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Fear of fishers: anti-predator behaviour of coral reef fish and its relevance to fisheries management and conservation

Thesis submitted by

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STATEMENT ON THE CONTRIBUTIONS OF OTHERS

This thesis includes collaborative work with Dr Nick Graham, Dr Joshua Cinner, Professor Garry Russ, Dr David Feary, Dr Rebecca Lawton, Kirsty Nash and Taudinoya Morove. I led these research collaborations and was responsible for the project design, data collection, data analysis and interpretation. My collaborators provided intellectual guidance, financial support, and assistance with fieldwork, technical instruction and editorial assistance.

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ABSTRACT

Responding appropriately to predators is essential for prey animals to maximise fitness and survival. Non-lethal predator-prey dynamics can have large effects on how animals use and perceive their environment. The understanding of predator escape behaviour in animals can play an important role in conservation and management, with implications for human/wildlife interactions, particularly hunting and tourism. In this thesis I use coral reef fish as model organisms to examine our existing knowledge of factors influencing prey flight response in the context of marine ecosystems. I go on to examine how fishing and protection from fishing influences the flight behaviour of fishery target coral reef fishes through the use of no-take reserves (NTRs) and periodically harvested closures (PHCs).

Flight initiation distance (FID - how close a predator can get to an animal before it flees) is widely used when investigating how prey animals respond to predation, and has been utilised in systems where humans are predators or otherwise disturb wildlife (e.g., through tourism such as bird watching). However, the use of FID in the marine realm prior to this thesis was limited. Studies investigating FID vary in methodology and many of the potential confounding effects inherent to in-water estimation of FID have yet to be investigated. In Chapter 2, I compared the relative effects of spear guns, dive gear (SCUBA vs. free diving), observer bias and protection from fishing on estimates of FID. FID in areas protected from fishing was, on average, 141 cm lower than in fished areas, with no difference found between treatments for either dive gear or speargun. Management status explained 60% of the variation in FID estimates, while differences between observers only accounted for 4%. Size was highly significant, with larger fishes being associated with greater FID in every treatment. These findings imply that fishes use only limited predator attributes as cues for flight, and that the response of fishes to these attributes is amplified in areas of higher predation risk.

In Chapter 3 I examined how FID changed across a range of families and fishing pressures on coral reefs in Papua New Guinea. I surveyed FID, fish size, group size and pre-flight behaviour of two families commonly targeted by spearfishers - Acanthuridae and Scaridae - and four families that were less common in the spearfish catch – Balistidae, Lutjanidae, Mullidae and Serranidae (groupers) across four levels of fishing pressure. Increases in fishing pressure were associated with increases in FID for Acanthuridae, Balistidae, Mullidae, and Scaridae, while FID of Lutjanidae and Serranidae showed no relationship with fishing pressure. Notably, mean FID of Lutjanids was greater than the mean effective range (MER) of spear guns, while the mean FID of Serranids was lower than other families. Larger individuals tended to flee earlier, particularly at moderate or high fishing pressures, while group size and pre-flight behaviour differed between families, but showed low concordance with fishing pressure. These findings indicate that the relationship between size and FID of coral reef fishes is more complex than has previously been presented, and that an interaction between predation experienced by fish families and traits such as territoriality or trophic level, may be important in determining FID.

One of the benefits expected from NTRs is spillover of adult biomass to adjacent fishery grounds, through density dependent export or random movement of fishes across NTR borders. Fishes with little experience of predation may transport non-wary behaviours across the borders of marine reserves, resulting in a gradient of increasing FID with distance from the reserve border. In Chapter 4 I examined FID and biomass of Acanthuridae and Scaridae, and one non-target family (Chaetodontidae) across the borders of three NTRs and three control borders within fished areas in the Philippines. FID only increased significantly with distance from the NTR centre for the two fishery families at NTRs, and remained below FID recorded in fished areas until 140 m outside the NTR, significantly further than spillover of biomass. These reductions in FID are likely to lead to increased catchability of fishes near NTRs. While this may increase local support for management, changes in catchability may give rise to inaccurate estimates of NTR effects on fish biomass and abundance.

Across the South Pacific, PHCs are often utilised in place of NTRs, with the specific aim of taming fishes to increase catchability and produce high yields during harvests. Using a before-after-control-impact-pair design, in Chapter 5 I investigated whether PHCs in Vanuatu had similar effects on fish FID and biomass as NTRs, and the effects of a single harvest. Catch per unit effort was higher during the harvest than for regular fishing, and this was linked to FID of Acanthuridae being lower than MER of spear guns in PHCs. Acanthuridae also increased as a proportion of the catch, and showed substantially lower biomass in PHCs than NTRs, even with no detectable effect of the harvest on UVC estimates of biomass. The effects of PHCs are attuned to the expectations of local communities. However, differences in the magnitude of behavioural changes between fishery-target families may result in contrasting outcomes of PHC management regimes.

In Chapter 6 I tested whether predictions of increased FID with increased predation risk, size of individual and availability of refuge were consistent across a broad range of fishing pressures around protected areas and inside fished areas. I included FID of fishes from the Chagos Archipelago, which is a completely unfished population, and FID from areas in Vanuatu, Philippines and Papua New Guinea. FID in fished areas was consistently higher than protected areas across the spectrum of fishing pressure. Both in fished areas and protected areas, fishing pressure had the most support explaining FID, followed by fish size then refuge availability. Life-history stage was not a significant predictor. These results show that fishing effects such as increases in wariness can be imported into marine reserves, and supports predictions of increases in FID with increased predation risk and size (as a loose proxy for reproductive values).

Previous studies have shown increases in FID with hunting, a result confirmed here for coral reef fishes. Experience of predation and some prey conditional and environmental factors can all have significant influences on FID. In contrast, little evidence was found for other factors such as predator attributes or group size. In general, I found that the level of predation risk in the environment tends to have the largest effect on FID (Chapters 2), while fish family, prey size and environmental variables had small but significant effects (Chapters 3, 6). These results have important implications for management, showing that changes in fish behaviour can positively influence fishing on during the harvest of PHCs (Chapter 5), and around the borders of NTRs (Chapter 6), both of which may help increase stakeholder support for management. Temporary changes in behaviour caused by management may increase the susceptibility of fishes to fishing gears, and reduce the impacts of protection. Furthermore, borders of NTRs are porous to behaviour, and fishery mediated behavioural changes may be ubiquitous within smaller NTRS within heavily fished seascapes (Chapter 6).

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CHAPTER 1: GENERAL INTRODUCTION

Most animals have predators. For those that do, responding appropriately to predation risk is critical for enhancing fitness and reproductive success. For example, if an animal is slow to respond to the presence of predators, injury or death is likely to result. Alternatively, if an animal responds too early, or disproportionally (i.e., flees too far) to predation, it may forego mating and feeding opportunities (Ydenberg & Dill 1986). The experience of prey, the type of predator and other physiological and environmental attributes (such as crypsis and resource availability) can potentially influence an animal's decision to flee, and play important roles in mediating animal behaviour (Stankowich & Blumstein 2005).

These types of non-consumptive predator-prey behavioural dynamics can affect how humans interact with and benefit from nature by influencing tourism and hunting opportunities, human and wildlife conflicts, and through the alteration of key ecosystem processes upon which people depend. For example, in the absence of natural predators, prey animals may become less wary, reducing vigilance levels and causing them to venture further from shelter when foraging (Halofsky & Ripple 2008; Madin et al. 2010a). This can result in large changes in ecosystem structure, such as in the northern United States of America where the extirpation of grey wolves in the mid 20th Century resulted in overgrazing of aspen, cottonwood and other trees by elk (Beschta 2003; Ripple & Beschta 2004), an effect reversed when the reintroduction of wolves changed fine-scale predation risk of elks (Halofsky & Ripple 2008). After re-introduction of wolves, elk changed their habitat use, moving to higher elevations, denser forests and steeper slopes. These areas are relatively inaccessible, and are likely to decrease both the likelihood of tourists encountering elk, and hunting success of wolves (Creel et al. 2005; Proffitt et al. 2010).

The role of prey decision-making about habitat use and when to flee in response to predation risk and anthropogenic disturbance has been widely studied in terrestrial and freshwater taxa (reviewed in Brown 2003; Stankowich & Blumstein 2005). This understanding of the behavioural ecology of animals has the potential to play an important role in conservation and management. Flight behaviour has informed the creation of buffer or set back zones to reduce disturbance to breeding birds or avoid the stress of an encounter with an observer that may be mistaken for a predator (Fox & Madsen 1997; Miller et al. 2001; Glover et al. 2011). Investigating how animals will react to different stimuli has also been used to regulate the type of interactions to minimise disturbance [e.g., type of vehicle used for tourism (reviewed in Stankowich 2008; Weston et al. 2012)]. However, there is still relatively little consideration given to how non-lethal effects of predation impacts can be utilised in natural resource management (Cromsigt et al. 2013).

Predation by humans is often a strong structuring force in ecosystems, primarily through reducing the density and abundance of target species. The effects of such depletions can have important consequences for humans and ecosystems, and have been well studied (e.g., Castilla 1999; Wilkie & Carpenter 1999; Jackson et al. 2001; Ward & Myers 2005; Worm et al. 2009; Babcock et al. 2010). For example, many of the world's fisheries are overexploited, with stocks a fraction of historical sizes (Mora et al. 2009; Worm et al. 2009). In order to exploit smaller and smaller stocks, fishers will invest in new technology, move to new areas, or practice techniques that may previously have been considered destructive. At lower levels of exploitation than that imposed by industrial fisheries, behaviour of prey may be modified substantially. Small amounts of variability in hunting pressure can lead to large differences in escape responses in many animals hunted for recreation or at subsistence levels. For example, significant increases in vigilance behaviours and flight responses were observed in two Impala populations in Zimbabwe, where hunting pressure increased from ~ 0.7% of the population being killed annually to ~ 2% (Matson et al. 2005). Similar results have been shown between Roe deer populations in the Netherlands, where areas where ~ 3% of the population were removed each year showed flight initiation distance (FID) approximately 50% lower than areas where ~ 10% of the population were removed each year (de Boer et al. 2004), Similarly, temperate and tropical reef fishes have shown changes in escape response even with relatively low increases in fishing pressure (Cole 1994; Gotanda et al. 2009). Knowledge by prey of appropriate behavioural responses can negatively influence success rates of hunters and fishers (Askey et al. 2007; Grau & Grau 1980). While undoubtedly useful in conservation and animal welfare contexts in the terrestrial realm, due to the role of humans as major predators in many marine ecosystems adoption of predator escape behaviour into marine natural resource management may be of particular value.

1.1 DECISION MAKING AND ESCAPE BEHAVIOUR

The primary method by which predator escape behaviour is quantified is using the metric flight initiation distance (FID). This is a measure of how closely a predator can approach a prey animal before it flees. The economic model of prey flight has largely guided the use of FID in assessments of prey-escape decision-making (Fig. 1.1). In this model, FID occurs at the distance where cost of leaving (which increases with distance from predator) is equal to the costs of remaining (which decrease with distance from predator) (Ydenberg & Dill 1986). The rates of change for these costs are altered by various factors such as resource quality (e.g., leaving a high-quality food source increases the cost of leaving), or predator characteristics (e.g., the speed of approach will cause the costs of remaining to increase more rapidly). While this model was the foundation for research into prey-escape behaviour for 20 years, it is considered conceptually flawed because a prey animal can do no better than ‘break-even’ during an encounter with a predator. Optimal escape models, which presume animals act in a manner to maximise benefits, allow for more complete explanations about how interactions between attributes such as life-history strategy, predator characteristics, lethality of encounter and levels of predation risk in the landscape influence FID (Cooper & Frederick 2007; 2010). While neither the economic or optimal models allow quantitative predictions to be made about FID due to imperfect knowledge of fitness functions and the prey animal's imperfect knowledge of the environment, predictions from both models have been useful in assessing relative influences of variables influencing the FID of prey animals.

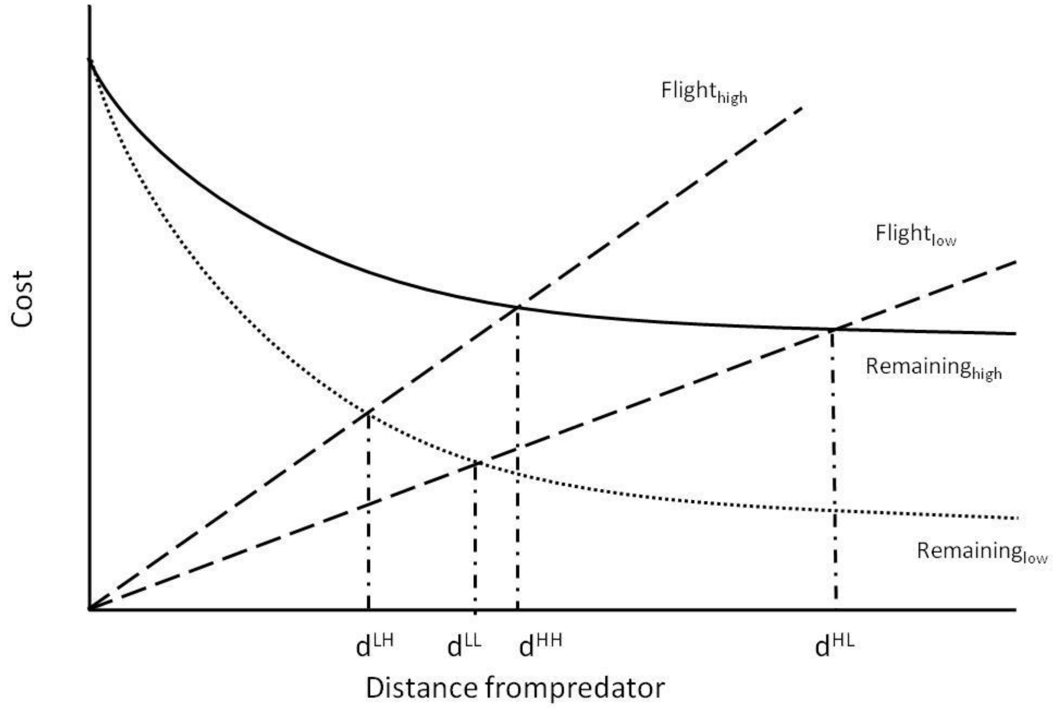

Figure 1.1 The economic model of flight initiation distance (FID). The probability of capture by a predator is proportional to distance of the prey from the predator (cost of remaining), and reaches a maximum when distance = 0. Energetic costs of fleeing are considered to be negligible and therefore cost of flight is equivalent to opportunity costs and increases linearly with distance from the predator (Flight). Therefore, increased cost of flight decreases FID (dLL < dHL) while increased probability of capture has the opposite response (dHH > dLH) (adapted from Ydenberg and Dill 1986).

How prey species perceive the intensity of predatory threat in the landscape is one of the major factors influencing FID. The importance that prey animals place on predator, prey and environmental attributes will determine the level of perceived risk, and FID should increase with increasing levels of perceived predation risk (Helfman 1989). While the influence of various factors on FID varies in magnitude among species and taxa, in general the effects are unidirectional. A meta-analysis of studies measuring FID identified predator characteristics, refuge availability and prey experience as having the largest effects and most statistical support in predicting FID, along with other factors such as patch quality, ground cover, reproductive state, prey morphology, and prey group size (Stankowich & Blumstein 2005). Individual attributes, such as prey size (which may be a proxy for ability to escape) have also been shown to be influential in other studies (Ydenberg & Dill 1986).

Larger (Dill 1974; Helfman & Winkelman 1997), and more direct predators (Burger & Gochfeld 1990; Cooper 2003a; Bateman & Fleming 2011), along with speedier approaches (Lord et al. 2001, Cooper 2003a, b; Stankowich & Coss 2007) will all induce flight earlier in an encounter. There is also evidence of discrimination between predators by some prey species. For example, Thomson's gazelle (*Gazella thomsoni*) show highest FID for wild dogs as predators, then sequentially diminishing FID for cheetahs, lions, hyenas and jackals (Walther 1969). Similar effects have been shown for the Alpine marmot (*Marmota marmota*) where a human with a dog initiated flight earlier than a human alone (Louis & Le Berre 2000). Interestingly, there is little evidence that prey animals are able to differentiate between threatening and non-threatening behaviour of natural predators within species (Helfman & Winkelman 1997), or between hunters and hikers (Stankowich & Coss 2007; Thiel et al. 2007). However, Ibis were able to identify the gaze direction of an approaching human observer, with direct gaze leading to larger FID (Bateman & Fleming 2011).

As with predator characteristics, some environmental characteristics may also have significant effects on FID. In a study on parrotfishes the distance to the nearest refuge (ledge, hole in reef) was a significant determinant of FID in response to approaching SCUBA divers, with higher distances being associated with higher FID (Gotanda et al. 2009). Similar effects in response to a human observer have been shown for other fishes (McClean & Godin 1989), lizards (Cooper 2003a) and marmots (Louis & Le Berre 2000). Other important environmental factors include patch quality, with animals being more reluctant to leave higher quality areas, and increased FID with longer lines of sight (reviewed in Stankowich & Blumstein 2005).

Reproductive state and animal morphology can also be important, with gravid female lizards showing lower FID (due to increased energetic costs of escape), while cryptic colouring and armour are also thought to reduce FID (Ydenberg & Dill 1986; Stankowich & Blumstein 2005). The effect of group size is less clear-cut. There is non-robust evidence for increase in FID with group size in ungulates (Stankowich 2008), which may be due to increased vigilance, or increased likelihood of a wary individual in a given group (discussed in Stankowich & Coss 2007; Stankowich 2008). However, the dilution effect in large groups (which reduces per-capita risk) is likely to result in lower FID than in small groups, and seems to be prevalent in the aquatic realm. Schools of fish tend to show reduced FID compared to individual fish (Abrahams 1995; Helfman & Winkelman 1997), and exhibit compaction effects (Magurran & Pitcher 1987). The effect of the size of the prey individual on FID is similarly less than robust and may vary by species (Stankowich & Blumstein 2005). Size is likely to be affiliated with fitness, and larger individuals will realise lower relative benefits from remaining (Ydenberg & Dill 1986). Evidence for the effect of size from aquatic studies, show this relationship is inconsistent (e.g., Gotanda et al. (2009) found a significant effect of size on FID of reef fishes, while Feary et al. (2011) did not). Gotanda et al. (2009) grouped fishes into two size classes depending on likelihood of being targeted by fishers, and the increased FID in larger fishes may be due to target status, rather than an assessment of risk based on initial fitness.

Overall, prey experience has arguably the largest influence on FID (Stankowich & Blumstein 2005). More frequent interactions with predators or witnessing of predation events are likely to increase perception of predation risk, and thus FID. The majority of studies that investigate prey experience have used density of predators as a proxy for prey experience and density of humans as a proxy for disturbance stimuli (Stankowich & Blumstein 2005), under the assumption that they will induce similar risk assessments as natural predators (Frid & Dill 2002). However, many of these studies appear to show the effect of habituation to human presence, with lower FID when density of humans is high, an effect that does not hold for species that are hunted. For these species, FID is higher in areas where hunters are present (de Boer et al. 2004; Stankowich 2008; Gotanda et al. 2009; Feary et al. 2011) or during hunting seasons (Thiel et al. 2004).

1.1.1 Flight initiation distance and marine fishes

Studies using FID to assess the impacts of fishing on predator escape behaviour are few. Prior to beginning my PhD, only two studies (Cole 1994; Gotanda et al. 2009) had previously looked at FID in response to fishing, and a third was published shortly after my starting (Feary et al. 2011). The role of various factors in altering FID, including fish size, group size, predation threat and predator recognition in such a context remained unclear. Significantly, the three studies mentioned above only tested FID in the presence and absence of fishing and did not assess gradients of predation risk either through varying predator attributes, or for different levels of predation threat in the landscape (i.e., across a gradient of fishing pressure). Furthermore, these studies were conducted on SCUBA and without the presence of fishing gears (e.g., a spear gun). This may not be an accurate facsimile of fishers on coral reefs, who generally fish using breath-hold diving and with a spear gun or other gear (Gillett & Moy 2006). Fishes have been shown to recognise and respond to acoustic cues from SCUBA (Chapman et al. 1974; Cole et al. 2006), and have the visual acuity to see if a diver is or is not holding a spear gun (McGill & Mittelbach 2006). If a fish is able to discern the presence or absence of these cues from an approaching diver, and thus act appropriately by either increasing FID in the presence of threat cues or decreasing FID in their absence, it should gain a fitness advantage over those fishes that do not (Cooper & Frederick 2007).

