutes, a diver swims a linear distance of 1,350 m² with an alert “bubble” of influence covering 5400m² in a dive, or 22.5 % of the total divable area. Assuming a random location, an individual fish has a .23 probability of encountering any given diver.

Supplemental Figures

Parameter Values (Per day)	Current Diving Activity	No habituation	Diver Behavior "Targets" fish
Ave. chord length (c)	3.33	5.71	NA
Ave. length of encounter (sec) (c/s)	6.66	11.43	120
No. divers per day (N_d)	87	120	87
Tot. no. expected encounters (N_e)	20.01	27.60	87
No. expected encounters that result in vigilance (N_v)	13.87	10.87	87
Vigilance (min) (T_v)	1.54	5.26	174
No. bites lost to vigilance	2.77	9.46	313.20
Proportion bites lost to vigilance (C_v)	0.00	0.00	0.10
No. expected encounters that result in flight (N_f)	6.14	16.73	NA
Tot. time fleeing (min) (T_f)	1.53	8.36	NA
No. bites lost to flight	11.50	62.73	NA
Proportion bites lost to flight (C_f)	0.00	0.02	NA
Total no. bites lost in a day	14.27	72.19	313.20
Proportion of daily feeding lost (Cost of diver encounter (C_d))	0.005	0.023	0.099

S1: Calculations of the daily (unless otherwise noted) parameter values used to estimate the cost of diver encounters to fish in terms of the proportion of daily feeding lost under three different diver encounter and fish behavior scenarios.

Anti-predator Behavior	Description
Stop	Interruption of whatever behavior fish was engaged in at start of trial
Look	Fish looks directly at diver
Turn	Fish turns its body toward or away from diver
Flick	Fish flicks its tail
Bump	Fish moves, but slowly, and stops <1 m away
Flight	Clear, directed motion away from the diver, sometimes accompanied by a fast-start escape response (<i>sensu</i> Domenici & Blake 1997)

S2: Descriptions of the anti-predator behaviors observed during diver approach trials

Behavior	Description
Bite Rate	Fish bites substrate
Clean	Fish is being cleaned by shrimp or cleaner fish that the diver see, sometimes accompanied by changes in color, an open mouth, and flared gills
Clean Ask	Body positioned vertically (perpendicular to the substrate), dorsal fins moving, sometimes accompanied by an open mouth and flared gills (<i>sensu</i> "cleaning invitation", Hanley, 1984)
Chased	Fish clearly pursues another fish (van Rooij et al., 1996)
Chased by	Fish flees from an approach by another fish
Defecates	Fish defecates

S3: Descriptions of the behaviors observed and timed in time budget trials.

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¹Four individual spearing licenses are currently issued by the Cayman Islands Department of the Environment to Little Cayman residents with long family histories of residential status. These fishers primarily spear lobsters during the legal season, and do not fish within the marine park. Otherwise, the only spearing that takes place on these reefs is by highly trained divers from DOE, other local agencies and tour operators, targeting the invasive lionfish population only. These culls take place at dusk, and no other fish species has been caught by spear during a cull (DOE and Central Caribbean Marine Institute Staff, personal communication).

CHAPTER THREE

Differential predation by the invasive predator *Carcinus maenas*: a potential mechanism for facilitating invasions

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Abstract

As multiple invasions accumulate in marine systems, identifying the species traits and interactions that affect invasion success is critical for predicting the outcomes of multiple species introductions. Facilitation is a major mechanism for invasion success that can increase the magnitude of impact of an existing invasion. Marine predators can facilitate invasions and may be more likely to tip the balance of dynamics between species in an invaded system via top-down effects. Here we examine the effect of predation by an introduced crab, *Carcinus maenas*, on the native snail *Cerithidea californica* and the invasive snail *Ilyanassa obsoleta*. Laboratory experiments revealed that *Carcinus maenas* predation was strongly and significantly greater on the native species as compared to the invasive. While the frequency of crab attacks was not significantly different between snail species, the predator was 5.45 times more successful at killing the native *C. californica* than the invasive *I. obsoleta* given an attack. This differential predation success drives the higher overall mortality in native snails.

Given the competitive displacement of the native snail by the invasive in this system, our study demonstrates that the introduced predator *C. maenas* can have both direct negative impacts on native species and indirect positive impacts on other invaders via facilitation. Our results provide unique information about a predator's potential to indirectly influence the success of an invasion, and contribute to our understanding of the role of introduced predators in influencing the dynamics of multiple invasions in marine systems.

Introduction

Humans continue to introduce species to marine ecosystems worldwide, and at an accelerating rate (Grosholz and Ruiz, 1996; Ruiz et al., 2000, 1997). Over 500 nonnative species are considered established in U.S. coastal ecosystems and some marine systems, particularly estuaries, have become so invaded that the majority of their biomass is comprised of non-native species (Cohen and Carlton, 1998; Ruiz et al., 1997). As invasions accumulate, the interactions among multiple introduced species and can bring both unexpected and long-lasting change to those ecosystems. Although much has been learned about the mechanisms and consequences of single introduced species in marine systems, ecologists are still trying to disentangle the complex interactions between multiple introduced species and their subsequent effects. Of particular interest are the species traits and ecological interactions that affect invasion success of one or many species when multiple introductions occur. While the enemy release hypothesis – the idea that introduced species experience a decrease in regulation from predators and other natural enemies and a concomitant rapid increase in population abundance and distribution- has long been cited in the successful