Pre-flight behaviours of an animal after detection of a predator can be indicative of risk assessment. Pre-flight behaviour can take various forms, such as inspection behaviour (Pitcher et al. 1986), or alteration in body position (Magurran & Higham 1988). These behaviours may pass on information to other prey animals in the vicinity, thus providing a general alarm signal, or can inform a predator that prey are aware of its presence, but may be detrimental to individual survival. For example, inspection behaviour as described in Pitcher et al. (1986), whilst allowing a prey fish to gauge a predator's intent, might increase vulnerability to spearfishers because it reduces the range. Similarly, alteration of body position to maintain eye contact with a spearfisher potentially increases the profile of a fish, and thus the target area. Pre-flight behaviours that convey a fitness disadvantage are likely to be less common under increased predation risk. Refuge choice has also been shown as vulnerable to change with increased predation pressure, although the relationship between refuge and FID is complex: Gotanda et al. (2009) considered only the reef structure as a refuge, despite open water being an effective refuge from spearfishers (Guidetti et al. 2008). For behaviour to be useful as a tool in fisheries management and conservation on coral reefs, FID, pre-flight behaviour, and refuge choice are important factors to consider when discussing how protection and fishing alters behaviour and susceptibility to fishing gears.

1.2 FISHERIES AND FISH BEHAVIOUR

Fish behaviours have evolved under pressure from predators and environmental constraints to maximise chances of survival to maturity and subsequent reproductive success. While many of these behaviours were no doubt adaptive in the face of natural predators such as piscivorous fishes, birds and mammals, humans fishing (fishers) now exploit several of these behaviours. Schooling behaviour can reduce overall mortality from predators such as sharks that can only take one or a few individuals from a school, or can increase reproductive output. However, when predators that can exploit such concentrations of prey efficiently (e.g., humans) are introduced into the system, this behaviour no longer mitigates predation risk, with fishers using trawls or purse seines able to capture large portions of fish schools (Parrish 1999; Pitcher & Hart 2000). Artisanal fishers often take advantage of more predictable aggregations of fishes. For example, In the South Pacific, spawning aggregations of the Serranids *Epinephelus fuscoguttatus*, *E. polyphekadion* and *Plectropomus areolatus* are targeted due to their predictable occurrence around the new or full moon (Hamilton et al. 2005) and high value (Sadovy 2005; Rhodes & Tupper 2007). Artisanal night-time fishing of these aggregations when fish are resting can be up to 30 times more efficient than during normal fishing activities, with two spearfishers able to catch between 15 and 30% of *Plectropomus areolatus* biomass at the aggregation over only two nights of fishing (Hamilton et al. 2012). Other fishing techniques are designed to exploit fish behaviour by turning adaptive behaviour into maladaptive responses to stimuli, which result in capture of the fishes (Ferno 1993). By using attractive cues such as sound (e.g., sprinkling water on the ocean surface in order to mimic baitfish schools – Rodríguez-Marín et al. 2002), object attraction (many species are attracted to, and will gather under floating objects in the open ocean – Hunter & Mitchell 1966) or light, schools of fish can be concentrated to increase fishing efficiency (reviewed in Parrish 1999). Once concentrated, fishes can be prevented from fleeing through the use of repulsion cues. Such cues include perceived barriers like palm fronds in subsistence fisheries or air curtains/bubble barriers (e.g., in the Japanese setnet fishery) which enhance harvesting success. It is here that predator-prey behaviour becomes important. By using lessons learned from predator-prey interactions, fishing gears and techniques can be refined to become more efficient, but species in heavily fished areas may alter their behaviour after repeated exposure to gears, which will in turn reduce catchability.

Fish behaviour can change in response to fishing pressure, either at the population level, or at the level of individual fishes. Fishing can exhibit bias by preferentially catching fishes that display certain behaviours (e.g., aggression towards intruders – Philipp et al. 2009), which can lead to overall shifts towards less aggressive or active behaviours across the population (Alós et al. 2012). Because fishes are being removed, they are not able to pass on learned experiences concerning fishing events, and less aggressive fishes become dominant in the population. In contrast, Askey et al. (2006) showed that in a catch and release fishery, that catchability of fishes reduces during the course of the fishing season. However, at the start of the next season, catchability is once again high. This effect most likely comes about due to strong short-term aversion learning by fishes that have experienced a fishing event. In marine systems, Cod (*Gadhus morhua*) have been shown to alter their position in the water column in response to trawl vessels, showing significant horizontal flight when the warps of a trawl are close (Handegard et al. 2003). In spearfishing areas in the Mediterranean, Sparid fishes (*Diplodus* spp.) chose flight to open water as refuge from intruders, while in no-take marine reserves (NTRs) embedded within the fished seascape, fish tended to choose holes in the substrate as refuge (Guidetti et al. 2008). Similarly, in NTRs on coral reefs, fish FID is substantially lower than in fished areas (Gotanda et al. 2009; Feary et al. 2011). In fact, outside NTRs mean FID of target species tends to be beyond the effective range of spearguns, while inside the NTRs FID is well inside speargun range (Fig. 1.2). These differences in behaviour between NTRs and fished areas may not be a result of population level effects, but rather learning at the level of individual fishes, because fishes recruiting to both NTRs and fished areas are likely to originate from the same population (Harrison et al. 2012).

1.2.1 The role of no-take reserves in fish behaviour and fisheries

NTRs are a popular and widespread conservation tool, and have attracted considerable attention for their potential as a fisheries management tool, particularly on coral reefs. Abundance of targeted species is generally significantly higher inside NTRs, and fishes often attain greater sizes (Lester et al. 2009; Graham et al. 2011). These effects are thought to have two significant consequences for fisheries management (Russ 2002). Firstly, preservation of large, fecund fishes will result in NTRs providing a supply of eggs and larvae to the wider population disproportionately large relative to the size of the reserve (Harrison et al. 2012). Secondly, the build-up of fish densities within a reserve will result in density-dependent movement of fishes across the boundaries of NTRs (as fish density increases in a NTR fishes will be displaced towards and then over NTR boundaries), replenishing adjacent fished areas (Zeller et al. 2003; Abesamis et al 2005; Goni et al. 2010). While there are many studies demonstrating increased abundance of fishes just outside NTR boundaries, using this as a proxy for spillover (Abesamis et al. 2005), there are very few studies that are able to directly relate increased catch per unit effort (CPUE) to increased abundance (but see Russ et al. 2004; Alcala et al. 2005). The most convincing evidence for spillover often comes from studies that use CPUE as a proxy for abundance (Russ et al. 2004; Alcala et al. 2005; Francini-Filho & Moura 2008; Goni et al. 2010). If catchability of fishes is greater when they have been resident in a NTR prior to being displaced to the fishery (Feary et al. 2011), differences in CPUE may reflect behavioural in addition to abundance effects. If, and how behavioural effects transfer across NTR boundaries is unknown.

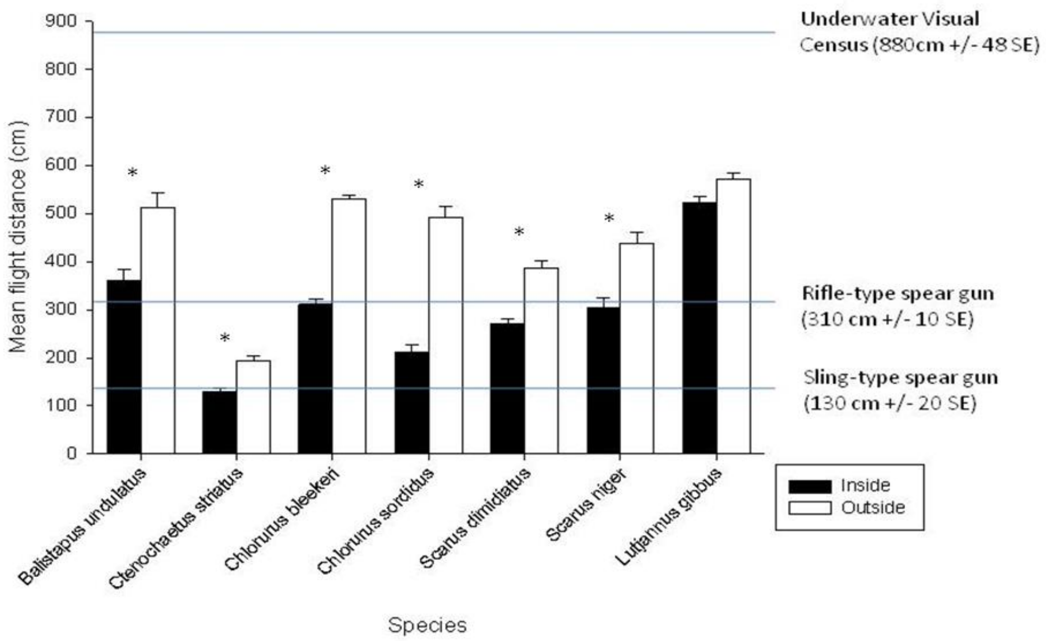

Figure 1.2 Mean flight initiation distance for selected species inside and outside a customary fishery closure area in Papua New Guinea (* - significant difference). Grey lines indicate the mean distance (± SE cm) over which underwater visual census (n = 13), rifle-type spear guns (n = 7) and sling-type spear guns (n = 7) are effective. Figure from Feary et al. (2011), a paper on which I am an author.

Potentially, the mobility of species may drive both the spatial extent and the magnitude of reserve influence, with more mobile species showing little difference in FID across the boundary, whilst those with smaller ranges showing the greatest difference, as is proposed for spillover of biomass (Kaunda-Arara & Rose 2004). Alternatively, species-specific traits and species and family level responses to fishing may be more important, with the intrinsic level of wariness within a family as drivers. For *Lutjanus gibbus*, in which FID changes little between fished and unfished areas, may show no gradient in FID compared to *Chlorurus sordidus,* which shows a large influence of fishing on FID (Fig. 1.2). If naive behaviour does increase catchability of fishes just outside NTR boundaries, fishers may rapidly acquire a large proportion of biomass exported from the NTR. This mechanism may explain why there can be steep declines in biomass across the boundaries of marine reserves such as Apo Island in the Philippines, despite relatively light fishing in the area adjacent to the reserve (Abesamis et al. 2006a, b). This minimal reserve effect on abundance or biomass may hide more spatially extensive effects of marine reserves on the fish community through behaviourally mediated processes. For example, if fishes displaced from NTRs through density-dependence processes, or moderately vagile fishes with a portion of home-range inside NTRs, retain fisher-naive behaviour learned in marine reserves, can escape the immediate surrounds of the marine reserve the distance to which the reserve can have a positive effect on the local fishery could be extended.

1.3 TRADITIONAL CORAL REEF MANAGEMENT AND FISH BEHAVIOUR

In much of the South Pacific coral reefs play an important role in food provision and livelihoods. In particular, coral reef fisheries make substantial economic and social contributions. Coral reef fisheries supply up to 90% of the protein requirement in some countries (Bell et al. 2009), and provide cash income through local and international markets for reef goods and tourism (Birkeland 1997; Moberg & Folke 1999; Sadovy et al 2003). Many coral reefs, particularly in island nations, are overexploited (Newton et al. 2007). Inarguably, the major reasons for this decline in coral reef fishery health is increased access to local and international markets and increased population pressure (McClanahan et al. 2008; Mora 2008). In concert with climate change and other anthropogenic pressures, this has led to global degradation in coral reef health (Hughes et al. 2003) and subsequently increased interest and effort in the management of coral reefs (US Coral Reef Task Force 2000; Coral Triangle Initiative 2008; Hughes et al. 2010; Graham et al. 2011).

One of the primary management tools that has been promoted as a method to restore and maintain coral reef ecosystems is through the use of customary and co-management systems. Much of the South Pacific has strong marine tenure or access and use rights over their coral reef fisheries (Johannes 2002). In such a societal context, consulting with and allowing resource user input into management rules is thought to increase social and ecological success of management (Brooks et al. 2012; Cinner et al. 2012). There is significant evidence that co-management or protected areas instituted under customary traditions can improve compliance with rules (Alcala & Russ 2006; McClanahan et al. 2006), and can maintain fish biomass and coral cover similar to that of permanent NTRs implemented by governmental or non-governmental actors (Cinner et al. 2005; McClanahan et al. 2006; Cinner et al. 2012). Many of these management arrangements include a mechanism by which protected areas are periodically or rotationally harvested, in keeping with customary management rules (Govan et al. 2009; Cohen & Foale 2013). In fisheries management theory, periodic closures are proposed as tools to increase harvest efficiency (McCallum 1988) and support ecosystem processes by maintaining an increased biomass of fish groups that are targeted by local fisheries (Game et al. 2009). The evidence that periodic or rotational closures can have comparable effects for the conservation of coral reef resources is ambiguous. Williams et al. (2006) reported significant declines in fish abundance within the rotational portion of a marine park in Hawai'i when compared to the permanently closed area. In comparison, McClanahan et al. (2006) showed significant increases in fish biomass in periodic harvested areas that were two to six times greater than those seen in national parks or co-managed areas. A third study (Bartlett et al. 2009) reported similar effects of permanent NTRs and periodic harvested closures on fish biomass. None of these studies reported any significant influence of management on the benthic community. Within a customary management context, social and utilitarian goals may have higher priorities than the biological and ecosystem benefits that may accrue from management of marine resources; often temporarily increasing yields in order to produce large amounts of fish for a feast is the goal of a periodic closure, rather than enhancing ecosystem health or biodiversity (Aswani et al. 2007; Macintyre and Foale 2007).

The studies mentioned above, and the other studies that have been conducted on the effects of rotational or periodic closures, demonstrate the expectation that these types of management increase fishing efficiency through increased biomass and abundance of target species due to protection. There is evidence that this mechanism does act to increase fishing efficiency, with fishes caught inside a periodic closure in Manus province in PNG significantly larger than those caught during other fishing activities (Cinner et al. 2005). However, in the South Pacific, it is often the perception that periodic closures work by making fishes more catchable, with relief from predation resulting in a taming effect, whereby fishes become more approachable (Cinner et al. 2005; Macintyre & Foale 2007). While there is no direct evidence for this theory, recent studies showing that FID of fishes inside periodic closures are often within the effective range of spear guns, unlike in fished areas (Feary et al. 2011, Fig. 1.2), provides some support. However, fishes can acclimatise to increases in predation risk rapidly, and show appropriate predator responses after observing or otherwise sensing the alarm cues conspecifics (Suboski & Templeton 1989; Brown & Laland 2003). Increases in catchability due to behavioural change may be short-term, and thus increases in fishing efficiency may be rapidly reduced.

Harvests of periodic closures are often intense, and can capture significant proportions of the fish population. For example, in Manus, Papua New Guinea, a single harvest afternoon resulted in approximately 10% of the fish biomass being removed (Cinner et al. 2005). In Fiji a four week opening of a periodically harvested closure resulted in a reduction of fish biomass of approximately 50% immediately post-harvest and almost 80% one year post-harvest (Jupiter et al. 2012). While these openings may only occur once per year, or even less frequently, species harvested may not fully recover if the period between openings is shorter than replenishment time (Russ & Alcala 1998; Cohen & Foale 2013). Furthermore, the impacts of this form of management on species that serve important functional roles on coral reefs, such as Scarids and Balistids (Bellwood et al. 2004) may be of concern, due to their vulnerability to spearfishing (Cinner & McClanahan 2008). Between rapid removal of biomass, and short-term behavioural effects, periodic closures may show only temporary benefits, while decreasing overall sustainability of reef ecosystems in comparison to NTRs. Understanding how the mechanisms inherent in how periodic closures increase fishing efficiency to meet social goals, whether by increasing abundance and size of fishes, their catchability, or a combination of both, is necessary to ensure the ecological sustainability of periodic closures as they are promoted throughout the South Pacific region.

1.4 AIMS AND THESIS OUTLINE

The overall goal of this thesis is to determine if variations in fishing pressure and protection from fishing alters coral reef fish behaviour, and the subsequent implications of this knowledge for both conservation and fisheries management. To address this goal, I addressed the following questions:

1. How is fish flight initiation distance (FID) influenced by diving techniques, fishing gears and observers – are fishes able to identify and respond appropriately to threatening and non-threatening human intruders?

2. How do FID and other anti-predator responses of fishery target species change with fishing pressure, and how do prey characteristics such as size and group size influence FID?

3. Are the boundaries of no-take marine reserves porous to learned behaviour, and if so, across what spatial scale?

4. Do periodically harvested closures have significant impacts on fish behaviour, and what influence do any changes in behaviour have on harvest efficiency and the fish community?

5. What is the relationship between FID and fishing pressure over a wide gradient of fishing pressure both inside and outside marine reserves?

The various components of this thesis are laid out in the following five data chapters, four of which correspond to publications arising from this thesis. I start in Chapter 2 by establishing a standardised and robust method to estimate FID, assessing the relative effects of spearguns, dive gear, observer bias and no-take protection on FID estimates. In Chapter 3 I observed fish behaviour across a gradient of subsistence fishing pressure, investigating how both FID and pre-flight behaviour, of 6 fishery target families of coral reef fishes vary. This chapter enhanced my understanding of variation in vulnerability of reef fish families to different fishing gears. In Chapter 4 I investigated the export of fisher-naïve fish behaviour beyond the boundaries of NTRs, showing that reduced FID, and potentially increased catchability of coral reef fishes extends further than biomass spillover. I expand on these results, discussing their importance for stakeholder support, modelling of benefits from reserves and how they may help to explain disparate measures of the importance of spillover from observational and catch surveys. In Chapter 5 I conducted a before-after-control-impact pair experiment on two PHCs, where FID and fish community composition were assessed both prior to and post-harvest of the PHCs, and compared with nearby open fishing grounds, and NTRs. Linking this data with creel surveys recording the biomass and composition of catches, this study enabled me to assess the extent by which protection altered fish behaviour, and the effect on fishing efficiency. Finally, in Chapter 6 I analysed FID data from 24 sites across four countries to assess how FID varies across a wide gradient of fishing pressure on both fished reefs and protected reefs embedded within a wider fished seascape, and in an isolated, unfished population. I also compared the relative influence of other important characteristics, such as fish size and refuge availability to the effects of fishing pressure on FID. The chapters in this thesis were deliberately written as pieces of work suitable to be taken individually, but have an underlying theme that weaves them together into a coherent whole: demonstrating that anti-predator behaviour of coral reef fishes has implications for management and conservation.

1.5 STUDY SITES

The work in this thesis was conducted at sites across four countries. Data for Chapters 2 and 5 were gathered in Vanuatu where the openings and closings of multiple PHCs were predictable and had a documented history, and the unique situation of both NTRs and open fished areas also situated within the same community tenure areas as the PHCs. For Chapter 3, I worked in New Ireland Province in Papua New Guinea (PNG). This area is home to human communities with a range of dependency on coral reef fisheries, giving rise to a wide gradient of fishing pressure in a relatively small geographic area, and where data about fishing pressure was available from a previous study in which I was involved. To estimate spillover of behaviour from NTRs in Chapter 4, I chose to work in the Philippines, where boundaries of NTRs are well defined and often demarcated by lines of buoys, in contrast to both PNG and Vanuatu, where the exact extent of NTRs can be more nebulous. Chapter 6 combined data collected in all three of these countries and added a fourth, Chagos, which is an expansive wilderness area (~10,000 km^2) with populations of fishes that have never experienced fishing (Graham & McClanahan 2013).

CHAPTER 2: INFLUENCE OF SPEAR GUNS, DIVE GEAR AND OBSERVERS ON ESTIMATING FISH FLIGHT INITIATION DISTANCE ON CORAL REEFS[1]

2.1 INTRODUCTION

Various aspects of the behaviour of fishes, such as schooling (Parrish 1999) and spawning aggregations (Hamilton et al. 2012), are exploited to increase fishing success. However, while evidence that fishing alters fish behaviour, and potentially fishing success has been reported from freshwater recreational fisheries (Cox & Walters 2002; Askey 2006) and commercial trawls (Pyanov & Zhuykov 1993), knowledge of the influence of behavioural changes on catchability of coral reef fishes is lacking despite indications that fishing can influence fish detectability (Kulbicki 1998). Using the metric flight initiation distance (FID), which estimates how close an animal can be approached before it flees (also referred to as flight or approach distance - Ydenberg & Dill 1986), it has been established that fishes on near-shore, shallow reefs open to fishing consistently flee from an observer at a greater distance than fishes in no-take marine reserves (NTRs) (Cole 1994; Gotanda et al. 2009; Feary et al. 2011; Chapter 3 & Januchowski-Hartley et al. 2011). Other factors have also been shown to influence FID, such as fish size (Gotanda et al. 2009; Chapter 3 & Januchowski-Hartley et al. 2011), distance from shelter (Gotanda et al. 2009), and vulnerability to fishing gear [e.g., mean Lutjanidae FID does not increase with fishing pressure and is consistently greater than the range of spear guns even in NTRs (Feary et al. 2011; Chapter 3 &

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[1] Published as: Januchowski-Hartley FA, Nash KL, Lawton RJ (2012) Influence of spear guns, dive gear and observers on estimating fish flight initiation distance on coral reefs. Marine Ecology Progress Series **469**:113-119. FA Januchowski-Hartley designed the study, collected and analysed data interpreted results and wrote the paper.

Januchowski-Hartley et al. 2011)]. However management status appears to have the most consistent and largest influence.

Low fishing intensity or occasional poaching can have significant effects on coral reef fish communities (Jennings & Polunin 1996). However, methods such as underwater visual census (UVC) can show considerable variation when estimating fish abundances and biomass (McClanahan et al. 2007a) even at low fishing pressures (Jennings & Polunin 1996) and lack of compliance within NTRs may be obscured by this variation. In contrast, fish FID is more tractable to high levels of replication, is sensitive to even low levels of fishing (e.g., Feary et al. 2011; Chapter 3 & Januchowski-Hartley et al. 2011) and, consequently, may be an alternative, more powerful tool to gauge levels of compliance with NTRs. Management may be further informed through the implications changes in FID have for success of certain fishing gears (e.g., increased FID may result in decreased efficiency of spear guns), and subsequent impacts on fisher decision-making (Feary et al. 2011). If this is to occur, knowledge of how possible biases may confound my interpretations of fish FID is essential.

Fish FID is estimated by an observer using either SCUBA gear or free-diving, who directly approaches a fish until it flees, and then measures the distance between him or herself and the location from which the fish fled (Feary et al. 2011; Chapter 3 & Januchowski-Hartley et al. 2011). Much of the fishing with spear guns on coral reefs is conducted by free-diving (Gillett & Moy 2006); in contrast the majority of fish FID studies investigating fishing effects have been conducted while using SCUBA (Cole 1994; Gotanda et al. 2009; Feary et al. 2011). There is convincing evidence that fishes will actively avoid SCUBA divers (Dickens et al. 2011) and will potentially allow closer approaches by snorkelers (Welsh & Bellwood 2012). Consequently fish FID estimated while using SCUBA could provide an inaccurate measure of FID in response to spearfishers. Additionally, in all studies of fish FID in response to fishing, FID has been estimated without either a spear gun or simulated spear gun substitute and for only one observer (Cole 1994; Gotanda et al. 2009; Feary et al. 2011; Chapter 3 & Januchowski-Hartley et al. 2011). If fishes recognize a spear gun, or discern it as an extension of the diver's body, this could result in increased FID, particularly in fished areas. In order for FID to be appropriately tested, questions about the effects of dive type, spear gun presence and observer error/bias need to be answered. The aim of the present study was to examine the influence of these factors on estimates of fish FID, and to compare them between a permanently fished area and an NTR. Scaridae (parrotfishes) were used as the focal fish group, because: 1) they are commonly targeted with spear guns on coral reefs; 2) were locally abundant; and 3) are known to exhibit behavioural changes as a result of fishing (Gotanda et al. 2009; Chapter 3 & Januchowski-Hartley et al. 2011).

2.2 METHODS

2.2.1 Study sites and design

This study was conducted during December 2011 on exposed fringing reefs in the Nguna-Pele Marine Protected Area Network, Vanuatu (17°29'S, 168°23'E). The area is lightly populated, with most of the population relying on fishing, gardens or small-scale tourism for income (Bartlett 2009). This study was conducted in a permanent NTR that had been protected since 2004, and adjacent fished area. The NTR was 14 hectares in size and characterised by a continuous fringing reef that slopes from approximately 2 m depth at the reef crest to sand at approximately 12 m, with large detached sections of reef outside the main fringing structure. The fished area (approximately 21 hectares) has a very shallowly sloping reef, which extends 250 m out from the crest to between 14 and 16 m depth. Both areas had similar levels of coral cover (NTR: 5.4 ± 0.8 % (S.E), fished area: 3.5 ± 0.5 %) and habitat rugosity (NTR: 3.1 ± 0.1, fished area: 2.4 ± 0.3) (Chapter 5 & Januchowski-Hartley et al. 2013a). Rugosity was visually appraised on a

6-point scale where: 0 to 5, where 0 = no vertical relief, 1 = low and sparse relief, 2 = low but widespread relief, 3 = moderately complex, 4 = very complex with numerous fissures and caves, 5 = exceptionally complex with numerous caves and overhangs (Polunin & Roberts 1993). All FID trials were conducted on the reef slope between 2 and 10 m depth in both the NTR and the fished area. Spearguns were the predominant gear used on these fringing reefs, with only one fisher out of 17 interviewed reporting using a different gear (gill net) and then only rarely (Chapter 5 & Januchowski-Hartley et al. 2013a). To avoid potential spillover of naive fish behaviour from the NTR, all observations in the fished area were conducted at greater than 200 m from the border with the NTR.

I chose a nested design for the study, with three observers nested within two levels of gear use (presence/absence spear gun), within two levels of dive gear (free-diving/scuba), within two levels of management (NTR/fished area). This resulted in eight different treatments (2 x fishing gear * 2 x dive gear * 2 x management), with three replicates at the observer level within each treatment. Each area was surveyed once per day, with time of survey (morning/afternoon) equally distributed across areas. The treatment (spear gun presence and dive type) was selected at random for each survey. Spear guns in this area of Vanuatu are rifle-style spear guns, which propel a metal spear via use of rubber tubing, and vary between 120 and 180 cm in length. As it was not appropriate to take spear guns into the NTR, all observers used a piece of wood of approximately the same thickness and length as the locally used spear guns as a simulated “spear gun” in both the fished area and the NTR. All three observers wore similar dive gear throughout the study, consistent with clothing of local spearfishers.

2.2.2 Flight initiation distance

To develop a standardized and repeatable method of approaching target fish that closely mimicked subsistence spearfishing techniques, I consulted with local spearfishers in the region and observed them during fishing activities. Many spearfishers have idiosyncratic behaviours, and here I developed my method by conserving similarities between spearfishers. When free diving, a potential target fish was first identified from the surface. The observer (myself or a field assistant) would descend directly from the surface to the reef at approximately the same depth as the targeted fish, with a minimum horizontal distance of 8 m separation from the fish. The observer would lie horizontal just above the substrate and reorientate to the fish, ensuring that the fish had not been disturbed by the descent. Fishes were not targeted if they were engaged in territorial, mating or predator escape behaviour, or were obviously aware of observer presence before the approach began (e.g., had turned towards the observer). The observer then swam directly towards the fish at a constant speed (approximately 0.75 m s^{-1}). When the fish fled, the observer placed a marker on the substrate directly beneath the point where their head was at the time of flight, and then a second marker on the substrate directly below the location of the fish when it fled. The distance (cm) between these markers was measured and recorded as the FID. Only fish that were close to the substrate were approached in order to minimise error through misidentifying the part of the substrate that was directly below the fish when in fled.

Flight was considered to occur when either a fast-start escape response (“C-start” Domenici & Blake 1997) or a noticeable increase in swimming speed in conjunction with a change in behaviour or orientation away from the diver was observed. While free-diving care was taken at every stage to minimise other flight cues by minimising sounds generated by air bubbles and breaking the surface, while keeping movements slow and deliberate. When using SCUBA, potential target fishes were identified from ~ 10 m distance at a similar depth to the diver, using the same criteria, and estimating FID using the same protocol. When simulated “spear guns” were present, observers would hold the spear gun horizontally in front of their face and pointing directly at the target fish prior to beginning the approach, imitating the approach of local spearfishers. For both snorkel and SCUBA diving trials a dive buddy remained in the vicinity, but did not move with the observer, and remained further away than the observer from the focal fish at all times.

Prior to approach observers estimated fish total length (cm TL) and only targeted individuals greater than 15 cm TL; there was no upper limit on body size. Observer fish TL estimates were validated daily by estimating lengths of PVC pipes until estimates were consistently within 2 cm of actual length. If line of sight between the diver and fish was broken prior to flight, or the target fish was chased by or chased a con- or hetero-specific competitor during the approach the observer abandoned the trial. To minimise the chance of approaching a target fish that had been disturbed by a previous trial, consecutive trials were conducted a minimum of 10 m apart, and in the opposite direction to which a disturbed fish fled. To establish the sample sizes required to detect differences in FID, I performed a power analysis in the MiniTab 14 statistical package. This analysis used data on the differences and variance in mean FID of Scarids obtained from a separate study with one observer using free-diving in the same fished area and NTR (Chapter 5 & Januchowski-Hartley et al. 2013a). Data were analysed in a one-way ANOVA model, with a total of 24 levels (8 treatments * 3 observers), and tested for an n of 5, 10, 15 and 20. At a sample size of $n = 15$, a power of 0.98 was achieved, compared to 0.86 at $n = 10$ and 0.99 at $n = 20$; therefore a sample size of $n = 15$ was selected for this study.

2.2.3 Data analysis

Mean fish TL ± SE was 24.8 ± 0.4 cm inside the NTR (range 14 – 55 cm) and was significantly larger than the mean of 22.3 ± 0.3 cm (range 15 – 37 cm) in the fished area (one-way ANOVA, $F_{1,358} = 18.54$, $P < 0.001$). Therefore I included fish size as a covariate in an analysis of covariance (ANCOVA) to control for potential differences in FID due to size, and assessed differences in FID between treatments using a four-level nested analysis where observer was nested within spear gun presence, nested within dive type, nested within management. FIDs were square root transformed to meet assumptions of normality and homogeneity of variance. Variance components were calculated to assess the relative contributions of each level in accounting for differences in FID. Mean changes in FID (adjusted for size) between gear, dive type and management were calculated to find absolute differences in FID estimates.

I also evaluated two components of error. First, I determined if there were systematic errors in FID estimation between observers within treatments using ANCOVA. Post-hoc Tukey's tests were used to identify which observers were significantly different from each other and to identify if one observer consistently estimated longer or shorter FID compared to other observers (observer bias). Second, I evaluated the variability in FID estimation between factors and observers (precision) by calculating a coefficient of variation (CV) for each observer in each of the eight treatments. I used a one-way ANOVA to test for differences in CV between observers, gear use, dive gear, and management.

2.3 RESULTS

The mean FID of parrotfishes in the NTR was 284.3 ± 6.7 cm compared to the fished area average FID of 417.4 ± 7.6 cm. The nested ANCOVA revealed significant differences in fish FID between management regimes and observers (Table 2.1). However, neither the presence of a spear gun, nor whether the observer was free-diving or using SCUBA gear was associated with significant differences in FID (Table 2.1). FID in the fished area was consistently higher than for the same treatment in the NTR and did not significantly vary within each management area, either by dive type or through spear gun presence (Fig. 2.1). Fish TL was a highly significant covariate ($F_{1,335} = 63.07$, $P < 0.001$; Table 2.1). Inspection of variance components confirms that management status had the largest influence on FID, explaining almost 60% of the variance (Table

2.1). The mean (± SE) fish FID was 141 cm ± 13.2 greater in the fished area than in the NTR for the same combination of gear and dive type, compared to an increase of 26± 8.9 cm, when only spear gun presence differed between treatments, and 21 ± 17.9 cm when snorkel was used rather than SCUBA (Fig. 2.2).

Table 2.1 Results of nested ANCOVA of flight initiation distance for treatments. Observer was nested inside spear gun presence, nested inside dive type, nested inside management.

Treatment	**d.f.**	***F***	***P***	**Variation explained (%)**
Management	1	34.13	0.027	58.9
Dive Type	2	2.84	0.171	2.3
Spear gun Presence	4	1.18	0.358	0.4
Observer	16	2.71	< 0.001	4.0
Error	335			34.4
Covariate				
Size	1	63.07	< 0.001	

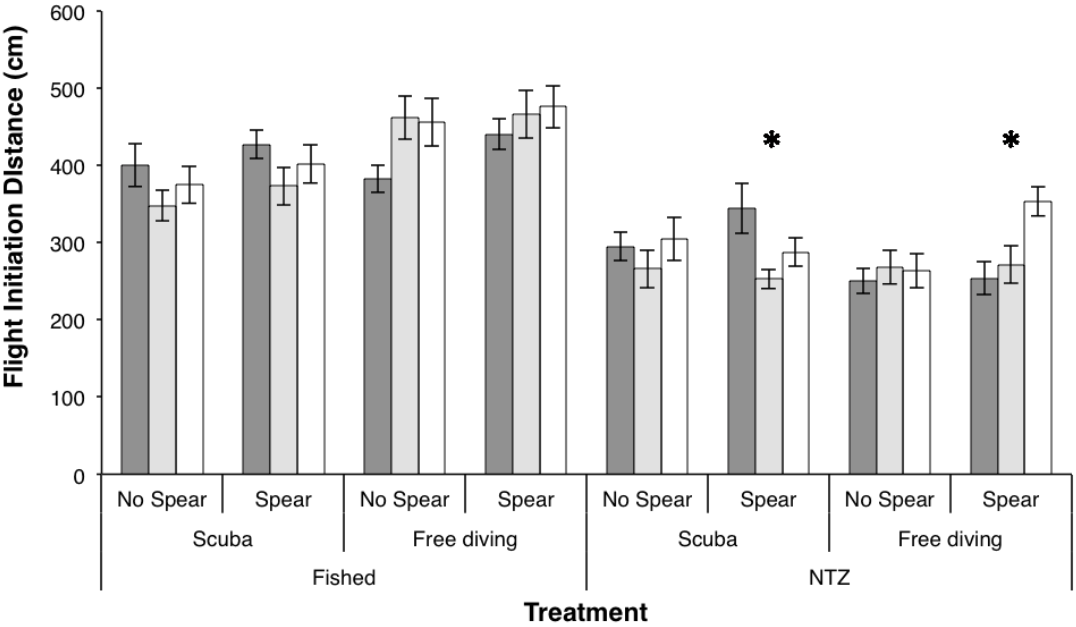

Figure 2.1 Mean flight initiation distance estimates in centimetres for each observer (indicated by different levels of shading) for each of eight treatments (2 management * 2 dive types * 2 gear types). Asterisks indicated where significant

differences were found between observers within the same treatment (one-way ANCOVA). Error bars represent ± 1 SE.

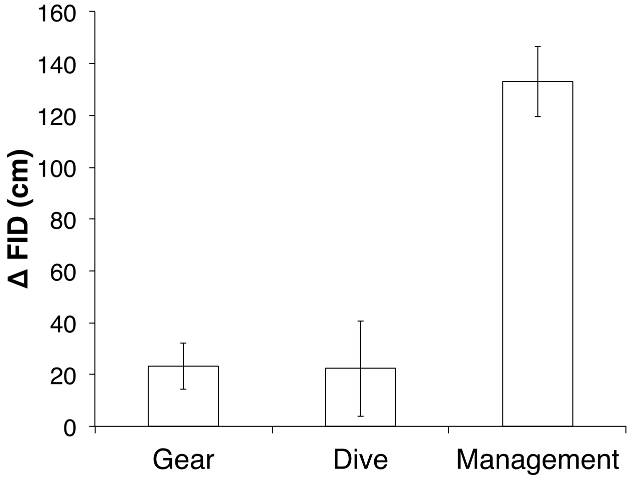

Figure 2.2 Change in flight initiation distance (ΔFID) in cm for each factor. The ΔFID for 'Gear' is the mean difference in FID between the 4 treatments with a artificial spear gun compared to the 4 treatments with no spear gun; for 'Dive', the mean difference between the 4 treatments free-diving compared to the 4 treatments using SCUBA; and for 'Management', the mean difference for the 4 treatments in the fished area compared to the 4 in the MPA. Data for the three observers is combined for each factor. Error bars represent ± 1 SE.

Table 2.2 Results from analysis of covariance between observers for each treatment including Tukey's post-hoc comparison.

Management	**Dive Type**	**Gear Presence**	***df***	***F***	***P***	**Size**	**Tukey's**
NTR	Snorkel	No spear	2, 44	0.48	0.624	NS[a]	
		Spear	2, 44	10.45	< 0.001	***	FJ > RL
	SCUBA	No spear	2, 44	0.18	0.838	**	
		Spear	2, 44	0.39	0.680	***	
Fished	Snorkel	No spear	2, 44	4.72	0.014	NS	FJ < KN
		Spear	2, 44	3.03	0.059	**	
	SCUBA	No spear	2, 44	0.29	0.752	**	
		Spear	2, 44	0.51	0.607	***	

[a] NS = not significant; ** = $P < 0.01$; *** = $P < 0.001$

Within treatment ANCOVA for observer differences identified statistically significant differences between observers for two treatments; inside the NTR with a spear gun both using SCUBA ($F_{2,44} = 4.72$, $P = 0.014$), and snorkel ($F_{2,44} = 10.45$, $P < 0.001$) (Table 2.1, Fig. 2.1). In both cases the differences occurred between a different pair of observers (Table 2.2), and there was no evidence that one observer was consistently estimating longer or shorter FID than either of the others (Fig. 2.1). Analysis of CVs showed that there were no significant differences in precision between observers, spear gun presence or dive gear; however precision was significantly lower (CV significantly higher) in the NTR, compared to the fished area (Table 2.3).

Table 2.3 Summary of coefficients of variation (CV) of estimates of fish flight initiation distance for each observer, gear, dive, and management type and ANOVA test of significance.

Factor		***CV***	***d.f.***	***F***	***P***
Observer	FJH	22.84	2, 21	0.80	0.461
	KN	24.00			
	RL	26.67			
Gear	Spear	23.23	1, 22	1.77	0.198
	No Spear	26.43			
Dive	SCUBA	24.77	1, 22	0.00	0.964
	Free-diving	24.89			
Management	Fished	21.60	1, 22	9.56	0.005
	NTR	28.06			

2.4 DISCUSSION

This study demonstrates that fisheries management status has the strongest influence on estimates of parrotfish FID, and that these estimates are relatively robust to the influences of dive type, spear gun presence, and inter-observer variation. The significantly higher parrotfish FID in the fished area compared to the NTR is consistent with other studies of FID (Gotanda et al. 2009; Feary et al. 2011), while the non significant influence of dive type (consistent with that found by Miller et al. 2011 when comparing their results in the Barbados Marine Reserve while free-diving to those of Gotanda et al. 2009) and spear gun presence on FID estimates suggests that neither of these factors act as flight stimuli for parrotfishes. The lack of difference between free-diving and SCUBA was unexpected as there is significant evidence that SCUBA negatively influences parrotfish density estimates (e.g., Dickens et al. 2011) and snorkelers may more closely approach at least one of the species of parrotfishes (*Chlorurus microrhinos*) present in this study (Welsh & Bellwood 2012). However, these differences may be due to distinct snorkelling techniques – it is unclear if Welsh & Bellwood (2012) free-dived or approached parrotfishes on the surface. While I attempted to minimize noise due to observers breaking the surface when free-diving, this may have acted as a pre-flight stimulus that raised fish awareness (Ydenberg & Dill 1986), resulting in higher FID than expected for this treatment. This theory is given some limited support by results suggesting that free diving while conducting UVC may result in parrotfishes fleeing the area (Dearden et al. 2010).

As in terrestrial taxa (Stankowich & Coss 2006), there was a lack of influence of weapon presence on FID. While this is possibly due to unfamiliarity with weapon, this is unlikely to be the case in the fished area in this study, and implies that fishes are taking their flight cue from some other stimulus associated with the body of the observer rather than the extension added by the spear gun. As reef fishes can discriminate predator characteristics, such as mouth size and distance between eyes

(Karplus & Algom 1981), it is unlikely that the visual acuity of adult parrotfishes is insufficient to resolve the spear gun at the starting distances in this study (Renee Lara 2001). The cue to flee may potentially be triggered by movement and exceeding an Apparent Looming Threshold (proportional to the attack speed and frontal profile of a predator), rather than direct assessment of predator characteristics (Wisenden & Harter 2001; Domenici 2002). Alternatively, my artificial spear guns may not have adequately imitated the spear guns used in the fished area. However, while I believe this unlikely, in future research it would be useful to validate whether there is a difference in the responses of fish to real and artificial spearguns in fished areas.

Although I had considerably more experience with FID estimation, my results indicated that observer bias had a negligible effect on magnitude or variation of FID estimates. Although there were significant differences between observers in two of the eight treatments, these differences were not consistent in direction and did not occur between the same observers. This source of error appears to be random, and only accounted for 4% of the variation in FID. The precision of FID estimates was not found to differ significantly between observers, dive type or fishing gear. These findings imply that while observer effects should be considered when designing and analysing studies that have more than one observer, or comparing results among studies, FID estimation can be achieved with a high level of rigor across observers and study designs.

My results suggest that comparison between FID studies conducted on different dive gears and with multiple observers may be valid. Estimates of mean FID within geographic regions appear to be consistent across studies and gears (Caribbean: Gotanda et al. 2009; Miller et al. 2011; Indo-Pacific: this study, Feary et al. 2011; Chapter 3 & Januchowski-Hartley et al. 2011), although there appear to be differences between regions. This could be due to potential differences in duration of protection of the NTRs in the studies (26 years in the Caribbean, Gotanda et al. 2009; 2-8 years in Indo-Pacific studies) resulting in fishes with differential exposure to fishing across their lifespan, to differences in fishing gear, fisher practices and fishing pressure in these two regions.