establishment of introduced species (Crawley, 1997; Williamson, 1996), facilitation between species is increasingly recognized as a major potential mechanism for invasion success (Bruno et al., 2003). Facilitation between separately introduced organisms creates a positive feedback that increases the likelihood of survival for one or both species, or accelerates the rate of one or both of their invasions, and can operate by increasing the magnitude of impact of an existing invasion(s). These positive feedbacks between species can have ecosystem-level effects, and have been hypothesized to lead to an accelerating increase in the number of invasions in the system, causing an “invasional meltdown” (Simberloff, 2006; Simberloff and Von Holle, 1999) in which invasive organisms become dominant. Despite limited evidence demonstrating “meltdowns” in marine systems, it remains a useful framework for thinking about the long-term consequences of multiple invasions (Simberloff, 2006). We know that functional replacement of native species by invasive ones can drastically alter trophic structure, population and community processes, and interfere with ecosystem functions (O’Dowd et al., 2003; Ruiz et al., 1999, 1997). Yet all introduced species do not replace native flora and fauna or even have a measurable negative effect. Likewise, the interactions between introduced species do not necessarily result in facilitation between invaders. In fact, while facilitation among multiple invaders has been demonstrated in various terrestrial systems, (Nuñez et al., 2008; O’Dowd et al., 2003; Parker, 2006) examples from marine systems are limited (Grosholz, 2005; Levin et al., 2002). Identifying the ecological contexts in which facilitation occurs between introduced species in marine systems is central to our understanding of invasion

dynamics in estuaries and coastal ecosystems, where introduced species accumulate, and multiple re-introductions are common.

One key factor in predicting the likelihood of invasive facilitation may be the relative trophic positions of the interacting species (Thomsen et al., 2014). Considering the role of trophic position in the direction and magnitude of invasive species interactions, including the potential for invasive facilitation, is essential to understanding the changing landscape of repeatedly invaded systems. Indeed, a meta-analysis of terrestrial systems provides evidence that introduced herbivores facilitated increased richness and abundance of introduced plant species through selective grazing on native species, suggesting that as native predators are replaced with invasive ones, the likelihood of invasive facilitation and a state of “meltdown” increases (Parker, 2006). Likewise, marine predators have been shown to facilitate invasions and may be more likely than organisms in other trophic groups to tip an invaded system into a state of “meltdown” (Grosholz, 2005; Veiga et al., 2011). As marine predators not only continue to be transported to new habitats by human intervention, but experience range shifts related to global climate change (Johnson, 2015; Kelley et al., 2013), there is an urgent need to understand the impact that their predation can have on the invasions of other introduced species.

Here, we examine the effects of an introduced predator, the European green crab (*Carcinus maenas*) on two species of consumers in San Francisco Bay (SFB): one a native snail and the other an invasive snail. The San Francisco Bay represents a natural experiment in the effects of multiple invasions and provides an opportunity to study the

dynamics between invasive species at different trophic levels. One of the most highly invaded marine systems in the world, up to 99% of the biomass in some of SFB's communities is comprised of introduced species (Cohen and Carlton, 1998). *Carcinus maenas* has been a resident in SFB since 1989, where populations are now well-established and self-sustaining (Cohen et al., 1995). An omnivorous predator, *C. maenas* has disrupted native food webs in nearby estuaries by preying upon and displacing a number of native species, and in one case by accelerating an existing invasion in the system (Grosholz, 2005; Grosholz et al., 2000). Little is known about its impacts in SFB, however, including its potential to prey on native consumers and its interactions with the multitude of invasive species in the system.

Two of the most common snails in SFB are the native California horn snail (*Cerithidea californica*) and the invasive eastern mud snail (*Ilyanassa obsoleta*). *Cerithidea californica* populations, once highly abundant in some California estuaries, have dwindled drastically in recent years across the species' range in California (Byers, 2000, 1999). In contrast, *I. obsoleta* was first reported in SFB in 1907 (Carlton, 1979) and has since established populations there that can reach densities of > 3000 individuals/m² in some areas (max density, 2009 surveys = 3345.5 individual/m²; Weiskel, unpublished data). The established invasion of *I. obsoleta* in SFB has previously been shown to have negative impacts on the native *C. californica* through competitive interactions, including physical displacement and direct predation on native eggs and juveniles by the invasive snail (Race, 1982; Weiskel, 2012) but nothing is known about the potential impacts of the more recently introduced predator *C. maenas* on either population.

To determine the effects of the predatory crab, we used laboratory experiments to test whether *C. maenas* preys equally on the native *C. californica* and the invasive *I. obsoleta*. Where the two species co-occur on the east coast of the United States, *C. maenas* are most successful in preying on *I. obsoleta* of smaller size classes (10-15 mm) by sheering their spire or chipping away at the lip of their thick shell (Ashkenas and Atema, 1978). Adult *I. obsoleta* require a comparatively high degree of force to crush outright in comparison to other local snail species (Tucker et al., 1997). The native snail, on the other hand, has an elongated spire and thinner shell, both of which are morphological characteristics that crab predators exploit by utilizing spire sheering and crushing techniques (Vermeij, 1979; Zisper and Vermeij G J, 1978). Based on this evidence and the obvious differences in morphology of the native and introduced snail shells included in our study, we hypothesized *C. maenas* would exert greater predation pressure on native snail, and greater pressure on smaller (juvenile) snails of both species.