Estimation of fish FID is a robust method, which shows high precision and low variation between observers and dive gears, and may be sensitive to small differences in fishing pressure, thus providing a useful tool to assess fisher compliance to NTRs (Chapter 3 & Januchowski-Hartley et al. 2011). Currently, monitoring of fish communities in NTRs is an expensive process, requires complex analysis of data, suffers from logistical constraints (e.g., availability of SCUBA gear and expense) and from a shortage of trained monitors while impacts of fishing may be masked by natural variation (McClanahan et al. 2007a). In comparison, estimating FID is a relatively simple procedure, is directly associated with fishing pressure, and is tractable to high levels of replication, allowing for sampling designs of higher power for less cost in time or resources (indeed in this study each of the three observers was able to sample 15 fishes within an hour for each treatment). In addition, there exists a pool of experienced spearfishers that are already engaged in co-management of local NTRs that can be easily trained in this technique. Although, there may be a limited suite of fishing gears that will impact on FID (e.g., spear guns, drive-in gillnets), these gears are commonly used globally in artisanal fisheries. FID does not, however, inform managers or communities of fish density, community composition or size, all of which are important in assessing the success of a NTR in helping maintain ecosystem function or in providing benefits to other areas through spillover or larval dispersal. While the influence of confounding factors, most importantly size, should be considered when designing monitoring protocols, FID may provide a novel, inexpensive and intuitively simple compliance monitoring tool for near-shore marine reserves.

2.5 ACKNOWLEDGEMENTS

Thank you to the Nguna-Pele MPA Network for allowing me to conduct this study in their fishing grounds and marine reserves. Special thanks to J. Ronneth for field support during this work, and John and Lapakoa of the Pauvina Guesthouse.

2.6 SUMMARY

- Fish flight initiation distance (FID) is emerging as a useful metric of the response of fishes to fishing, with significant differences in FID demonstrated between fished and no-take marine reserves.

- Studies investigating FID vary in methodology and many of the potential confounding effects inherent to in-water estimation of FID have yet to be investigated.

- I examined relative effects of spear guns, dive gear, observer bias, and protection status on FID estimates. Three observers estimated FID of parrotfishes in both a fished area and no-take marine reserve, via both SCUBA and free diving, and with and without a simulated spear gun (eight treatments).

- FID was significantly influenced by protection status, increasing by 141 cm on average in the fished area compared to the no-take marine reserve, but not by either dive type or spear gun presence.

- There was no evidence of observer bias, nor were there any significant differences in the precision of FID estimates between observers. Overall, management status explained almost 60% of the variation in FID estimates, while observers accounted for only 4%.

CHAPTER 3: FEAR OF FISHERS: HUMAN PREDATION EXPLAINS BEHAVIORAL CHANGES IN CORAL REEF FISHES[2]

3.1 INTRODUCTION

Appropriate response to predation risk is one of the most important factors in enhancing fitness and reproductive success among animals (Ydenberg & Dill 1986; Cooper & Frederick 2007). The most commonly used metric to assess prey decision-making and wariness in the light of predation is flight initiation distance (FID) – the distance to which a predator can approach prey before the prey animal flees (Blumstein 2003). Research using this metric has given rise to an extensive theoretical framework, culminating in the theory of optimal FID, which states, "a prey animal will flee at the stage of an encounter at which maximal fitness is achieved" (Cooper & Frederick 2007). There is a range of factors that may influence when a prey animal makes the decision to flee from a predator (Stankowich & Blumstein 2005). These include: environmental factors such as: food patch quality (Stankowich & Blumstein 2005); refuge availability (Cooper 1999); previous experience of predation (Kelley & Magurran 2003); morphological defences (Cooper et al. 2009); social defences (Walther 1969); and transmission of information through the prey population (Magurran & Higham).

Increased wariness of prey species in the context of higher predation has been reported for both natural (Giles & Huntingford 1984; Madin et al. 2010a) and human predation (de Boer et al. 2004; Feary et al. 2011). Although this understanding of FID in predator/prey relationships has improved our ability to manage terrestrial animal populations, for example through the use of setback and buffer zones to minimize

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disturbance (Blumstein et al. 2003), there is a paucity of research on the impacts of human predation on the FID of marine species. Studies to date consistently show that fishing activity does influence FID. For example, coral reef fishes normally targeted by spearfishers showed lower FID within areas protected from fishing pressure (Gotanda et al. 2009; Feary et al. 2011), while in New Caledonia, detection distance (mean distance from the transect line at which fishes were observed) was found to increase with intensity of fishing (Kulbicki 1998). In parallel, within a New Zealand marine reserve, it was found that “approach distance” (synonymous with FID) of targeted fishes increased with distance from the centre of the marine reserve (Cole 1994). Although previous studies agree that fishing intensity directly influences FID, the role of body size and group size is more contested. In Papua New Guinea (PNG), fishes’ body size was found to be non-significant as an explanatory factor for FID (Feary et al. 2011), contrary to studies elsewhere (Gotanda et al. 2009), which found that larger sized fishes exhibited greater FID/mean detection distance. In the terrestrial literature, increased group size tends to be accompanied by increased FID (Stankowich & Blumstein 2005; Stankowich 2008) contrary to data available on fish, where increased group size has generally been found to be associated with lower FID (Stankowich & Blumstein 2005; Domenici 2010).

Prey species wariness to predators may also be expressed through behaviours other than flight (Kelley & Magurran 2003; Guidetti et al. 2008) Fishes are well-equipped for social learning and transfer of information, and alarm signals are often communicated through visual and other sensory systems (Brown & Laland 2003). Visually transmitted alarm signals can originate as a result of predator inspection behaviour, where a prey fish fixates on a predator, and slowly swims towards it (Pitcher et al. 1986). While inherently risky, this behaviour may allow assessment of predator intent (Licht 1989) and dissuasion of predation (Godin & Davis 1995), while also advertising fitness to potential mates (Godin & Dugatkin 1996). However, this behaviour may make fishes particularly vulnerable to spearfishers, because it brings the fish closer to the fisher, and highlights the fish as a target. Although there is little empirical data, at higher fishing pressures fishes' behaviour prior to flight would theoretically be expected to show declines in occurrence of 'less wary' behaviours (e.g., inspection), with 'more wary' behaviours (i.e., immediate flight or movement towards a refuge), becoming more frequent.

Despite over a decade passing since the effects of differing human predation on coral reef fish behaviour were first identified in the literature (Kulbicki 1998), the importance of human-induced fish behaviour in structuring fish communities is rarely considered within the conservation and fisheries management literature (Jennings et al. 2000; Higgins et al. 2008; Lester et al. 2009). Although levels of artisanal fishing can vary widely, even low levels of subsistence fishing have been associated with dramatic declines in fishery target species (Jennings & Polunin 1996). While underwater visual census (UVC) of abundance and catch survey data are often used to assess the success of management in small-scale subsistence fisheries, they are subject to high variance (Connell et al. 1998) or may not provide the information necessary to accurately assess and manage the ecosystem over short temporal scales (Maunder et al. 2006). Changes in the structure of fish communities due to altered management practices may occur over multi-year to decadal scales (Russ et al. 2005; Babcock et al. 2010). However, behavioural responses to altered fishing practices may express themselves over much shorter temporal scales (Lima & Bednekoff 1999), and the assessment methods above do not lend themselves to identifying such temporally rapid changes within reef fish communities. If differences in FID or other behaviours are driven by changes in management or compliance, monitoring of behaviour may prove to be a tool that can quickly and accurately identify and assess the results of such changes. This may be particularly useful in the assessment of compliance with no-take reserves (NTRs) or gear bans in coral reef and similar fisheries.

This study aims to clarify whether predictions made by anti-predator escape theory are reproduced within coral reef fisheries, and ascertain how different factors influencing FID interact as fishing pressure increases. The relevant predictions made by FID theory are: 1) as the intrinsic risk of predation and lethality of encounters increase FID should likewise increase; and 2) as prey increase in size, FID should also increase. I hypothesize that as fishing pressure increases, fish targeted by fishers will show increased wariness, and that this will be reflected in increases in FID and the type and frequency of pre-flight behaviour. To explore these hypotheses, I examined FID at four coastal communities in PNG along a gradient of fishing intensity.

3.2 METHODS

3.2.1 Study sites and design

FID of coral reef fishes was assessed at four sites in the Tigak and Tsoi Islands of New Ireland Province, PNG between July and September 2010. I surveyed three communities with varying levels of fishing pressure (Ungakum - low, Nusa - intermediate, and Mongol - high), and one community (Kavulik) who comply with a NTR that has been in place since February 2008 (TM, personal observation). Previous research indicated that these areas were appropriate for this study because spearguns were a commonly and frequently used gear in the Kavieng area (JE Cinner, unpublished data). Each of the communities have exclusive access rights to their fishing ground, with the exception of Mongol, which, as a community of migrants and located adjacent to the provincial capital of Kavieng, has seen adherence to customary tenure rights fade (FAJ, TM, personal observation).

To estimate fishing pressure within each community, I used data gathered during previous studies of household fishing practices in these communities (Cinner & McClanahan 2006; Cinner et al. 2012). To obtain the average number of reef-associated fishing trips per week per household I removed gears that target pelagic fishes (e.g., trolling), and gears commonly used in lagoons, such as nets. Because spearguns and hand lines are often used during the same fishing trip, it was not possible to disaggregate these to provide a spearfishing only fishing pressure. Therefore fishing pressure estimates presented in this study are for spearguns and hand lines combined on the fringing reef. To account for population growth since the earlier surveys (2002 in Mongol and Nusa, 2009 in Kavulik and Ungakum) I re-counted the total number of households in each community in 2010. To calculate fishing ground size, the limits of fringing reef that were claimed as exclusive fishing grounds by each community were marked by GPS and linear reef distance estimated by digitally tracing the reef edge using Google Earth. I multiplied the average fishing trips per week by the total number of households and divided this by the length of each community's respective fishing ground to develop a measure of fishing trips per linear kilometre of reef per week for each community, and used a finite population correction factor to estimate the error associated with each estimate. The estimate of fishing pressure at Mongol obtained by this method is potentially lower than the actual fishing pressure, due to loss of tenure rights and fishing within the fishing ground by non-residents of nearby Kavieng town. Mongol's relative position as the site of highest fishing pressure means that any underestimates of fishing pressure at this site should not affect my interpretation of the results.

To allow comparisons of FID across all four communities, I conducted surveys along approximately one linear kilometre of continuous fringing reef at each area. The majority of spearfishing in the region occurs between the crest and the 10 m depth contour on the reef slope, and all surveys were conducted in this reef zone. Within each area surveyed, benthic complexity was assessed visually using 8-10 replicate 50m transects (to control for availability of potential refuge for fishes between areas). Each transect was given a benthic complexity score between 0 and 5 (Polunin & Roberts

1993): 0 = no vertical relief; 1= low and sparse relief; 2 = low but widespread relief; 3 = moderately complex; 4 = very complex; and 5 = exceptionally complex. This method is highly correlated with the linear versus contour complexity measure, reef height and abundance of holes 10 – 70 cm diameter when conducted by experienced observers (Wilson et al. 2007), and captures the important characteristics of coral reef substrates as refuge.

3.2.2 Selection of focal families

I selected focal families based on records of fishery catches by local communities in Kavieng (Kaly & Opnai 2005) and other areas of PNG (McClanahan & Cinner 2008). Focal families were also tractable to investigation (i.e., diurnally active, reef resident), and were present in sufficient abundance at the study areas to meet power requirements. Six families/subfamilies were chosen for this research: Acanthuridae (surgeonfish), Balistidae (triggerfish), Lutjanidae (snapper), Mullidae (goatfish), Scaridae (parrotfish) and Serranidae (groupers, subfamily Epinephelinae). Acanthuridae and Scaridae make up the majority of the spear gun catch in PNG, while the Balistidae, Lutjanidae and Serranidae are primarily caught by hook and line (Kaly & Opnai 2005; McClanahan & Cinner 2008). Mullidae are caught by both gears at approximately the same frequency (McClanahan & Cinner 2008). FID was measured for 680 coral reef fishes that ranged in size from 10 to 50 centimetres total length (cm TL), encompassing 54 species across the six families.

3.2.3 Behaviour and flight initiation distance

Although previous studies on FID of reef fishes have used SCUBA divers as predation stimuli (Cole 1994; Guidetti et al. 2008; Gotanda et al. 2009; Feary et al. 2011), all FID surveys within this work were based on free diving as my interest was in how fishes respond to local spearfishers (who do not use SCUBA) (NFA 2007). I used the methodology outlined in Chapter 2 (Januchowski-Hartley et al. 2012) to estimate fish

FID. The maximum FID obtained by Feary et al. (2011) in Papua New Guinea was approximately 8 m; consequently, in order to avoid beginning trials within FID of target fishes, all trials began outside this distance, and were conducted only when visibility was ≥ 10m.

Fishes were only targeted for approach if they exhibited normal daily behaviour (i.e., were not obviously alert to observer presence, fleeing from predators, or engaged in competition with con- or hetero-specifics). If line of sight between myself and the target fish and observer was broken prior to flight, or if during the approach the target fish was chased by another fish, the trial was abandoned. Only fishes greater than 10 centimetres TL were approached because spearfishers will rarely target fishes under this size (FAJ, personal observation). For each fish, size (cm TL), behaviour exhibited prior to flight (hereafter "pre-flight behaviour"), group size, life-history phase (for Scaridae only) and refuge choice were recorded. Pre-flight behaviour was assigned into five broad types of behavioural response, ranging from most wary to least-wary behaviour, based on perceived increase in vulnerability to fishers. These were: "none" – the fish fled without changing behaviour; "tacking" – the fish halted activity and slowly swam away tacking from side to side before fleeing; "orientation" – the fish orientated to flee to a refuge; "watch" – the fish stopped current activity and turned towards the observer; and "inspect" – the fish moved towards the observer prior to flight.

To minimize the chance of approaching a target fish that had been disturbed by previous surveys, consecutive trials in the same area were conducted a minimum of 10 m apart. A pilot study found that after approximately 20 minutes of repeated FID surveys, most target fishes had vacated an area of approximately 30 linear metres of reef. Therefore, I moved steadily along the reef front during each sampling session, and did not revisit areas on consecutive days, in order to avoid both this response and habituation of fishes to my non-threatening presence in areas where I was the only free-diver (e.g., in no-take areas).

3.2.4 Data analysis

All data analyses were performed using MINITAB Version 14, with a significance level of $P \leq 0.05$. FID data was inspected for normality through quantile-quantile plots, while homogeneity of variance was determined using Levene's test. It was necessary to square root transform Acanthuridae FID data in order to meet assumptions of normality and homogeneity. To investigate FID for each family between areas, I used analysis of covariance (ANCOVA), with fish body size, group size and life history stage (Scaridae only) as covariates in the model. Where differences in FID were significant, I used a post-hoc Tukey's test to identify where FID differed. Regression slopes were homogenous for all families. Where fish size or group size was significant in the model, I analysed the effect of these continuous variables across all areas and independently within each area, using linear regression. This was done in order to partition the effects of fishing pressure from either body size or group size. In addition, separate one-way analyses of variance (ANOVA) were conducted to investigate whether there were differences in substrate rugosity between survey areas. Lastly, pre-flight behaviour and refuge choice were analysed using Pearson's Chi-squared to test the hypothesis that fishes in more heavily fished areas would show more wary behaviour when confronted with a spearfisher. For the purposes of analysis the "watch" and "inspect" behaviours were merged.

3.3 RESULTS

Fishing pressure was highest at Mongol (147 ± 38 trips km^{-1} $week^{-1}$), followed by Nusa (110 ± 23 trips km^{-1} $week^{-1}$), then Ungakum (29 ± 8 trips km^{-1} $week^{-1}$). FID increased with fishing pressure in the Acanthuridae, Scaridae, Balistidae and Mullidae (Table 3.1). Acanthuridae and Balistidae showed significant increases in FID at the highest fishing pressure (Mongol) when compared to all other areas (Fig. 3.1). Scaridae and

Mullidae showed a steady trend of increasing FID, with low FID at unfished and lightly fished areas (Kavulik and Ungakum), moderate FID at intermediate fishing pressure (Nusa) and the highest FID at the highest fishing pressure (Mongol). FID did not significantly vary with fishing intensity for Lutjanidae or Serranidae. Rugosity did not differ significantly between grounds (One-way ANOVA; $F_{3,36} = 1.74$, $P = 0.176$), with a mean value across all areas of 2.83, indicating moderately complex reef systems in each area.

Table 3.1 Analysis of covariance (ANCOVA) results of flight initiation distance (cm) with fishing pressure as a fixed factor and fish body size (cm TL) and group size as covariates

Family (d.f.)	**Factor**	***F***	***R*²**	***P***
Acanthuridae (3, 158)	fishing pressure	35.38	0.618	***
	body size	43.88		***
	group size	10.94		**
Scaridae (3, 234)	fishing pressure	47.65	0.504	***
	body size	66.81		***
	group size	1.05		0.306
	life history stage	1.79		0.149
Balistidae (3, 56)	fishing pressure	5.26	0.357	**
	body size	22.51		**
	group size	0.04		0.845
Lutjanidae (3, 75)	fishing pressure	1.86	0.074	0.143
	body size	3.17		0.079
	group size	0.14		0.709
Mullidae (3, 76)	fishing pressure	18.08	0.487	***
	body size	10.70		**
	group size	2.01		0.160
Serranidae (3, 41)	fishing pressure	2.30	0.224	0.092
	body size	10.15		**
	group size	1.20		0.965

[a] *** = $p < 0.001$; ** = $p < 0.01$ and; * = $p < 0.05$

Overall, FID ranged from 27 to 722 cm. When compared to the maximum effective range of spear guns used in this region (310 cm) (Feary et al. 2011) only the Lutjanidae had a mean FID greater than spear gun range at all levels of fishing pressure, while Serranidae mean FID was never greater than spear gun range (Fig. 3.1). Only at the highest fishing pressure did other families show mean FID greater than maximum effective spear gun range (Fig. 3.1).

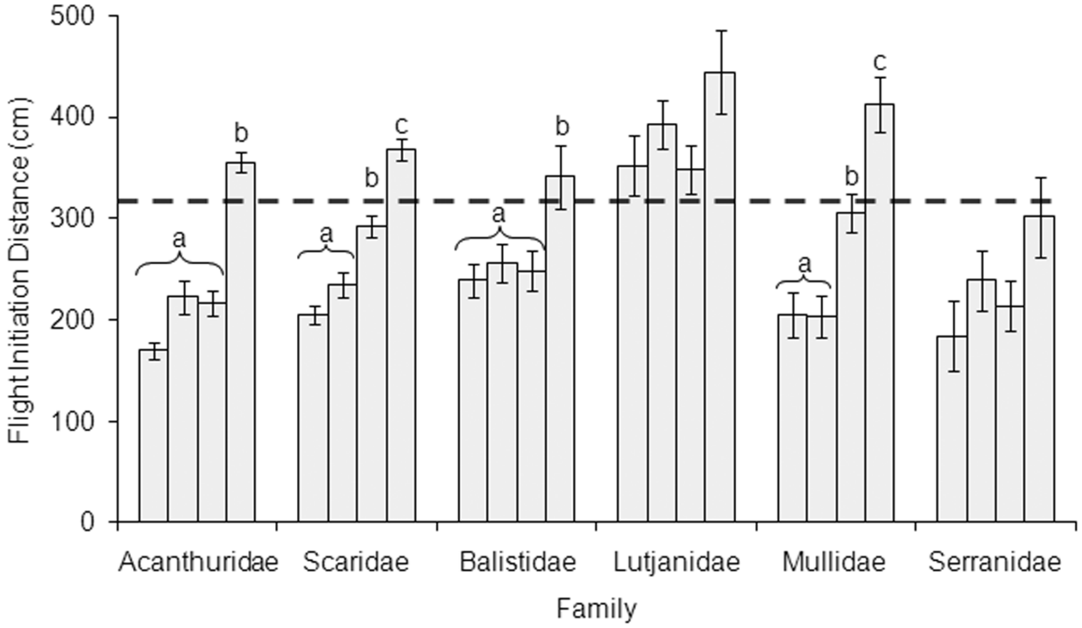

Figure 3.1 Mean flight initiation distance (FID) (cm ± S.E) at each fishing ground for six coral reef fish families. FID was estimated for individuals of six families of coral reef fishes at four different fishing pressures. From left to right within each family, bars are: Kavulik NTR (no fishing); Ungakum (low fishing pressure); Nusa (intermediate fishing pressure); and Mongol (high fishing pressure). If significant differences existed in FID within families at different fishing grounds, grounds were grouped by similarity (a, b and c). Dashed line is maximum distance at which rifle-style spear guns used in New Ireland province are considered effective [approximately 310 cm, Feary et al. (2011)].