Based on our results, we discuss whether a difference in predation pressure on these two prey species could further facilitate or accelerate the invasion of *I. obsoleta* populations in SFB. We further discuss the implications of our findings in the context of declining *C. californica* populations across its native range and, more broadly, the potential for introduced predators to facilitate the invasions of marine species through differential predation on native prey.

Materials and Methods

Collection

Adult *C. maenas* individuals of both sexes were collected with baited traps from SFB, Bodega Harbor, and Bolinas Lagoon, California during a two-week period in July of 2008. Responsive, non-gravid crabs with all legs and both claws were selected for use in the study. They were separated by sex and size class and housed in an outdoor flow-through seawater system at Bodega Marine Lab in Bodega Bay, CA. Individuals were fed squid and anchovies both as bait in the traps and while housed in the tanks, but each was starved for a minimum of 24 hours prior to the start of the trial in which it was used.

Cerithidea californica and *I. obsoleta* individuals of both juvenile and reproductive (hereafter adult) status were collected from a mudflat in SFB at Robert's Landing in San Leandro, CA during the second week of July 2008. Active individuals with intact opercula and shells were separated by species and housed in aerated 10-gallon aquaria in a static seawater system at Bodega Marine Lab. To determine the effect, if any, of size and sex on the predation behavior of *C. maenas*, equal numbers of crabs of each sex were separated into three size categories based on carapace width (CW): small (30-40 mm CW), medium (41-60 mm CW), and large (≥ 61 mm CW). To determine if *C. maenas* predation affects adults in each population differently than juveniles of the same species, snails were separated into juvenile (*C. californica*: 8.5-14.0 mm, 11.5 mm average; *I. obsoleta*: 8.5-15.0, 11.6 mm average) and adult (*C. californica*: 15.0- 24.0 mm, 21.3 mm average; *I. obsoleta* 16.0 – 24.0 mm, 18.8 mm average) size classes based on

the length of their shell from the spire to the tip of the lip (McCloy 1979 and Race 1981 for *C. californica*; Curtis & Hurd 1983 for *I. obsoleta*).

Predation Trials

Four trials were conducted using plastic Ziploc® “Large Rectangle” containers (2.25 L each; 26 cm L x 15 cm W x 6.5 cm H) with approximately 1 cm of sifted sediment from Bodega Harbor and approximately 4.5 cm of filtered natural sea water (32 psu) at Bodega Marine Lab from 14 July to 29 July 2008. Small (30 mm), equally spaced holes were drilled in the container lids and approximately 1 cm of air was left at the top of each container. Containers were thoroughly scrubbed and new sediment, snails, and crabs were used for each trial. Natural light conditions were simulated with sunlight spectrum bulbs and a 12-hour light/dark cycle in order to maintain the crabs’ circadian rhythms. Each trial began at 7 am, so natural daytime corresponded with the lighted 12-hour period in the lab. The trials therefore reflect daytime predation behavior for *C. maenas*.

In order to test whether crab size or sex had an effect on crab predation on both snail species, each crab of a given size class (small, medium, large) and sex was simultaneously offered five snails of each species of a uniform size class (e.g., 10 juvenile snails). This arrangement resulted in a fully crossed multifactorial design with 144 crabs, 1,440 snails and 24 replicates of the crab size by snail size treatment.

Every 6 hours, the containers were opened, the crab removed, and the sediment sifted

through by hand to find all living snails in each container. The total number of living snails and any shell fragments present were recorded for each snail species. The condition of each living snail's shell was inspected for evidence of predation attempts (e.g., punctured shells and evidence of chipping on the shell) and recorded. All relevant behavior observed upon opening each container (e.g., snails climbing the walls or a crab grabbing a snail in its chela) was also noted.

To gain further insight into whether the introduced predator selectively targeted either prey species or snail size, we also recorded evidence of attacks on individual snails. Any shell damage that was unambiguously the result of attempted predation by green crabs was recorded as evidence of an attack. Using shell scarring as evidence of an attack provides accurate data about attempted predation events, and is a standard method for recording predation attempts by crabs in field experiments (Yamada and Boulding, 1996; Zisper and Vermeij G J, 1978), although it does not account for multiple attacks on the same individual over time. We compared these results to successful predation events. We hypothesized that where there was a difference in mortality between snail species or size classes, it would result from *C. maenas* attacking more of the most vulnerable snails.

A 48-hour control trial (no crabs present) was run with identical conditions as those described above prior to the main experiment in order to test the lab set-up and conditions. In control treatments, no snail of either species died for up to 48 hours, which was four times the length of the experimental treatments.

Although predation trials were run for 24 hours, our analysis concentrates on the

effects of predation up to hour 12, which is the time at which approximately half of the prey were eaten. This value reflected the potential for *C. maenas* predation occurring in one tide cycle and provided enough time for differences in predation effort to become apparent, while avoiding predator satiation effects (Wong et al., 2010).