All families except Lutjanidae showed a significant effect of fish body size on FID (Table 3.1). Linear regression analysis across all areas indicated that for all families, greater body size was predictive of greater FID (Fig. 3.2). When linear regression analysis was conducted for each family partitioned by fishing area, there was no significant relationship between fish body size and FID for the majority of families surveyed in unfished and lightly fished areas (Table 3.2). The heavily spearfished Acanthuridae and Scaridae, showed a significant relationship between body size and FID at higher fishing pressures, while the less heavily spearfished families only showed a significant relationship with intermediate fishing pressure (Balistidae and Serranidae), and at the highest fishing pressure (Mullidae) (Table 3.2). Group size only had a significant effect on FID for Acanthuridae (Table 3.1). Linear regression analysis for group size and FID for Acanthuridae indicated a significant relationship for all areas combined ($R2 = 0.091$, $F_{1,162} = 17.28$, $P < 0.001$) (Fig. 3.3), but not within grounds (Table 3.2). There was no effect of life history stage on FID of Scaridae (Table 3.1). Pre-flight behaviour varied among families (Fig. 3.4), but only Acanthuridae and Mullidae showed changes in pre-flight behaviour with increasing fishing pressure. Chi-squared tests indicated that least-wary behaviour (“inspect/ watch”) showed significant differences among areas for Acanthuridae ($\chi2 = 39.36$, d.f. = 9, $P < 0.001$). Within this family, focal fishes least-wary behaviours (“watch/inspect”) became less frequent as fishing pressure increased, while the more-wary behaviours (“orientation” and “tacking”) became more frequent (Fig. 3.4a). Mullidae showed a similar response to increased fishing pressure ($\chi2 = 39.55$, d.f. = 9, $P < 0.001$), with least-wary behaviour decreasing as fishing increased (Fig. 3.4e). Although there was no significant difference in pre-flight behaviour between fishing areas for Serranidae, this family exhibited less-wary behaviours, even at the highest fishing pressures (Fig. 3.4f).

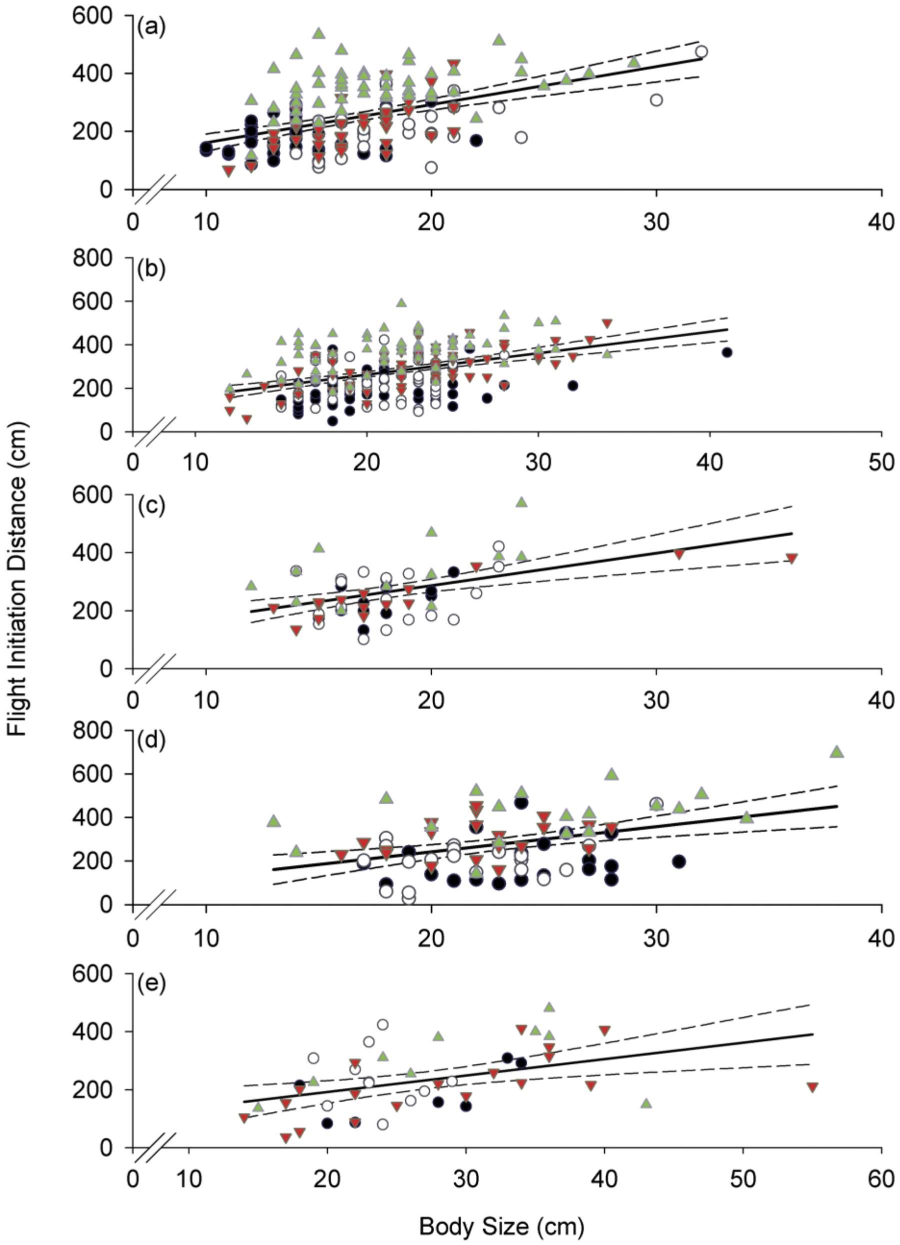

Figure 3.2 Effect of body size (cm TL) on flight initiation distance (cm). Flight initiation distance plotted against fish body size for: (a) Acanthuridae; (b) Scaridae; (c) Balistidae; (d) Mullidae; and (e) Serranidae. Black circles, open circles, inverted red triangles and upright green triangles represent Kavulik NTR (no fishing), Ungakum (low fishing pressure), Nusa (intermediate fishing pressure) and Mongol (high fishing pressure) fishing grounds, respectively. Solid lines are significant linear regression across all grounds and dotted lines are 95% confidence intervals. For significance and R^2 values see Table 3.2. Note that scales differ on both X and Y-axes.

Table 3.2 R^2 values of linear regression analysis of flight initiation distance with body size (cm TL) and group size reported by family and fishing ground

	Kavulik	**Ungakum**	**Nusa**	**Mongol**	**All**
Body Size					
Acanthuridae	0.055	0.296**[a]	0.347***	0.139**	0.216***
Scaridae	0.156**	0.038	0.435***	0.188***	0.179***
Balistidae	0.245	0.060	0.762***	0.295	0.243***
Mullidae	0.024	0.173	0.047	0.244*	0.155***
Serranidae	0.415	0.026	0.315**	0.151	0.190**
Group Size					
Acanthuridae	0.015	0.027	0.064	0.060	0.091***

[a] *** = $P < 0.001$; ** = $P < 0.01$ and; * = $P < 0.05$

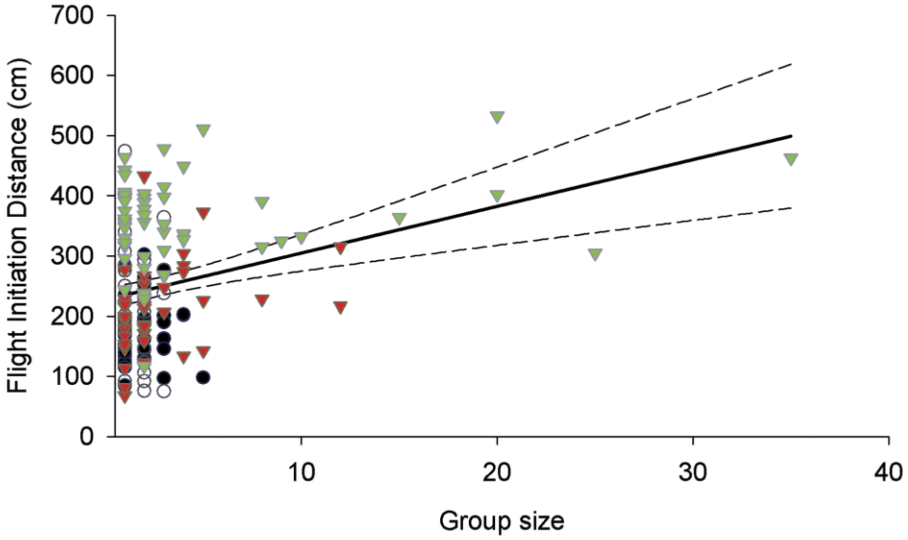

Figure 3.3 Effects of group size on flight initiation distance of Acanthuridae. Group size (number of individuals) plotted against FID (cm) for Acanthuridae. Black circles, open circles, red triangles and green triangles represent Kavulik NTR (no fishing) Ungakum (low fishing pressure), Nusa (intermediate fishing pressure) and Mongol (high fishing pressure) fishing grounds respectively. Solid line is significant linear regression across all grounds and dotted lines are 95% confidence intervals. For significance and R^2 values see Table 3.2.

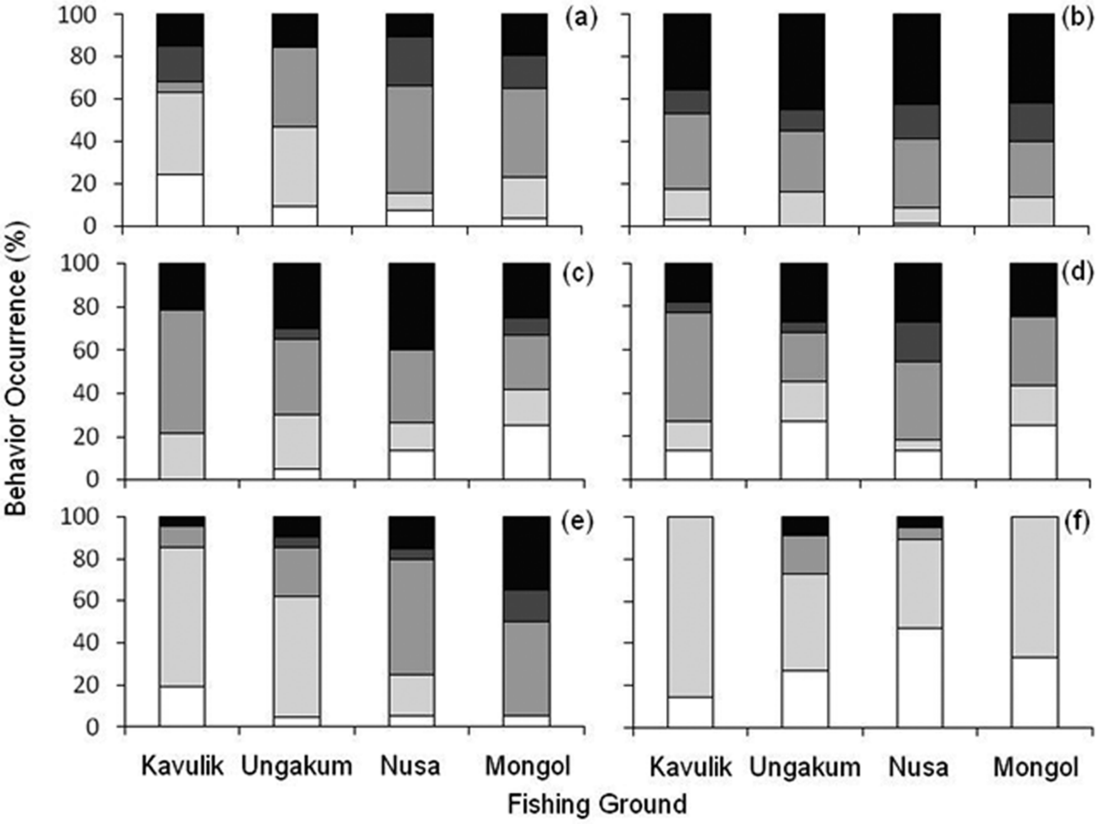

Figure 3.4 Pre-flight behaviour of six reef fish families across four fishing grounds with different fishing pressures. Total occurrence (%) of fishes displaying each category of pre-flight behaviour for: (a) Acanthuridae; (b) Scaridae; (c) Balistidae; (d) Lutjanidae; (e) Mullidae; and (f) Serranidae across four reef areas in Papua New Guinea. Darkest shading indicates no notice behaviour, followed by tacking away, orientating towards refuge, watching, and inspecting as shading becomes lighter

3.4 DISCUSSION

Predator escape theory predicts that as intrinsic level of threat increases in an organism's surroundings, wariness (e.g., FID) will also increase (Cooper & Frederick 2007). This is supported by both experimental studies (Huntingford & Wright 1989; Botham et al. 2008) and field observations (Thiel et al. 2007; Feary et al. 2011) I found that this prediction also holds true in the context of increasing human predation on coral reef fishes, although the behavioural response of fishes to increasing fishing pressure varied by family, and with target status. For example, Acanthuridae and Scaridae, which are the 1st and 3rd most commonly spearfished families in the region (McClanahan & Cinner 2008), showed the highest sensitivity to increased fishing pressure, while Lutjanidae and Serranidae, both of which are primarily caught by hook and line and more rarely caught by spear gun, showed no significant changes in FID between fishing pressures. This concurs with FID estimates for *Lutjanus gibbus* in a previous study in PNG (Feary et al. 2011). Serranidae, by contrast, showed a FID less than the effective range of spear guns at all sites. This lack of wariness may be due to the Serranidae being some of the predominant natural predators on coral reefs, and the low number of natural predators for this family (Parrish 1987), or due to territorial defence postures to perceived competitors (Shpigel & Fishelson 1991).

I found little difference in FID between Kavulik NTR and the low fishing pressure area (Ungakum) across all families in this study, which could have several plausible explanations. First, these similarities could be explained by poaching occurring in the Kavulik NTA. However, the NTA is situated directly in front of the village, which facilitates monitoring (McClanahan & Cinner 2008), and community members report high compliance. Consequently poaching is an unlikely explanation for the similarities in FID between Kavulik and Ungakum. A second, alternative explanation could be the low levels of fishing at Ungakum. Both Ungakum and Kavulik are exposed to the northwest monsoon, which blows from November to April. During this time, fishers rarely venture beyond sheltered lagoonal waters (FAJ personal observation); fishing grounds at Ungakum may only be fished for six months of the year, and may not have been regularly fished prior to the study commencing due to unseasonably bad weather. Therefore, the impact of fishers within the Ungakum fishing area may not be high enough for wariness of fishes to be impacted, and subsequently FID to be affected. A third likely, but unconfirmed explanation is that similarities in FID between the two areas may be associated with the age of the Kavulik NTR (~2 years at the time of this study) relative to age of the fish population. Prey fishes are able to gather information about the threat context in which they are present through both experience and social learning (Brown & Laland 2003), and recall of predator attributes has been shown to occur after a gap of two years between encounters in minnows (Magurran 1990). *Ctenochaetus striatus* individuals surveyed at Kavulik would be between 5 and 10 years of age (Trip et al. 2008), while the species of Scaridae surveyed are predicted to be from 3 to 5 years old (Choat et al. 1996). Thus, the relatively recent no-take status at Kavulik means that fishes with previous experience of human predation, and consequently higher FID, were likely to still be present within its boundaries. At this point, it is not known how long fishes recall threats and adjust their FID accordingly. Future research into recall of appropriate flight response will be necessary to confirm this potential explanation.

The broad results from this study (that FID in fishes increased with fishing intensity) are consistent with previous research, but some details differ. In particular, Feary et al. (2011) reported relatively greater FID within areas open to fishing for all target fishes than estimated in the present study (with the exception of the Acanthuridae). Likewise, estimates of Scaridae FID were lower than either this study or by Feary et al. (2011), both inside and outside a 26 year old NTA in Barbados (Gotanda et al. 2009); the latter may be explained by low exploitation pressure in fished areas near the Barbados NTA (Chapman & Kramer 1999) compared to fished areas in Papua New Guinea. Differences in approach technique may make direct comparisons between studies difficult. The methods of approach used in this study were designed to emulate a spearfisher. These included descending away from the target fish and keeping flat and close to the substrate. These techniques may reduce the distance at which a fish becomes aware of the approaching observer and therefore initiates flight; such techniques were not used in either Gotanda et al. (2009) or Feary et al. (2011). Although I found no differences in FID between SCUBA and free diving in Chapter 2 (Januchowski-Hartley et al. 2011), reports show that fishes can learn to associate the noises generated by SCUBA equipment, or the appearance of divers, with increased food availability (Chapman et al. 1974; Cole 1994). Differences in exploitation history, tourism use and human density between geographic locations could be driving these inter-site differences.

At no/low fishing pressures, size was not a factor explaining variation in FID, but at higher fishing pressures this factor became significant in explaining FID. The role of body size in determining FID in fish remains poorly understood (Domenici 2010). Optimal fitness theory predicts an increase in an animal's FID with increasing levels of initial fitness at the start of an encounter (Warner 1998; Cooper & Frederick 2007). In fishes, greater fitness (residual reproductive value) is closely related to size, and a larger individual should therefore flee earlier in an encounter with a predator than smaller individuals. However, there is still conflicting evidence for the application of this theory to coral reef fishes. For example, body size in Caribbean parrotfish was the largest single determinant of increases in FID (Gotanda et al. 2009), while within Indo-Pacific reef fishes body size was unimportant in determining FID (Feary et al. 2011), and has been shown to be negatively correlated with reaction distance (the distance at which an animal shows awareness of a predator, not flight - Helfman 1998). Here I have reported results that, while supporting the theoretical role of body size on FID, indicate that the relationship between body size and FID varies with fishing pressure.

The eco-morphology of predator/prey relationships should be taken into account when considering how body size may impact FID (Gill 2003). Smaller prey is more cryptic, harder to identify, and metabolically less profitable to target than larger sized prey (Gill & Hart 1994). These attributes are likely to reduce attractiveness of prey to predators, and result in lower prey FID (Ydenberg & Dill 1986). As fishes grow larger, their locomotive ability grows, and their ability to avoid a predator increases, which potentially decreases FID (Domenici 2002). Predator prey-size preference is also influential; fishes generally tend to consume prey whole (Gill 2003), which places restrictions on the upper limit of prey size they can ingest. For example, a study on the reaction of a small coral reef fish (*Dascyllus trimaculatus*) to models of a predator, demonstrated that larger individuals were less wary (Helfman 1989), possibly because they are larger than can be handled by the size of predator.

The optimal size of prey for a predator is when prey body depth ~ 0.6 gape width (Gill & Hart 1994), although during a food deficit, predators may take larger prey (Gill 2003). Therefore, I hypothesize that FID will slowly increase with body size until body depth exceeds 0.6 gape width of the largest predator before: 1) remaining constant; or 2) decreasing as predation becomes less common due to increased handling time. Due to depletion of reef sharks (Robbins et al. 2006; Graham et al. 2010), predation escape via increased body size in coral reef fishes may be increasingly common, or may be occurring at lower prey body sizes. Given this assumption, I would not expect a significant impact of body size on FID in NTRs, a hypothesis supported by both this study and Feary et al. (2011). In fished areas however, humans may play a similar role to sharks by targeting larger fishes. Thus, FID would likely increase with body size, as reported here and in the Caribbean (Gotanda et al. 2009). This may explain the non-significant impact of FID where fishes' exposure to fishing is low, but the increased impact when exposure to fishing is higher. In fact, spearfishers may preferentially target larger fishes due to increased body depth providing a greater target area. This may partially explain why the "taller" bodied Acanthuridae make up a large proportion of the spearfishing catch (McClanahan & Cinner 2008). While body-depth may not be a limiting factor in human predation, there are other limits of handling capacity (e.g., power of spear gun, preference for fish size) that may afford a size refuge for fishes in fished areas, but most likely at larger body sizes than found for fishes surveyed in the present study.

There are alternative explanations for increasing FID with increased body size (discussed in Gotanda et al. 2009), including the importance of observer starting distance and increased visual acuity of prey fishes. Observer starting distance can be positively correlated with FID, because prey individuals are aware of predator focus earlier, and for longer (Blumstein 2003). As larger individuals are more easily identified from distance, compared to smaller prey, this may positively bias FID. In my study I controlled for this factor by standardizing starting distance across all fish sizes. Visual acuity of prey fishes may impact FID due to physiological changes with maturity, with visual acuity increasing with body size (McGill & Mittelbach 2006). Similar to Gotanda et al. (2009), I do not believe my results were impacted by differences in visual acuity between different sized fishes, due to all studies being accomplished in clear tropical waters and target fishes being close to or mature adults.

Theoretically, as animals form larger groups both their field of view and total time spent scanning for predators increase (Elgar & Catterall 1981). This leads to higher alertness, identification of predators at greater distances, and a correspondingly increased FID (Ydenberg & Dill 1986). However, within fishes increased group size tends to reduce FID (Stankowich & Blumstein 2005), with risk dilution the primary benefit (Godin 1986; Krause & Godin 1994). Within the present study only Acanthuridae showed increasing FID with increasing group size. This response only occurred across, and not within areas, and could indicate an independent anti-predation response to increased fishing pressure.

This is the first study to examine pre-flight behaviour in the context of increased fishing pressure. I demonstrated that pre-flight behaviour varies by family, but that variance with fishing pressure is not universal, with both trophic group and life history mediated responses. Lower trophic level families (i.e., Acanthuridae, Scaridae) displayed a higher proportion of wary behaviours (i.e., swimming away or immediate flight), while the highest trophic level family (Serranidae) showed almost exclusively less-wary behaviour. The prevalence of immediate flight – the most wary behaviour - in Scaridae may stem from fishes in this study generally being close to, or of terminal phase size, with correspondingly higher initial fitness rewarding increased wariness although life history stage did not influence FID. In addition, while both the Acanthuridae and Mullidae showed the most obvious changes in behaviour across fishing pressure, both families may have different vulnerabilities that drive change in behaviour. Acanthuridae are one of the most heavily targeted families by spearfishers (McClanahan & Cinner 2008), and this status militates against non-wary behaviours being retained at even low fishing pressures. In comparison, Mullidae will rest on corals or rocks during the day, and in the Kavulik NTA one species, *Parupeneus crassilabris*, would often watch and not flee until the observer was within 100 cm, and would return to their perch within 30 seconds, often while the observer was still in the immediate area (FAJ, personal observation). This lack of wariness would make Mullidae an attractive target, despite being arguably a more difficult to target family due to relatively small body depth. Any reduction in the occurrence of this behaviour, making them even more difficult to catch, is likely to have a large impact on frequency of targeting by spearfishers.

The basic prey model of optimal foraging theory predicts that a predator (i.e., in the present case a spearfisher) chooses prey based on profitability (potential energy gain per unit of handling and search time) (Sih & Christensen 2001). This theory suggests that predators will concentrate on the most profitable prey, and as prey abundance decreases (and thus search/handling time increases) will switch to primarily targeting what was previously the next most profitable prey. However, this assumes that all prey are equally vulnerable to capture, which is rarely the case, while profitability will change with consideration of prey attributes (Sih & Christensen 2001). Theoretically, increases in FID in target fishes represent increasing difficulty of capture by spearfishers; therefore as FID increases, reducing the profitability of targeting a particular prey type, fishers will shift target preferences. As preferentially targeted families show higher FID, families with lower catchability due to smaller target areas (e.g., Mullidae) or greater intrinsic wariness (i.e., Mullidae or Lutjanidae) may play a greater role in the fishery; one speculative interpretation of my results may point to some preliminary support for this theory. FID for all but one family exceeded the effective range of spearguns at the highest fishing pressure, while Mullidae and Balistidae FID only differed when the FID of Scaridae or Acanthuridae equalled or exceeded this distance. Whether this is due to prey switching by spearfishers is unclear from my data, but presents an interesting avenue for future research. Currently, knowledge of how subsistence fishers prioritize which fishes they target is lacking. In order to better understand how changes in fish behaviour may influence fisher behaviour, factors that are important in fisher decision making, such as catchability, size, taste preference, cultural factors and ownership rights (Carrier 1981) will need to be explored more thoroughly. I have presented some interesting results that hint at prey switching by fishers due to fish behaviour influencing catchability, and complement predictions that changing FID of fishes can influence the prey choice of fishers.

Here I have presented the most comprehensive assessment to date of fishes' FID in relation to human predation. I have shown that fishes' FID varies with both fishing pressure and target status. Fish body size appears important in determining FID, however the relationship between size and FID of coral reef fishes is more complex than has previously been presented, and both prey and predator eco-morphology needs to be taken into account. While the data I present here indicates that pre-flight behavioural mechanisms may show promise in assessing fished status of some families of coral reef fishes, this behaviour differs markedly across families and trophic groups. There may be scope to integrate FID into assessment of compliance and effectiveness of management of reef fisheries; however, variation in FID between species and geographic location requires local validation of FID prior to implementation as a successful management tool.

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3.6 SUMMARY

- Prey flight decisions in response to predation risk are increasingly being considered in conservation and management decisions in the terrestrial realm, but are rarely considered in marine systems.

- This field-based study was conducted along a gradient of subsistence fishing pressure in Papua New Guinea to examine how fishing pressure was related to pre-flight behaviour and flight initiation distance (FID), and whether FID was influenced by body size (centimetres total length), group size (including both con- and hetero-specific individuals), or life-history phase.

- Fishing pressure was positively associated with higher FID, but only in families that were primarily targeted by spear guns. Among these families, there were variable responses in FID; some families showed increased FID monotonically with fishing pressure, while others showed increased FID only at the highest levels of fishing pressure.

- Body size became a more significant influence on FID at higher levels of fishing pressure. Although family-level differences in pre-flight behaviour were reported, such behaviour showed low concordance with fishing pressure.

- FID shows promise as a tool by which compliance and effectiveness of management of reef fisheries can be assessed.

CHAPTER 4: SPILLOVER OF FISH NAÏVETÉ FROM MARINE RESERVES[3]

4.1 INTRODUCTION

Evidence from both temperate and tropical marine ecosystems suggests that fish behaviour can be substantially altered as a direct response to fishing and protection from fishing (Handegard et al. 2003; Guidetti et al. 2008; Gotanda et al. 2009). Although natural fish behaviours such as aggregation for spawning have been exploited to increase fishery catches (Hamilton et al. 2012), knowledge of how human-induced changes in fish behaviour may influence fisheries and conservation science is sparse. Evidence from recreational angling suggests that learned hook-avoidance behaviour can develop in previously unexploited fishes (Askey et al. 2006). Similarly, lower fish flight initiation distance [FID - how close a human or natural predator can approach a fish before it flees (Ydenberg & Dill 1986)] has been found within no-take marine reserves (NTRs) than in fished locations, suggesting that fishes may be more easily caught by spearfishing within marine reserves (Gotanda et al. 2009; Feary et al. 2011). Given that NTRs are a frequently proposed management tool for coral reef fisheries (Russ 2002), it is imperative to understand how alterations in the behaviour of fish targeted by fisheries may influence fishery success.

An important fishery benefit from NTRs is likely to be spillover of adult fish biomass across reserve boundaries into adjacent fishing grounds (Russ 2002). Indeed, there is ample theoretical (Kramer & Chapman 1999; Pérez-Ruzafa et al. 2008) and empirical (McClanahan & Mangi 2000; Abesamis & Russ 2005; Francini-Filho & Moura 2008; Halpern et al. 2009; Goñi et al. 2010) support for density-dependent spillover of

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fishable biomass. For example, predictions of gradients of decreasing fish abundance from inside to outside NTR boundaries, based on fish home-range size and mobility (Kramer & Chapman 1999), have been observed in the field (Kaunda-Arara & Rose 2004; Abesemis et al. 2006b). However, recent diffusion models predicting fish abundance, biomass and fishery yields across boundaries of reserves (Halpern et al. 2009) assume that fishes do not vary in catchability, an assumption challenged by differences in FID both inside and outside NTRs, and at different levels of fishing pressure (Gotanda et al. 2009; Feary et al. 2011; Chapters 2, 3 & Januchowski-Hartley et al. 2011, 2012). I hypothesize that fish FID is also likely to vary in a predictable way across NTR boundaries. I predict that FID will increase, as one moves from reserve to fished areas. Consequently, export of fish naïve to exploitation, and therefore with greater catchability, from NTRs to fished areas may increase access to fishery benefits from reserves.

In this study, I quantify spatial patterns of fishes' naïve behaviour and biomass across the boundaries of three NTRs, and utilise a suite of candidate models (Table 4.1) to describe these patterns. Specifically, I surveyed FID and biomass of two key families targeted by local fishers (Acanthuridae and Scaridae) and one non-target family (Chaetodontidae) across the boundaries of three NTRs and three control 'boundaries' in nearby fished areas in the Philippines. I then compare the spatial extent to which fishes' FID and biomass extend beyond NTR boundaries into fished areas for both real reserves and "control" (fished) areas.

Table 4.1 Candidate ecological equations used to model fish flight initiation distance response across the boundary of marine reserves.

Model	Equation	Ecological Explanation
Linear	$b + md$	FID increases continuously from a minimum FID (b) at a constant rate (m) without limit
Logistic	$\frac{FID_m}{(1 + \left(\frac{FID_m - FID_0}{FID_0}\right) e^{-rd}}$	FID reaches a maximum (FID_m) at a maximum rate (r) through an initial exponential phase; FID_0 is minimum FID inside the NTR
Asymptotic	$FID_m + (FID_0 - FID_m)e^{-rd}$	FID reaches a maximum at a constant rate (r)
Exponential	$FID_0 * e^{rd}$	FID increases from an initial minimum (a) at an exponential rate r without limit
Piecewise Linear	$b_1 + m_1 d$ if $d < s_1$; $(b_1 + m_1 s_1) + m_2(d - s_1)$ for $d > s_1$	FID increases continuously from a minimum FID (b_1), at rate m_1 until distance s, after which it increases at rate m_2

4.2 METHODS

4.2.1 Study sites

Fish FID and biomass of three fish families (Acanthuridae, Scaridae, and Chaetodontidae) were surveyed from 200m inside to 200 m outside one boundary at each of three 6-10 hectare NTRs in the Bohol Sea area of the Philippines: Apo Island (9°84' N, 123° 81' E), Tandayag (9° 27' N, 123° 14' E), and Tubod (9° 8' N, 123°30' E); and across artificial "boundaries" at three fished control areas (Fig. 4.1). At Apo Island and Tubod NTRs, I chose control areas that were situated on continuous reef within the fishing grounds of the communities adjacent to the NTRs, separated by at least 750 m from the NTR. Tandayag has no suitable adjacent fished reefs because reefs on the coastline of Negros Oriental are patchy, and often under protection (Stockwell et al. 2009). Thus I chose the closest available fished site down the coast (~ 40 km) with sufficient contiguous habitat.

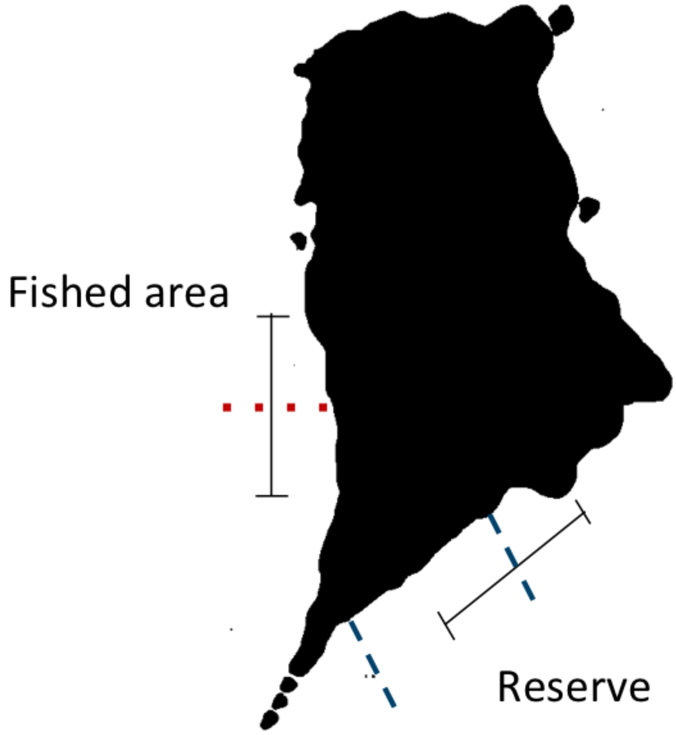

Figure 4.1 Schematic of one example NTR/control pair. The red dotted line is a artificial boundary established within a fished area, the dotted blue lines are boundaries of the extant NTR.

The spatial extent of the sampling was chosen based on previous work on Philippine reefs for these families, which showed that NTR effects can dissipate at scales of hundreds of metres (Abesemis et al. 2006b). At the time of the study, fishing had been effectively excluded from these NTRs for twenty-nine (Apo), six (Tubod) and five (Tandayag) years. While “drive-in” gill nets (where swimmers attempt to scare fish into a net) and hook and line are the primary fishing gears in these areas, spear guns are also commonly used (Abesamis et al. 2006a). Acanthuridae and Scaridae are both abundant on these reefs, targeted by local fisheries (Alcala et al. 2005; Abesamis et al. 2006a) and have shown increases in FID in response to increased fishing pressure (Feary et al. 2011; Chapter 3 & Januchowski-Hartley et al. 2011). While there are life history and behavioural differences between the target and non-target families (e.g., the dependence of Chaetodontidae on live coral as a resource), fisheries in the region encompass the majority of families on coral reefs limiting my choice of control families. I chose the Chaetodontidae because they rarely occur in fishery catches (although Chaetodontidae may be harvested for the aquarium trade, semi-formal interviews with fishermen did not reveal any aquarium harvest operations in my study areas), and are sufficiently abundant on reefs to use as a control fish group.

4.2.2 Fish behaviour and reef community surveys

I estimated fish FID via free diving, imitating spearfisher behaviour as described in Chapter 2 (Januchowski-Hartley et al. 2012). I recorded FID, species and total length (TL) for fishes > 15 cm TL in the fishery target families. This minimum size limit for the FID estimation was adopted because fishes smaller than this are unlikely to be targeted by the fishery. For the Chaetodontidae, individuals were targeted within the size range 10-18 cm TL. It was not feasible to survey only individuals > 15 cm TL due to the smaller maximum attainable sizes of species within this family. I considered flight to have occurred when the fish increased its swim speed to greater than my approach speed, either away, or into a refuge in the substrate. In order to estimate distance from the NTR or control boundary, each area was delineated into eight 50 m long sections (0-50 m, 50-100 m, 100-150 m and 150-200 m inside and outside the boundary) using 50 m tapes. FID estimates took place within visual distance of the tape, and distance from the boundary was estimated by drawing a perpendicular line from the marker at the point at which the fish fled, to the tape. FID was estimated for a minimum of four individuals of each family per 50 m section of reef (see Table 4.2 for sample sizes and species list).

I counted all individuals > 15 cm TL of the Acanthuridae and Scaridae and > 10cm TL of the Chaetodontidae within three 7 m radius point counts (Jennings et al. 1996) at nine distances from the boundary at each area (200 m, 100 m, 50 m, 25 m from the boundary both into and out of the NTR, and at the boundary). Fish were identified to species and size was estimated to the nearest cm TL. Larger mobile species and individuals were counted first, and any individual that left and re-entered the point count area was only counted once. Reef topology resulted in only two point counts being conducted at some sites. All data were collected by the same observer (FAJ). I converted fish length and abundance data to biomass using published length-weight relationships (Froese & Pauly 2011). Because habitat complexity and coral cover can affect both FID (Gotanda et al. 2009) and fish biomass (Friedlander & Parrish 1998), I assessed topographic complexity of the reefs and coral cover using a six point scale for the former (Polunin & Roberts 1993), and line intercept transects for the latter at the location of each fish point count.

4.3.3 Data analysis

Prior to testing the suite of models across NTR boundaries, I first established whether there was a significant relationship between distance from the NTR boundary and fish FID by performing linear regressions for each family inside and outside each NTR. FID was weighted using the residuals of a linear regression of FID and fish length at each area in order to control for increased FID with size (Chapter 3 & Januchowski-Hartley et al. 2011) prior to regression. I found that for all families at all NTRs there was no relationship of FID with distance inside the reserves. For both Acanthuridae and Scaridae I found a significant effect of distance on FID outside the NTR at two of the three NTR areas (Table 4.3). Five potential models were

Table 4.2 Species and number of individuals for which flight initiation distance was estimated at each area.

	No-take reserve			Control		
	Apo	*Tandayag*	*Tubod*	*Apo*	*Tandayag*	*Tubod*
ACANTHURIDAE						
Acanthurus leuococheilus	-	1	-	-	-	-
Acanthurus lineatus	-	1	-	1	-	-
Acanthurus nigricauda	12	3	10	-	2	-
Acanthurus pyroferus	1	7	-	-	5	1
Ctenochaetus striatus	18	20	25	30	17	28
Naso lituratus	-	-	2	9	-	2
Naso unicornis	1	-	-	3	1	1
Naso vlamingii	2	1	-	-	-	-
Total	**34**	**33**	**37**	**43**	**25**	**32**
CHAETODONTIDAE						
Chaetodon adiergastos	2	2	-	-	1	-
Chaetodon auriga	6	-	-	-	2	1
Chaetodon baronessa	1	6	6	4	1	5
Chaetodon ephippium	2	-	-	-	-	-
Chaetodon kleinii	1	2	2	2	2	2
Chaetodon lineolatus	2	-	-	-	-	-
Chaetodon lunula	2	2	1	2	3	1
Chaetodon lunulatus	1	2	9	4	-	10
Chaetodon melanotus	3	-	-	3	-	-
Chaetodon ocellicaudus	-	4	1	1	-	-
Chaetodon ornatissimus	-	-	-	-	2	-
Chaetodon oxycephalus	-	-	1	-	-	-
Chaetodon octofasciatus	-	2	-	-	-	-
Chaetodon punctatofasciatus	-	-	1	-	-	1
Chaetodon rafflesii	3	5	3	2	-	3
Chaetodon reticulatus	-	-	-	-	-	2

Table 4.2 cont.

	No-take reserve			**Control**		
	Apo	*Tandayag*	*Tubod*	*Apo*	*Tandayag*	*Tubod*
Chaetodon speculum	1	-	-	-	-	-
Chaetodon trifascialis	1	-	-	1	-	-
Chaetodon ulietensis	2	-	-	1	-	-
Chaetodon unimaculatus	1	1	-	4	2	-
Chaetodon vagabundus	3	1	3	5	7	5
Heniochus varius	1	5	4	5	5	2
Total	**32**	**32**	**32**	**34**	**25**	**32**
SCARIDAE						
Chlorurus bleekeri	27	14	20	17	11	18
Chlorurus bowersi	5	-	-	1	-	1
Chlorurus sordidus	2	7	-	2	1	1
Scarus dimidiatus	7	3	8	10	9	5
Scarus flavipectoralis	-	-	-	1	-	-
Scarus forsteni	-	-	-	1	-	1
Scarus frenatus	-	-	-	1	-	-
Scarus ghobban	-	0	1	-	-	1
Scarus niger	8	8	5	19	1	5
Scarus prasiognathos	2	-	-	-	1	-
Scarus psittacus	-	-	-	2	1	-
Scarus rivulatus	-	-	1	1	1	-
Scarus rubroviolaceus	-	-	1	-	-	-
Total	**51**	**32**	**36**	**54**	**25**	**32**

assessed to describe the spatial pattern of FID change across the boundaries of marine NTRs: linear, logistic, asymptotic, exponential and piecewise linear (Table 4.1).I fitted nonlinear models using maximum likelihood of the nonlinear regression (nls) routine in R 2.13.1, and piecewise models using the segmented function which tests for the existence of possible breakpoints and differences in slopes of linear models (R Development Core Team 2011). The starting value of the parameter FID_o (FID of a fish never exposed to fishing) was estimated as the minimum FID of the innermost 50 m section at each area, and fitted using a non-parametric bootstrap method (R = 9999). The parameter FID_m was the maximum FID for a specific area and family. If a breakpoint was evident in the piecewise models, I used the Davies Test to examine significant differences in slope. If a breakpoint was not evident, or if differences between slopes were not significant, the piecewise model was removed from further analysis. For each model, I calculated the proportion of the variation explained using an approximation for R^2, where R^2 is equal to 1 minus the residual sum of squares of the model over the total sum of squares. I also calculated a goodness of fit statistic (GOF) using a likelihood ratio test: $LRT = -2[\log_e(L_0) - \log_e(L_M)]$ which is approximately χ^2 with $k - 1$ degrees of freedom, where k is the number of parameters in the model, L_0 is the likelihood of the null model (no parameters) and L_M is the likelihood given the model used (McClanahan *et al.* 2007b). If GOF < 0.05 and if the percentage variation explained was > 10%, I considered the model to fit appropriately. I selected the best-fitting model using Akaike's Information Criterion corrected for small sample sizes (AICc), where the model returning the lowest AICc value was considered to have the majority of support if it was > 2 AICc values lower than the next lowest model (Burnham & Anderson 2002). If two or more models were within 2 ΔAICc of the highest ranked models, I selected the model with the highest R^2 value. Each model fit was plotted using the loess smoother function in R.