Data Analysis

All statistical analysis of the data was performed in R version R 2.13.2 (R Development Core Team, 2011). The effects of snail species, snail size class, crab gender and crab size class on snail mortality (binomial data) were analyzed using a generalized linear regression model assuming a quasibinomial distribution and fitted with all explanatory variables and interactions in the lme4 package. Odds ratios (OR) were then calculated by exponentiating the log likelihood coefficients. Where multiple pairwise comparisons revealed significant differences between variables, these were corrected using Tukey's HSD test via the Multcomp package in R and z values are reported. Effects of the above variables on crab attacks (shell damage, but not snail mortality) and successes (predation attempts resulting in snail mortality) were each likewise analyzed.

To determine the mechanism for the differential predation found between crab size classes and sexes, two metrics were calculated for each container: number of attacks and number of successful predation events given an attack. Successful predation was calculated per container by recording the number of snail deaths from the total number of attacks in that container. These calculations exclude snails that showed no evidence of scarring, and therefore no evidence of being attacked. In five containers, we found no

evidence of attack on any snails; for these containers, successful predation events (which represent attacks that result in predation) could not be calculated and were not included in the analysis of successful predation.

Results

Predation (mortality)

In all trials, *C. maenas* successfully preyed upon individuals of both species of snail. *Carcinus maenas* predation was strongly and significantly greater on the native snail as compared to the invasive snail: *C. californica* individuals were nearly five times more likely to be killed than *I. obsoleta* (OR= 4.98, $t= 6.29$, $p < 0.001$).

Snail size class

Snail size class was a significant predictor of mortality for snails of both species. Overall, juvenile snails were 3.4 times more likely to be preyed upon than adult snails ($t= 4.99$, $p < 0.001$). However, this result is strongly driven by the comparatively large difference in mortality between juvenile and adult invasive snails: *I. obsoleta* juveniles were nearly seven times more likely to be preyed upon (OR= 6.7, $t= 4.346$, $p < 0.001$), while juvenile *C. californica* were 2.65 times more likely to be killed than adults of the same species ($t= 3.04$, $p= 0.003$) (Fig 1). Importantly, there was no difference in the proportion of mortality between native adult snails and juvenile invasive snails ($z= -1.11$, $p= 0.67$, Tukey HSD).

Crab size class

Large *C. maenas* preyed most heavily on snails of both species: large crabs were five and seven times more likely to kill snails than medium or small crabs, respectively (OR= 5.04, $z= 5.79$, $p < 0.001$, Tukey HSD and OR= 7.01, $z= 6.44$, $p < 0.001$, Tukey HSD). This result is driven disproportionately by the differences in large crab predation on *I. obsoleta*: large crabs were 14 times more likely to inflict mortality on the invasive snail than small crabs and 12 times more likely than medium crabs (L to M OR=14.3, $z= 4.67$, $p < 0.001$, Tukey HSD; L to S OR= 12.17, $z= 4.67$, $p < 0.001$, Tukey HSD) as compared to 3.5 and 5.4 times more likely to kill the native snail ($z= 4.26$, $p < 0.001$ and $z= 3.44$, $p < 0.002$, Tukey HSD) (Table 2). Predation by medium crabs was not significantly different from small crabs for either snail species (OR= 1.39, $z= 0.99$, $p= 0.58$, Tukey HSD).

Crab Sex

Male *C. maenas* caused more overall mortality in both species of snail than females (OR= 1.92, $t= 2.78$, $p= 0.006$). This trend held within species, and the effect of crab sex on mortality was significant for *I. obsoleta* (*C. californica* OR= 1.83, $t= 1.92$, $p= 0.057$; *I. obsoleta* OR= 2.14, $t= 2.05$, $p= 0.042$). In fact, four individual male crabs were solely responsible for all of the adult *I. obsoleta* mortality in this experiment.

Crab size as measured by carapace width was not correlated to crab sex for any trials in this experiment ($t= 1.23$, $df= 284$, $p= 0.22$, Pearsons product-moment correlation).

No crab mortality occurred during the 12-hour experimental trials and all snail mortality included direct evidence of crab predation during all trials.

Attacks vs. Successful Predation Events

Evidence for unsuccessful *C. maenas* attacks on juvenile and adult snails of both species was found, and crabs attacked native and invasive snails with equal frequency (OR= 1.32 $t= 1.51$ $p= 0.132$). Despite equal attacks, crabs were 5.45 times more successful at killing the native *C. californica* than the invasive *I. obsoleta* ($t= 6.84$, $p < 0.001$); this differential success drives the higher overall mortality in native snails found here.

Snail size class

Juvenile snails were 6.92 times more likely to be attacked by *C. maenas* than reproductive snails ($t= 9.86$, $p < 0.001$), and once they attacked, crabs were twice as successful at killing juveniles as compared to adult snails (OR= 2.09, $t= 2.99$, $p= 0.003$). Importantly, this difference in successful predation with juvenile snails was driven entirely by differences in *I. obsoleta* success; there was no difference in the odds of successful predation on juvenile versus adult *C. californica* (OR= 1.44, $t= 1.12$, $p= 0.267$). Crabs attacked native juvenile snails at a much higher rate than adults of the same species, (OR= 8.85, $t= 7.169$, $p < 0.001$) but once they attacked a native snail, they had an equal likelihood of killing it, regardless of its size. By contrast, crabs were 5.24 times more likely to be successful in preying upon juvenile *I. obsoleta* than adults ($t= 3.946$, $p < 0.001$), and they also attacked the invasive juveniles at a higher frequency than their adult counterparts (OR= 5.67, $t= 6.550$, $p < 0.001$).