Table 4.3 Results of linear regression of fish flight initiation distance weighted by size inside and outside of no-take reserves and control areas for all families

Family	Area	Location	*F*	*p*	R^2	d.f.
Reserve						
Acanthuridae	Apo	Inside	1.43	0.241	0.087	1, 16
		Outside	5.06	0.042	0.280	1,14
	Tandayag	Inside	0.03	0.871	0.002	1,16
		Outside	0.09	0.770	0.007	1, 14
	Tubod	Inside	0.34	0.570	0.021	1, 17
		Outside	13.44	0.002	0.442	1, 18
Scaridae	Apo	Inside	1.11	0.302	0.046	1, 24
		Outside	4.66	0.041	0.163	1, 25
	Tandayag	Inside	0.48	0.499	0.033	1, 15
		Outside	6.53	0.023	0.318	1, 15
	Tubod	Inside	0.00	0.959	0.000	1, 16
		Outside	1.71	0.209	0.097	1, 15
Chaetodontidae	Apo	Inside	2.15	0.164	0.133	1, 15
		Outside	0.49	0.494	0.034	1, 15
	Tandayag	Inside	0.03	0.856	0.002	1, 15
		Outside	1.04	0.326	0.069	1, 15
	Tubod	Inside	0.35	0.562	0.027	1, 15
		Outside	2.99	0.106	0.176	1, 15
Control						
Acanthuridae	Apo Control	Inside	0.91	0.350	0.038	1, 24
		Outside	2.32	0.147	0.127	1, 17
	Tandayag Control	Inside	0.20	0.668	0.028	1, 8
		Outside	0.63	0.442	0.042	1, 15
	Tubod Control	Inside	1.29	0.274	0.085	1, 15
		Outside	0.73	0.407	0.050	1, 15
Scaridae	Apo Control	Inside	0.25	0.618	0.008	1, 34
		Outside	1.25	0.273	0.041	1, 30

Table 4.3 cont.

Family	Area	Location	*F*	*p*	R^2	d.f
Control						
Scaridae	Tandayag Control	Inside	0.00	0.954	0.000	1, 15
		Outside	1.33	0.268	0.087	1, 15
	Tubod Control	Inside	0.15	0.706	0.001	1, 15
		Outside	0.57	0.462	0.039	1, 15
Chaetodontidae	Apo Control	Inside	0.18	0.677	0.015	1, 15
		Outside	0.21	0.651	0.012	1, 19
	Tandayag Control	Inside	0.48	0.501	0.033	1, 15
		Outside	0.7	0.414	0.048	1, 15
	Tubod Control	Inside	0.12	0.734	0.009	1, 15
		Outside	4.39	0.056	0.253	1, 14

I used a randomisation-based multi-way analysis of covariance (ANCOVA) to determine if there were differences in biomass of Acanthuridae and Scaridae due to NTR locations, management status and benthos. NTR location was treated as a random factor with three levels (Apo, Tandayag, Tubod); management status as a fixed factor (three levels: NTR, adjacent to NTR, control), with rugosity and hard coral cover as covariates. Each recorded fish biomass value was randomly re-sampled with replacement 4999 times to produce an F-value distribution curve based on my data. I then compared the observed F-statistic to this distribution curve. A randomisation-based ANOVA avoids violating assumptions of the theoretical F-value distribution curve and is a more powerful statistical tool (Manly 1997). Where differences were found between management statuses I conducted post-hoc pairwise comparisons using randomized t-tests with a Bonferroni correction.

I fitted logistic decay and linear regression models to fish biomass data for both target families, and selected the best-fit model using the methods described above. The logistic decay model was fitted using the nls routine in R: $B = 1/(1 + e^{S(I-d)})$, where B is the proportion of the mid-reserve biomass, S is the slope of the logistic decay, I is the inflection point, and d is the distance from the NTR boundary (Kaunda-Arara & Rose 2004). I estimated 95% confidence intervals (CI) of parameters (S, I) from nonparametric nls bootstrap methods (R=9999) for each model. B was calculated for each NTR-family combination separately, prior to inclusion in the model. The mean biomass of each control area was also converted to a proportion of the mid-NTR biomass of its paired NTR. The model and CI were plotted using a loess smoother using the loess function in *R*. To determine the spatial extent of spillover of biomass and FID outside the NTR, I estimated the distance at which the modelled FID or biomass reached the mean FID or proportional biomass of the control fished areas. This is likely to be a more realistic measure of the spatial extent of NTR enhancement of fisheries adjacent to NTRs than estimated in other studies, which used the inflection point of a logistic decay curve of catch rate or biomass (Kaunda-Arara & Rose 2004; Abesemis *et al.* 2006b), or a proportion of the maximum or range of catch/biomass at the NTR centre to infer the spatial extent of spillover (Halpern *et al.* 2009). Using the mean biomass of control (fished) areas more accurately approximates the level of biomass that is maintained by normal fishing activities in these habitats.

4.3 RESULTS

Both fish families targeted by the fishery showed linear or weakly exponential increases in FID across the boundaries (from NTR to fished) at all three marine NTRs, demonstrating that naïveté of coral reef fishes to fishing extends outside marine NTR boundaries (Fig. 4.1, Table 4.4). In contrast, the non-target family, Chaetodontidae, showed no change in FID across NTR boundaries (Fig. 4.1, Table 4.3), and none of

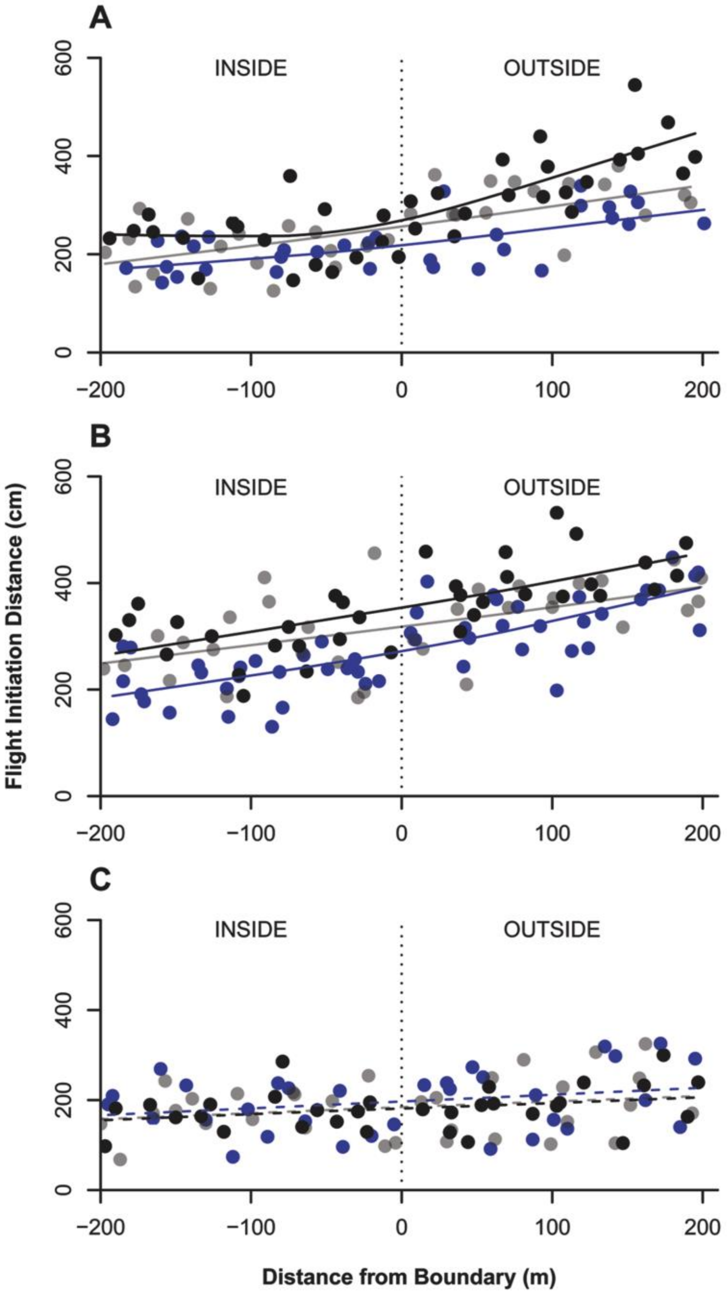

Figure 4.2 Fish flight initiation distance (FID) from 200 m inside to 200 m outside marine no-take reserve (NTR) boundaries for: (*A*) Acanthuridae; (*B*) Scaridae; (*C*) Chaetodontidae. FID is weighted by the residuals of the FID ~ Size relationship and rescaled by mean total length for the family and reserve. Lines represent best-fit models for each family at each NTR; solid lines represent significant relationships between FID and distance, while dashed lines indicate no significant relationship. Black, grey and blue circles and lines represent Tubod, Tandayag and Apo Marine Reserves, respectively. Dotted vertical line indicates marine reserve boundary. See Table 4.3 for results of linear regressions for all families at both reserve and control sites.

the sampled families displayed any trends at any control (fished) "boundary" (Table 4.3). FID for both Acanthuridae and Scaridae reached mean values for control (fished) areas approximately 140 m outside the NTR boundaries (Fig. 4.2, Table 4.5).

Both Acanthuridae and Scaridae biomass showed significant effects of NTR location (multi-way ANCOVA, Acanthuridae: $F_{2,148} = 16.42$, $P < 0.001$; Scaridae: $F_{2,148} = 11.05$, $P < 0.001$) and management status (Acanthuridae: $F_{2,148} = 6.49$, $P < 0.005$; Scaridae: $F_{2,148} = 4.37$, $P < 0.05$). Post-hoc t-tests indicated that for both of the target families there was significantly more fish biomass inside NTRs than in fishing grounds adjacent to NTRs (t-test, Acanthuridae: $P < 0.01$, Scaridae $P < 0.05$), but no differences in fish biomass between fished control areas and NTRs or fished control areas and areas adjacent to reserves.

Fish biomass fitted a logistic decay model across NTR boundaries for Acanthuridae, and a linear regression for Scaridae. (Fig. 4.2, Table 4.5). The mean biomass of control areas ranged from 54% of the mid-NTR biomass (Tubod) to 72% (Tandayag) for Acanthuridae, and from 59% (Apo) to 79% (Tubod) for Scaridae. The distance at which NTR biomass declined to a proportion of the mid-NTR biomass that was similar to the control area mean biomass was 89 m inside the NTR boundary for Acanthuridae, and 57 m inside the NTR boundary for Scaridae (Table 4.5). 95% confidence intervals for the spatial extent of FID spillover and biomass spillover did not overlap (Fig. 4.2).

Table 4.4 Best-fit models of the relationship between fish flight initiation distance with distance from the reserve boundary. See Table 4.1 for definition of parameter terms.

Family	Reserves	R^2	AICc Weight	GOF	Parameters							
					b		95% CI		m		95% CI	
Linear												
Acanthuridae	Tandayag	0.447	0.433	< 0.0001	180.7		(143.74, 217.60)		0.404		(0.236, 0.572)	
Scaridae	Tandayag	0.315	0.424	< 0.001	247		(200.89, 293.09)		0.359		(0.162, 0.556)	
Exponential					FID_o^*		$FID_o^†$	95% CI†	$R^†$		95% CI†	
Acanthuridae	Apo	0.438	0.485	< 0.001	165.7		169.3	(145.6, 194.3)	0.00140		(0.00084, 0.00197)	
Scaridae	Apo	0.587	0.638	< 0.0001	178.3		189.3	(167.4, 212.0)	0.00183		(0.00140, 0.00227)	
	Tubod	0.487	0.503	< 0.0001	258.7		266	(234.1, 299.2)	0.00137		(0.00091, 0.00299)	
Acanthuridae	All	0.404	0.799	< 0.0001	175.3		181.7	(162.6, 201.0)	0.00169		(0.00130, 0.00210)	
Scaridae	All	0.470	0.566	< 0.0001	208.1		219.1	(200.7, 238.3)	0.00165		(0.00134, 0.00198)	
Piecewise Linear					b	95% CI	m_1	95% CI	m_2	95% CI	s_1	95% CI
Acanthuridae	Tubod	0.632	0.656	< 0.0001	247.2	(185.67, 308.82)	-0.150	(-0.797, 0.498)	0.979	(0.620, 1.399)	-33.8	(-102.25, 34.70)

*starting parameter estimated from linear regression

† estimates derived from a non-parametric bootstrap (R = 4999)

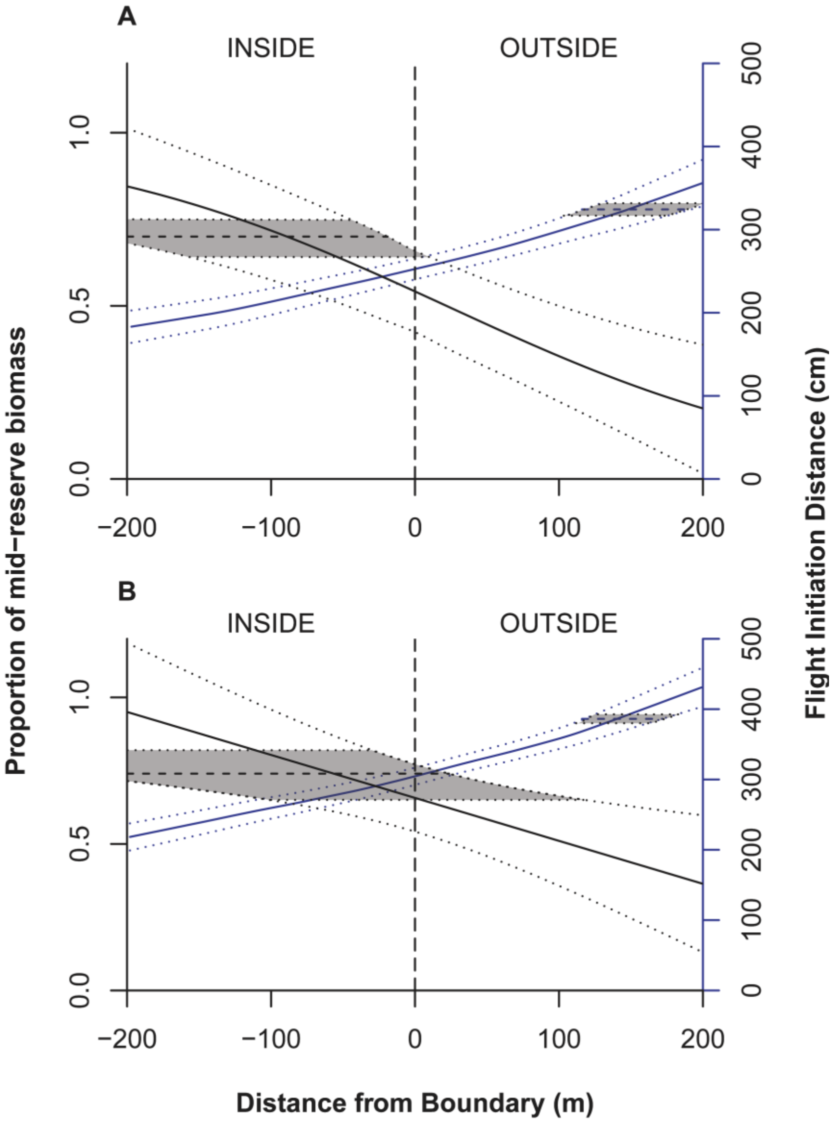

Figure 4.3 Fitted models for flight initiation distance (FID) and fish biomass across no-take reserve (NTR) boundaries. Loess smoothed best-fit models for flight initiation distance (blue lines), and biomass (black lines) against distance from NTR boundary for all NTRs combined (dotted lines are 95% confidence intervals) for: (*A*) Acanthuridae; (*B*) Scaridae. FID is weighted by the residuals of the FID ~ Size relationship and rescaled by mean total length for the family across all NTRs. Vertical black dashed line indicates the NTR boundary; dashed horizontal lines indicate mean FID (blue) and mean proportion of mid-NTR biomass (black) at the control sites. Grey shaded areas indicate where best-fit models intersect with mean ± SE for control FID and biomass.

Table 4.5 Details of best-fit models for pooled Acanthuridae and Scaridae biomass across marine reserve boundaries, and estimates for extent of spillover for both biomass and FID.

Family (model)	***R*²**	***P***	**GOF***	**Slope**	**SE of Slope**	**Distance at which biomass model = biomass of control (m) †**	**95% CI biomass intersection (m) †**	**Distance at which model FID = control FID (m)**	**95% CI of FID intersection (m)**
Acanthuridae (Logsitic decay)	0.155	0.006	0.002	-0.0076	0.0027	-89	(-200‡, 10)	142	(116, 191)
Scaridae (Linear)	0.101	0.006	0.006	-0.0014	0.0005	-57	(-200‡, 117)	142	(118, 172)

* GOF stands for goodness of fit
† negative values are distance inside the boundary of the marine reserve
‡ limit of the spatial scale of this study

4.4 DISCUSSION

I found that there were significant differences in both fish biomass and FID across the boundaries of three NTRs. A key and surprising finding from this study is that the reductions in FID extended beyond NTR boundaries, whereas the increases in biomass did not. For both targeted families, FID increased from inside to outside the reported maximum effective range for spearguns in a similar artisanal fishery in Papua New Guinea (310 cm) (Feary et al. 2011). The lack of a similar trend for the non-fishery family (Chaetodontidae), suggests the observed increase in FID is related to fishing. While increased fish density and larger fishes in areas adjacent to NTRs are mechanisms by which catch per unit effort (CPUE) can be increased (Russ 2002), I provide evidence of a previously overlooked mechanism that may also increase CPUE; increased catchability of naïve fishes.

Increasing FID with distance across the boundary (from NTR to fished) was found at all NTRs, and for both targeted families, suggesting that the export of naïve behaviour may be a general benefit of marine NTRs. A further interesting finding is the suggestion from biomass models that the fishing grounds immediately adjacent to NTRs had lower biomass than control areas. If fishes leaving marine reserves are more catchable, and density of fishes adjacent to reserves is low, any potential increases in fish biomass within reserves may being exported and captured rapidly, which may explain the relatively low biomass observed within the reserves in this study. This result is consistent with “fishing the line” behaviour observed in some NTRs, whereby fishing pressure is heaviest immediately outside NTR boundaries (Kellner et al. 2007; Francini-Filho & Moura 2008; Goñi et al. 2008). While spillover of biomass almost certainly occurs on Philippine reefs, evidence to date is limited to highly vagile fishes (e.g., Carangidae, Scaridae, *Naso vlamingii*) and to relatively few locations (Abesamis & Russ 2005; Alcala et al. 2005; Abesamis et al. 2006b). I suggest that the lack of biomass spillover in my study, and reduced near-NTR biomass compared to fished control areas, may be exaggerated by naïve fishes with lower FID being more easily caught.

Increased wariness outside NTRs could be facilitated through direct experience of a non-fatal encounter with a spearfisher, or through the linking of the visual image of a predator with olfactory cues (i.e., chemical alarm cues released when a spear pierces a fish), with repeated exposures resulting in larger effects (Brown 2003). An alternative mechanism increasing FID outside NTRs could be preferential removal of naïve fishes in fished areas, with density-dependent export of non-wary fish from the NTR maintaining lower FID closer to the NTR boundary. Indeed, spillover of fishes through density dependent mechanisms has previously been demonstrated from my study location (Abesamis & Russ 2005; Abesamis et al. 2006b). However, as distance from a NTR increases, the proportion of the fish population that will have escaped/witnessed a fishing event is expected to increase, leading to FID increasing more gradually with distance away from the NTR boundary. Furthermore, my results suggest that individuals may be highly susceptible to capture if they are exposed to fishing, but have a significant proportion of their home range inside NTRs, thus reducing their FID. As such, anticipated increases in biomass may be slower than predicted by many marine NTR models, especially for more vagile species and in smaller NTRs (Kramer & Chapman 1999).

Interestingly, for at least one target family (Acanthuridae), observed FID changes across NTR boundaries appear to be related to other processes besides short-term boundary crossings related to home range size. The selection of linear and weakly exponential models for Scaridae FID suggests wariness increases proportionally to risk over a spatial scale that is consistent with the moderate vagility of this family (Abesemis et al. 2006b; Welsh & Bellwood 2012). However, the distance from the NTR boundary that Acanthuridae continue to display naïve behaviour is similar to that of Scaridae, despite species in this family being considerably less mobile. For example, Acanthurid species typically have home range diameters < 100 m (Kramer & Chapman 1999; Claydon et al. 2012), compared with home range diameters of several hundred meters for Scarid species (Afonso et al. 2008; Welsh & Bellwood 2012). Although some highly vagile Acanthurid species included in this study (e.g., *Naso* spp.) might be expected to increase the distance outside the NTR that FID is reduced, visual inspection of the data indicated that individuals of these species showed similar FID to other Acanthurids regardless of distance from the NTR boundary. An alternative mechanism for the greater than expected distance that lower FID extends beyond the NTR boundaries for Acanthuridae is density-dependent home-range relocation whereby competitive interactions cause individuals to be displaced towards lower abundances (Kramer & Chapman 1999). Indeed displacement of the home range of fishes from NTRs to adjacent fished areas has been documented from the same location as the current study (Abesamis & Russ 2005), suggesting this is a plausible explanation.