Crab size class

Overall, large crabs were slightly more likely to attack snails than either medium or

small crabs (L v. M OR= 1.74, $z= 2.436$, $p= 0.04$; L v S OR = 1.76, $z= 2.487$, $p= 0.034$, Tukey HSD); medium and small crabs made an equal number of attacks (OR= 1.01, $z= 0.053$ $p= 0.999$, Tukey HSD). Medium and small crabs also showed no difference in predation success once they attacked a snail (OR= 1.46, $z= 1.194$, $p= 0.46$ Tukey HSD). Large crabs were, however, much more successful in preying upon snails once they had attacked (L v. M OR= 5.49, $z= 6.128$, $p< 0.001$, Tukey HSD; L v. S OR= 7.98, $z= 6.986$, $p< 0.001$, Tukey HSD). This difference in predation success relative to crab body size is strongly driven by crab successes with the invasive snail: large crabs are over 15 and 13 times more likely to be successful at preying upon *I. obsoleta* than medium and small crabs respectively (L v. M OR= 15.43, $z= 5.17$, $p< 0.001$, Tukey HSD; L v. S OR= 13.29, $z= 5.17$, $p< 0.001$, Tukey HSD). By comparison, large crabs were 3.73 and 6.03 times more likely to successfully prey on *C. californica* individuals than their medium and small counterparts (L v. M, $z= 3.57$, $p= 0.001$; L v S $z= 4.59$, $p< 0.001$, Tukey HSD) (Table 1).

Crab Sex

Male crabs attacked nearly twice as often as female crabs, (OR=1.99, $t= 3.76$, $p< 0.001$), and this result is significant with both native and invasive snail species. Overall, males are also nearly twice as successful as females at killing a snail once they attack it (OR= 1.82, $t= 2.592$, $p= 0.010$). However, this differential success between crab sexes is not significant for the native *C. californica*, (OR= 1.7, $t= 1.7$ $p= 0.091$); males simply attack native snails nearly twice as often as females (OR= 1.88, $t= 2.339$ $p= 0.021$). By contrast, males are twice as likely as females to kill the invasive *I. obsoleta* once an attack is made (OR= 2.20, $t= 2.218$, $p= 0.028$).

Discussion

The invasive predator *C. maenas* can successfully prey upon both the native and invasive snail species, and attacked individuals of both species with roughly equal frequency in this experiment. However, *C. maenas* predation was strongly and significantly greater on the native *C. californica* as compared to the invasive *I. obsoleta*. Native snails were nearly five times more likely to be preyed upon than invasive snails. The source of this highly differential predation on the native snail was the predator's higher degree of success in killing the *C. californica* individuals they attacked. This higher predation success with the native snail is likely driven by the differences in shell morphology between the two species: *C. californica* has a comparatively thin and elongate shell, which likely makes for a more easily handled and accessed prey item and may entail reduced energetic costs for a range of *C. maenas* chela sizes. Increases in the shell thickness of gastropods in response to chronic crab predation have been well documented, including a range of snail species responding to *C. maenas* predation specifically (Smith, 2004; Trussell, 1996). While *C. maenas* has overlapped *I. obsoleta* for decades on the east coast of the United States, allowing for potential co-evolution of these traits between predator and prey, *C. californica* have not co-occurred with this predator very long, which may contribute to their vulnerability to the introduced predator. In fact, other predators have been shown to ignore *I. obsoleta* as a prey source even where the snail is more abundant than other prey, due to the strength of their shells resulting in a high processing cost for the predator (Tucker et al., 1997). In contrast, while native predators of *C. californica*, including crabs, demonstrate size-

selective predation on the horn snail, (Lorda et al., n.d.; Sousa, 1993) they do not appear to be excluded from preying upon even the largest size classes of the native snail. Additionally, the introduced predator employs a range of techniques in accessing prey beyond outright crushing a shell, including sheering the spire and peeling back the lip in order to extract the soft body of the animal (Hughes and Elner, 1979) and the native snail's longer spire and thinner shell make it more vulnerable to these techniques than the thicker, squatter invasive snail.

Given this collective evidence, it is not surprising that *C. maenas* attacked juvenile snails of both species more frequently than their adult conspecifics, and were more successful at accessing only the smaller juvenile *I. obsoleta*. Importantly, however, the invasive crab not only exerted greater overall predation pressure on the native snail population, but its effect on snail mortality was equivalent between adult *C. californica* and juvenile *I. obsoleta* (Fig 1), highlighting the absence of an invulnerable size class in the native snail population. Thus, predation by *C. maenas* in SFB could result in significant mortality for the full range of *C. californica* individuals in the population, while its effect is limited primarily to the juvenile individuals in the invasive snail population. The comparative freedom from predation for the adult invasive snails has the potential to confer an obvious fitness advantage in terms of reproductive output, and may also result in less direct competition for resources with adult native snails as they are disproportionately removed from the system.

Body size influenced the frequency of attack and odds of successful predation for the

invasive crab with both snail species, and affected predation success much more strongly with the invasive snail (Table 2). Crabs of all sizes were able to prey upon *C. californica* individuals. No medium crabs and only one small individual preyed on adult *I. obsoleta* in all trials; interestingly, all of these successful predators were male crabs. While male *C. maenas* are known to reach larger body sizes than females in natural populations (Young et al., 1999), carapace width was not correlated to crab sex in this experiment. Although chela size was not measured in this study, male *C. maenas* have larger chelas than females of the same carapace width (Juanes et al., 2008), and relatively larger or stronger claws could confer an advantage to male crabs in breaking *I. obsoleta* shells (Bourdeau, 2012; Moody and Aronson, 2012; Smith, 2004). In this study, males were twice as likely to attack their prey as their female counterparts irrespective of body size, which we posit contributes to the difference in success for males, who repeatedly attack the same snail or are simply more aggressive in their initial attack. These results demonstrate that only male, and mostly large male (over 70 cm CW) *C. maenas* are effective predators of adult *I. obsoleta*, further underscoring the limited vulnerability of the invasive snail population in SFB to this introduced predator.

Population surveys taken at the time of this experiment found that where the two species overlap in SFB, average *I. obsoleta* densities were twelve times greater than those of the native *C. californica*, (invasive: 612.12 ± 546.81 snails/m², vs. native: 45.69 ± 16.07 snails/m²; Weiskel, unpublished data), and evidence for the competitive displacement of the native snail into higher marsh areas by the invasive snail were found as early as the 1970s (Race, 1982). Taken with the results of the current study,

we hypothesize that concentrated *C. maenas* predation of the type we report on the native snail population could facilitate the dominance of *I. obsoleta* in SFB. It is worth noting several challenges to discussing how these data relate to the species dynamics currently unfolding in the bay, however. First, we did not calculate a predation rate for *C. maenas* on either snail species; our study design did not include the manipulation of equal densities of snails throughout the experiment. Instead, our data show significantly higher overall predation on the native snail, even as the density of native individuals relative to invasive snails decreased over time in the containers. It is therefore likely that any effect of the decreasing density of native snails in our experiment mirrors actual field conditions, in which *C. californica* population densities are much lower than that of *I. obsoleta*. Even so, a predation rate calculated from lab experiments would not necessarily be directly transferable to true rates in the bay for other reasons. The distribution and movement of these species within the estuary, especially the highly mobile predator, is likely to influence the rate of contact between, and ultimately the effect of *C. maenas* predation on these two prey populations. Additionally, *C. maenas* is an omnivorous predator (Crothers, 1968), known to prey on other species in California estuaries (Grosholz et al., 2000; Grosholz and Ruiz, 1996) making it difficult to assess, even via field experiments, what the true rate of *C. maenas* predation on *C. californica* population currently is. However, a separate experiment in which tethered *C. californica* individuals were either protected or exposed to predators confirmed that crab predation is an important source of mortality for *C. californica* populations in SFB, especially in the more exposed cobble and mudflat areas that *C. maenas* has the greatest access to (Weiskel, 2012). As the native snail is competitively

displaced into higher marsh areas, then, it may also be enjoying a refuge from crab predation, and therefor persisting in a limited range. More site-specific data are needed to determine the actual trajectory of these species interactions in the SFB, but our results identify a novel potential mechanism for invasive-invasive facilitation both within the SFB and beyond.

Declines in *C. californica* populations are not limited to SFB, and have been reported in other California estuaries throughout the native's range: in at least one location this has been attributed to the effect of competitive interactions with another invasive snail species, the Asian Mudsail *Batillaria attramentaria* (Byers, 2000, 1999). *Cerithidea californica* populations are at risk of being replaced by this other invasive snail in marshes in its northernmost range, and the loss of these populations is particularly important both because they represent a race shown to be a genetically distinct from southern California populations (Byers, 1999), and because this may result in the loss of at least ten other native species that parasitize *C. californica* and are unable to use the invasive snails as hosts (Torchin et al., 2005). Given the scope and magnitude of *C. californica* population declines and the concomitant loss of biodiversity in California estuaries, the current findings provide novel evidence for an additional potential mechanism for the replacement of this native species, and highlight a specific additional stressor to local populations.

Importantly, the invasive predator *C. maenas* is also not confined to SFB: its current range on the west coast of North America covers 1600 km from Elkhorn Slough,

California to Grays Harbor, Washington, and local populations have been established in estuaries including SF Bay, Bolinas Lagoon, Tomales Bay and Bodega Harbor (Grosholz et al., 2000; Grosholz and Ruiz, 1995). We demonstrate that *C. maenas* predation on *I. obsoleta* is limited primarily to only the smallest snails in the SFB population, likely due to the thickness of their shells, which suggests that the invasive predator may prey instead on other, more accessible species in the bay in addition to the native snail. Indeed, *C. maenas* predation has been shown to exert “top-down” control in a number of other estuaries, significantly decreasing the abundances of common native species such as clams (*Nutricola tantilla* and *Nutricola confusa*) and shore crabs (*Hemigrapsus oregonensis*) (Grosholz et al., 2000). Again, because it is a highly mobile, omnivorous predator (Crothers, 1968) *C. maenas* will likely affect various populations of native species throughout its introduced range which have yet to be identified; our results shed light on some of the factors that lead to predation success for *C. maenas* with native prey.

The complexity inherent in multiple species interactions of the kind that are occurring during multiple invasions poses a challenge to predicting their outcome. Determining the conditions under which these species interactions lead to facilitation or acceleration of invasions remains a critical next step in our understanding of invasion dynamics in marine ecosystems. Few marine studies to date have demonstrated that the simultaneous effects of multiple introduced species in a system can result in an invasive facilitation or “meltdown” (e.g., Grosholz 2005); even fewer have explored the mechanisms underlying the displacement of native species by introduced ones (e.g.,

Byers & Goldwasser 2001). The current study provides clear evidence for differential predation on a native snail species by an invasive crab, and provides support for the idea that the more recently introduced predator can facilitate an established invasion and magnify its effects on a beleaguered native species. While we cannot conclude from these results alone that predation by the introduced crab will facilitate the invasion of *I. obsoleta* in SFB, we provide several lines of supporting evidence that suggest that this strongly differential predation pressure may be serving as a tipping point for the facilitation of the invasive snail in this ecosystem. More importantly, our results demonstrate that this marine predator can have both direct negative impacts on native species and indirect positive impacts on other invaders. The spread and establishment of green crab populations thus has the potential to accelerate the rate of historically benign introductions and facilitate future invasions through differential predation on native species (Grosholz, 2005), and our results provide unique information about this predator's potential to influence the trajectory of other invasions in marine systems wherever it occurs.

Our results also suggest that other marine invasive predators- with a narrower diet or fewer choices in their introduced range, for example- could be a primary mechanism for facilitation of invasions via preferential predation on native species. Records of introduced species that interact with both native and invasive species this way - posing a sort of double threat particularly in ecosystems with other established introduced species - are rare, and important to consider due to their potential to have broad impacts on coastal ecosystems worldwide.

Figures

Main Figures

Fig. 1: Proportion Mortality by Snail Species & Size Class

Fig. 2: Percent Mortality by Crab Size Class

Fig. 3: Percent Mortality by Crab Sex

Main Tables

T1: Odds Ratios of Crab Attacks and Successes by Crab Size

T2: Odds Ratios of Crab Attacks and Successes by Crab Sex & Snail Size Class

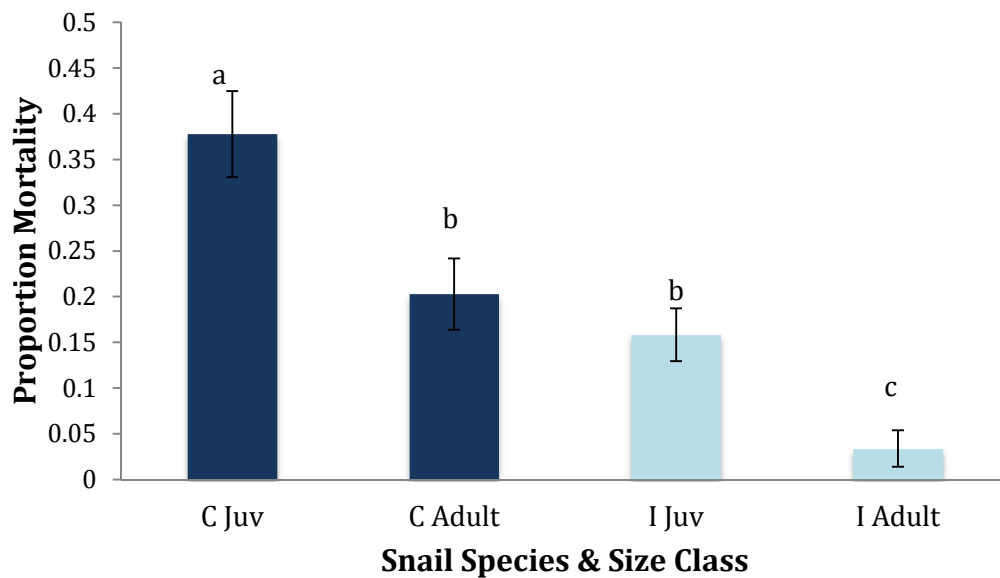


Fig. 1 Effect of *C. maenas* predation on the native *C. californica* (dark bars) and the invasive *I. obsoleta* (light bars) individuals, by size class. Bars represent the proportion of snails killed out of the total available to the crabs. Letters represent significant differences; error bars represent standard error.

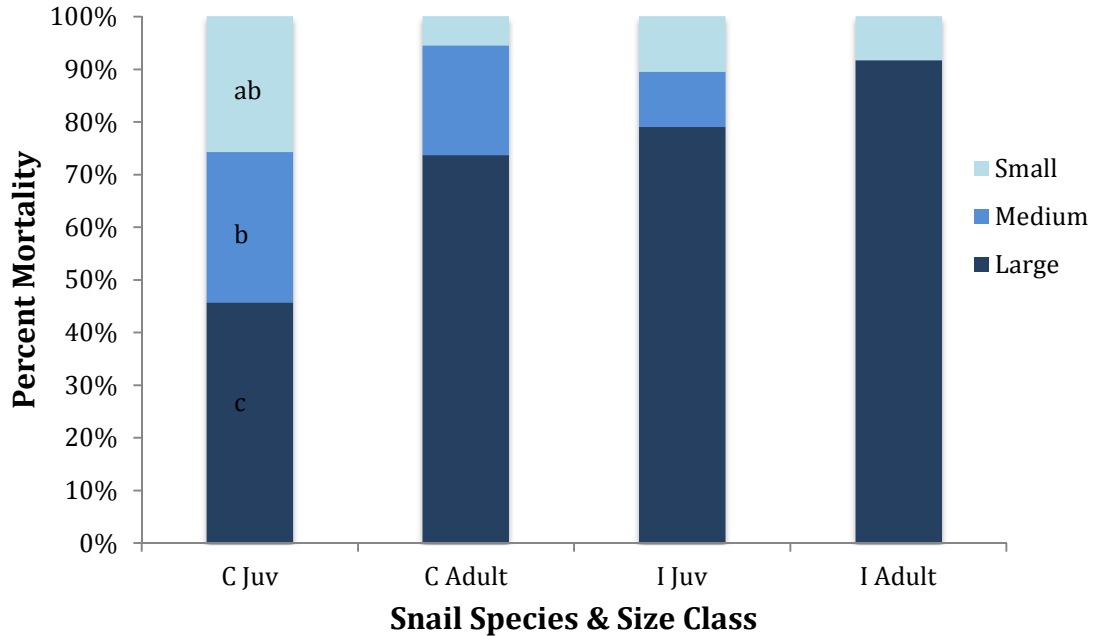


Fig. 2 Proportion of snails killed by large (≥ 61 mm CW, dark), medium (41-60 mm CW, light) and small (30-40 mm CW, lightest) *C. maenas*, by snail species and size class (C Juv = *C. californica* juveniles, etc.). Large crabs were the most effective predators, particularly with adult invasive snails. Letters represent significant differences for all snail species/size class combination (although only the first bar is labeled).

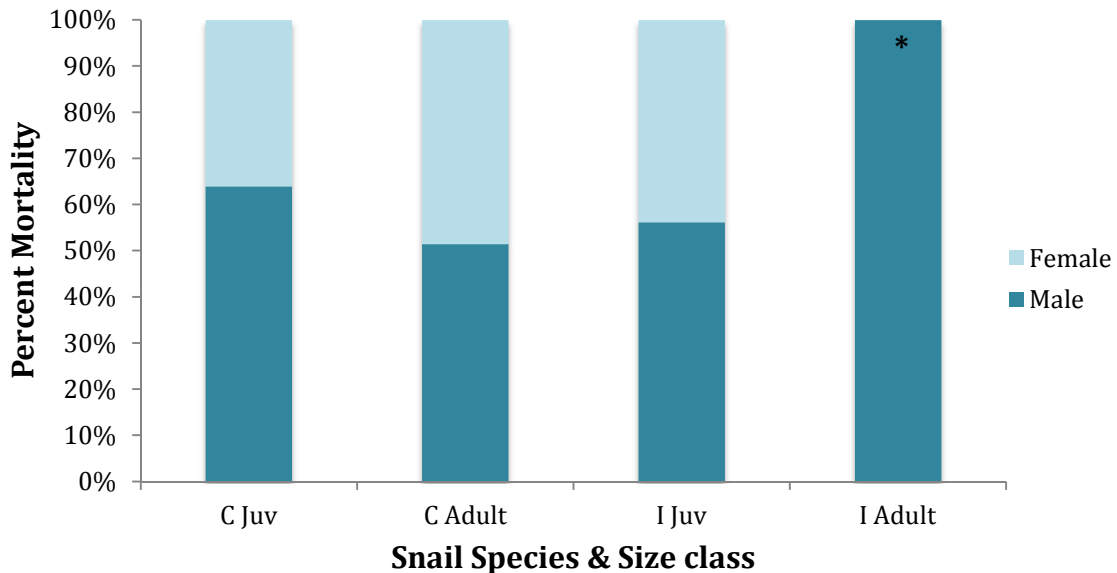


Fig. 3 Proportion of snails killed by female (light) versus male (dark) *C. maenas*, by snail species and size class (C Juv = *C. californica* juveniles, etc.). Male crabs were responsible for more overall snail mortality (trend), and solely responsible for mortality in adult

invasive snails (* indicates significant difference from all other combinations).

Factor	Odds Ratio	Lower CI 95%	Upper CI 95%	t	p
Attacks					
F	1				
M	1.99	1.39	2.85	3.76	0.0002
Successes					
F	1				
M	1.82	1.16	2.89	2.59	0.01007

Table 1. The effect of crab size on the odds of successful predation by *C.maenas* on the native *C. californica* and the invasive *I. obsoleta* once an attack is made (generalized linear regression model). Letters refer to crab size class (L=large, M=medium, and S=small)

Factor	Odds Ratio	Lower CI 95%	Upper CI 95%	z	p
<i>C. californica</i>					
M-S	1.62	0.65	4.12	1.21	0.45
L-S	6.03	2.14	15.10	4.59	<1e-04
L-M	3.73	1.57	8.85	3.57	0.001
<i>I. obsoleta</i>					
M-S	0.86	0.19	4.00	-0.23	0.97
L-S	13.30	4.15	42.59	5.19	<1e -06
L-M	15.43	4.49	53.07	5.17	<1e -06

Table 2. The effect of crab sex on the odds of attacks and successful predation events by *C. maenas* on both snail species (generalized linear regression models).

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