Recent modelling and empirical studies of biomass spillover imply that NTRs can help maintain sustainable fisheries outside their borders (Alcala et al. 2005; Abesamis et al. 2006a; Halpern et al. 2009; Goñi et al. 2010). The spatial extent of this reported spillover has generally been estimated as the distance at which mid-NTR biomass is halved (Kuanda-Arara & Rose 2004; Abesamis et al. 2006b), while here I estimate the extent of spillover by comparison with biomass at adjacent control fished areas. It is likely that the metric I use to estimate spillover is more conservative as fished area biomass appears to generally be greater than 50% of the mid-NTR biomass. Furthermore, little notice has been paid to how behaviour may influence export or accessibility of fishes to a fishery. My results indicate that robust predictions of expected NTR benefits require fish behaviour to be addressed explicitly. Most models assume the rate of fishing mortality (a function of fishing effort, modified by a coefficient of catchability) is constant, or may vary in response to fisher behaviour or management actions (Pérez-Ruzafa et al. 2008; Halpern et al. 2009). While fishing effort can be estimated with some degree of certainty, estimates of how catchability changes are less certain, hindering the adoption of a varying coefficient of catchability into models. While I did not directly measure catchability, I are confident that there is a relationship between FID and catchability based on other studies that have quantified FID changes with fishing pressure (Gotanda et al. 2009; Feary et al. 2011; Chapter 3 & Januchowski-Hartley et al. 2011). For spear guns I hypothesize that the approximately linear increases in FID with distance away from the centre of NTRs will be accompanied by a proportional decrease in catchability until FID exceeds the maximum effective range of spearguns. Incorporating behaviourally mediated catchability into population diffusion models should enable a more accurate estimate of how much NTRs enhance nearby fisheries, and what level of fishing effort is sustainable.

Another possible implication of my results is that fish abundance estimates in and around NTRs could be influenced by FID related behaviour. For example, given the assumption that lower FID increases catchability, some CPUE data could overestimate fish abundance near marine NTRs (Rakitin & Kramer 1996; Goñi et al. 2010). Specifically, the efficiency of spearguns is likely to be improved by reduced FID adjacent to NTRs, with high catches possible despite relatively low abundances. However, passive gears such as fish traps are less likely to be affected by FID. Conversely, results from this study and another (Feary et al. 2011) show that the distance at which reef fish are surveyed using UVC (~ 9 m) exceeds that at which targeted fishes flee (generally < 5 m). Thus, when water clarity provides > 5 m visibility, underwater fish counts should not be affected by differences in FID between NTRs and adjacent fished areas. Clearly, the likelihood that FID related behaviour will influence abundance estimates will depend on both survey methodologies and fishing gears in use.

Reductions in fishing ground area and perceived lost fishing opportunities can make fishers unwilling to support marine NTRs (McClanahan 1999). Indeed, resource user perceptions and access to initial and continuing benefits are key to the sustainability of management projects (Pollnac & Pomeroy 2005). Changes to the catchability of fishes, whether through learning or increased intrinsic wariness, may be particularly important where the utility and/or efficiency of widely utilised management tools (e.g., NTRs) and fishery gears (e.g., spear guns/drive nets) are potentially sensitive to fish behaviour (Cinner et al. 2005; Feary et al. 2011). I have demonstrated that reduced FID spills over NTR boundaries, and thus may provide a previously undocumented benefit to local fishers through greater access to catchable fish. While significant increases in biomass in NTRs may take several years, or even decades, to manifest (McClanahan et al. 2007b), the consistent behavioural response of fishes from NTRs of different ages suggests that behavioural changes may occur more quickly.

My results are primarily applicable to reefs where active gears such as spear guns are common, although these results may also be pertinent to the effectiveness of other active gears such as drive-in gill nets. Spearguns are a widely used, and there are substantial artisanal and recreational fisheries that use this gear. For example, approximately 90% of registered artisanal fishers surveyed in Chile rated spearguns as a highly important fishing gear (Godoy et al. 2010), while the quantity of fish harvested by recreational spearfishing in parts of the Mediterranean is equivalent to 40% of the commercial catch (Lloret et al. 2008). Furthermore, spearguns are an important gear relied upon by communities throughout the Pacific Islands (Cinner et al. 2006; Gillet & Moy 2006; Stoffle & Allen 2012). The results presented here have implications for both predicting accessible fishery benefits from NTRs, and how NTRs and adjacent fisheries should be managed. FID may not be the only anthropogenically induced behavioural change pertinent to fisheries. Changes in refuge choice, or in behaviour prior to flight (Guidetti et al. 2008; Chapter 3 & Januchowski-Hartley et al. 2011), may act to increase catchability of fishes, while other behaviours (e.g., “spill-in” of fishes fleeing high fishing pressures) may reduce diffusion of fishes from marine NTRs (Eggleston & Parsons 2008; Jupiter et al. 2012). I recommend explicit consideration of fish behaviour when predicting fishery impacts of NTRs and gear restrictions on local fisheries, in concert with careful monitoring of fisheries adjacent to NTRs to ensure that the fishery benefits of NTRs are appropriately quantified and managed.

4.5 ACKNOWLEDGEMENTS

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4.6 SUMMARY

- Spillover of adult fish biomass is an expected benefit from no-take marine reserves to adjacent fisheries.
- Here I show how fisher-naïve behaviour in reef fishes also spills over from marine reserves, potentially increasing access to fishery benefits by making fishes more susceptible to spearguns.
- The distance at which two targeted families of fishes began to flee a potential fisher (flight initiation distance - FID) was lower inside reserves than in fished areas, and this reduction extended outside reserve boundaries.
- Reduced FID persisted further outside reserves than increases in fish biomass.
- This finding could help increase stakeholder support for marine reserves and improve current models of spillover by informing estimates for spatial changes in catchability.
- Behavioural changes of fish could help explain differences between underwater visual census and catch data in quantifying the spatial extent of spillover from marine reserves, and should be considered in the management of adjacent fisheries.

CHAPTER 5: FISHERY BENEFITS FROM BEHAVIOURAL MODIFICATION OF FISHES IN PERIODICALLY HARVESTED FISHERIES CLOSURES[4]

5.1 INTRODUCTION

Allowing resource users a greater say in the development and enforcement of rules is thought to contribute toward both social and ecological dimensions of successful fisheries management (Brooks et al. 2012; Cinner et al. 2012). Consequently, there is an increasing movement to engage communities in collaborative management arrangements that allow resource users to develop rules that are appropriate for local social, cultural, and ecological conditions. As part of these collaborative management arrangements, a number of coastal communities have implemented periodically harvested fisheries closures (PHCs) and other temporal area restrictions (Govan 2009; Cohen & Foale 2012). PHCs are areas of fishing grounds where fishing is normally prohibited, but is occasionally permitted for a short period (as opposed to periodic closures, where areas of fishing grounds are normally open, and occasionally closed, or rotational harvests where the area open to fishing rotates on a fixed cycle). Critical questions remain as to whether periodically harvested closures can provide both social and ecological benefits.

There is empirical evidence that periodically harvested or rotational closures can maintain higher fish biomass and larger individuals, particularly of targeted species, than open fished areas (Meyer 2003; Cinner et al. 2005; McClanahan et al. 2006).

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However, additional information about the mechanisms and immediate effects of harvests are needed, particularly as there is potential for periodic harvests to remove a large proportion of standing biomass [e.g., up to 10% of the standing fish biomass in a single day (Cinner et al. 2005)]. If the fish community does not recover in the period between openings, many potential benefits from marine reserves such as spillover of biomass, recruitment subsidy, and increased resilience to stressors may be minimized (Russ 2002; Bellwood et al. 2004). For example in Hawai'i, the 2-year open/2-year closed cycle (later 1-year open/1-year closed) within the Waikiki-Diamond Head Fisheries Management Area probably led to an overall decline in fish biomass in the rotational area over the 24 years of monitoring, despite maintaining higher biomass than open areas (Meyer 2003; Williams et al. 2006). In contrast to Hawai'i, customary periodically harvested closures in Melanesia are often open to fishing for significantly less time (half a day to several weeks (e.g., Cinner et al. 2005; Jupiter et al. 2012)), and some have demonstrated similar or better ecological benefits (e.g., higher fish biomass) than comparable no-take reserves (NTRs) (McClanahan et al. 2006; Bartlett et al. 2009). However, the frequency and intensity of harvest, and the type of fishing activities (i.e., gear choice, target species) may affect different sections of the fish community (McClanahan & Cinner 2008; Jupiter et al. 2012). Understanding which parts of the fish community will be affected, and why, are necessary in order for the effective use of PHCs as a management tool.

Many communities that implement PHCs do so for utilitarian social goals (such as a short-term increase in harvests), which, in addition to metrics such as fish biomass or coral cover, require consideration as indicators of success. For example, some PHCs have the explicit goal of improving harvests by making fishes more approachable (Cinner et al. 2005; Macintyre & Foale 2007). Fishers expect that fishing success (catchability) will increase after an area has been closed as they can now readily approach fish that have lost their wariness to spearfishers (Cinner et al. 2005). This belief is supported by significant evidence from studies of fish flight initiation distance (FID) showing that fishes are less wary of divers in customary PHCs and recently (< 2 years) closed areas than in open fished areas (Feary et al. 2011, Chapter 3 & Januchowski-Hartley et al. 2011). This change in behaviour results in fish that remain outside maximum effective range (MER) of spearguns in fished areas allowing approaches to within MER in closed areas (Feary et al. 2011; Chapter 2, 3 & Januchowski-Hartley et al. 2011, 2012). This implies that these species of fish would be more easily approached and caught in a PHC, than in open fishing grounds. If increased catchability is a product of reduced wariness, rapid depletion of fish biomass that was built-up during the closed period may result during harvests, because fishing pressure is often intense (Cinner et al. 2005; Jupiter et al. 2012). Ecological functions associated with higher fish biomass may also be degraded if biomass fluctuates significantly (McClanahan et al. 2011). Clearly a better understanding of changes in fish behaviour and catch dynamics is important to assessing the efficacy of these PHCs to fulfil both utilitarian and conservation objectives, temporarily increasing fishing efficiency during openings, while maintaining high levels of fish biomass.

Here, I investigate the effect of harvesting events in PHCs in light of these unresolved questions regarding the role of fish behaviour, benefits that can be realized from changes in behaviour, and the effects of periodic harvests on fishery targeted families and total fish biomass. I conducted surveys of FID of two fishery-target families and one non-target family, as well as biomass of all fishes in two PHCs, two NTRs, and two open-access fished areas prior to and after harvest of the PHCs. Specifically, I investigated the following questions. 1) Do PHCs have an effect on fish FID? If so, 2) what is the effect of a harvest on FID? 3) What is the effect of management strategies (NTR; PHC; open fished area) and harvest on biomass of the fish community? 4) Is fish biomass significantly diminished after a harvest event? 5) Is catch per unit effort higher during a harvest event than in normal fishing in open fished areas? And 6) are there impacts on fish catches that can be related to changes in fish behaviour?

5.2 METHODS

5.2.1 *Study sites and management context*

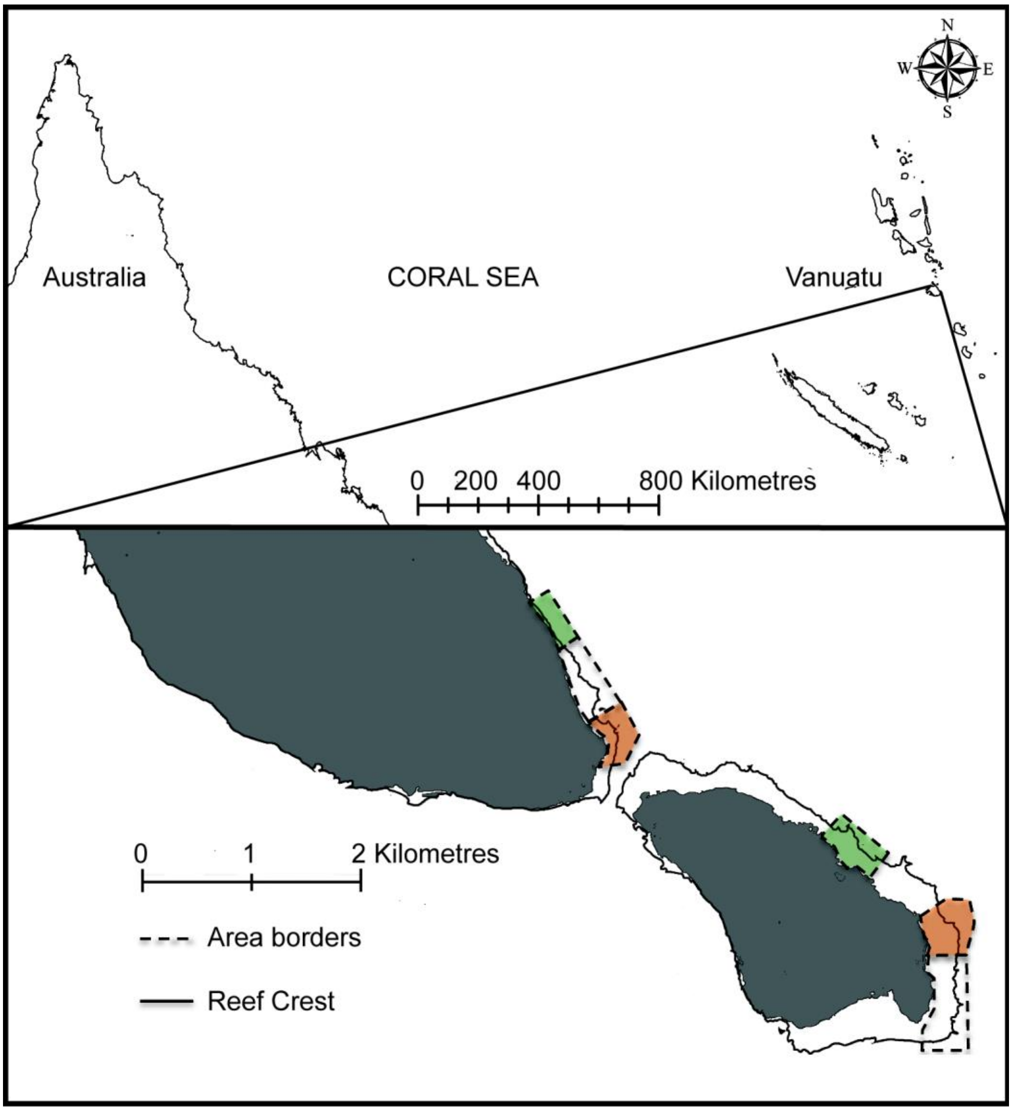

Figure 5.1 Study area in North Efate, Vanuatu, South Pacific. Large dark green areas are the islands of Nguna and Pele, open polygons are open fished areas, green polygons periodically harvested closures, and orange polygons permanent no-take marine reserves.

The six management areas in this study are situated on fringing coral reefs under the customary ownership (i.e., marine tenure) of two communities in the Nguna-Pele Marine Protected Area Network, North Efate, Vanuatu (17°29'S, 168°23'E). Each community has a permanent NTR that has been completely closed to all fishing for at least 6 years (since 2005), a PHC that is open to exploitation for between 1 and 3 days approximately every 6 months (species harvested during this time may be restricted), and areas open to fishing (Fig. 5.1). One of the PHCs in this study had been established since 2006 while the other had been under periodic harvest status for approximately 18 months (since mid-2010) prior to this study. Both areas had been harvested for either 3 or 7 days approximately 6 months prior to this study. All NTRs and PHCs enclosed between 8 and 10 hectares of fringing reef, while open fished areas enclosed between 14 and 16 hectares of reef. In both communities fished areas of at least 300m of linear reef separated NTRs and PHCs. During the study period (November – December 2012) both PHCs were opened for 3 days to spearfishers targeting all fish species. To answer the research questions above, surveys of fish behaviour and fish and benthic communities were conducted in all management areas pre and post-harvest of the PHCs, using a before-after-control-impact-pairs design (summarized in Table 5.1). Creel (fishery landings) surveys were conducted during regular fishing activities and periodic harvest events. The research agreement with the communities stipulates that resultant publications would not directly identify or name the communities. Therefore, the communities will be referred to as "Community 1" and "Community 2" when necessary.

5.2.2 Effects of periodically harvested closures on fish behaviour

All in-water surveys were conducted between 8:30 am and 5:00 pm. I estimated FID for individuals in three families (two fishery targets: Acanthuridae and Scaridae; one non-target: Chaetodontidae) in each of the three types of management in both communities, prior to openings of PHCs, and immediately after the harvests were completed. I only sampled species that occurred in the fishery catch for each target family, and sampled similar species from each area/time combination. A pre-study power analysis conducted on FID data for Acanthuridae and Scaridae obtained from similar reefs in Papua New Guinea (Chapter 3 & Januchowski-Hartley et al. 2011) indicated a sample size of 12 fishes per area/time combination would have a power of > 0.9 for both families. For the non-fishery target Chaetodontidae, power analysis on FID of this family from Philippine no-take reserves and fished areas (Chapter 4 & Januchowski-Hartley et al. 2013b) indicated over 300 individuals would need to be surveyed per area /time combination to obtain a similar power. Due to the non-target status of this family, the small effect of protection demonstrated from a relatively large sample size (> 100 individuals) in the Philippines, and time constraints, I sampled same number (12) of fishes per area/time combination as for the target families.

Table 5.1 Summary of indicators and methods used to answer research questions.

Indicator	*Method*	*Analysis*	*Research Questions*
Flight initiation distance (FID)	FID surveys of target and non-target families in all areas pre- and post harvest	Three-way orthogonal ANOVA	1, 2, 6
Fish biomass and abundance	UVC of fish community in all areas pre- and post-harvest	Three-way orthogonal ANOVA	3, 4, 6
Catch per unit effort	Creel surveys of normal and periodic harvest fishing trips	Two-way ANOVA	5, 6
Catch composition	Creel surveys of normal and periodic harvest fishing trips	χ-squared test of number of individuals of families in the catch	6

I obtained all estimates of FID through free diving. I identified a focal fish from the surface, before descending to approximately the same depth at > 8m distance. I than swam towards the fish at a steady speed. When the fish fled, I placed a marker on the substrate directly below my face, and then on the substrate directly below where the fish was when it fled. The distance between these markers was measured, and considered to be FID (see Chapter 2 & Januchowski-Hartley *et al.* 2012 for further details). Fishes were not selected for FID estimates if they were engaged in territorial, mating or predator escape behaviour, or were obviously aware of observer presence prior to approach (e.g., had turned to look at the observer). Trials were abandoned if line of sight between the diver and fish was broken prior to flight, or another fish chased the target fish during the approach.

Prior to approach, I estimated fish total length (cm TL), and only individuals larger than 15 cm TL for Acanthuridae and Scaridae, and 10 cm TL for Chaetodontidae were sampled; there was no upper limit on body size. Acanthuridae and Scaridae smaller than 15 cm TL were highly unlikely to be targeted by fishers in the study area. Due to the rarity of individual Chaetodontidae > 15 cm TL, a lower minimum size for this family was adopted. Observer fish TL estimates were validated daily by estimating lengths of PVC pipes (between 5 and 60 cm length) until estimates were consistently within 2 cm of actual length. In order to try and minimize the likelihood of repeated observations on the same individual, I noted size, group size and other characteristics (e.g., scars), and individuals with similar characteristics were not sampled. All FID estimates in an area were conducted on the same day.

5.2.3 Impact of periodically harvested closures on fish and benthic communities

Fish and benthic community surveys were conducted by two divers along eight 50 x 5 m transects at 6-8 m depth across all areas both before and after the harvest in the appropriate PHC. The first diver unrolled the transect tape and counted and estimated the size of all non-cryptic reef fishes > 10 cm TL to the nearest centimetre. Size estimation was validated as above. Fish biomass was calculated using published length-weight relationships (Froese and Pauly 2011). The second diver followed the first, classifying the benthic habitat directly beneath the transect tape at intervals of 0.5 m as: hard coral, soft coral, turf algae, macroalgae, crustose coralline algae, bare substrate, sand, rubble or other. The second diver also scored the rugosity of the reef for each transect between 0 and 5: 0= no vertical relief; 1 = low and sparse relief; 2= low but widespread relief; 3= moderately complex; 4= very complex; and 5= exceptionally complex (Polunin & Roberts 1993). This scoring approach shows high correlation with other methods of estimating reef rugosity, including the abundance of holes of appropriate size for fish refugia (Wilson et al. 2007).

5.2.4 Effects of periodically harvested closures on catch

I collected data on the abundance, species composition and lengths of fish landings in both villages. I estimated catch per unit effort (CPUE) and composition of the regular fishery by sampling as many fishing trips as possible to the open fishing grounds on fringing reefs over 10-12 days at each village. During the 3-day opening of the PHC, I surveyed all fishing trips to the closure to obtain estimates of the periodic harvest CPUE and composition. Although each community has access to other lagoon and reef areas, these areas were rarely fished during the study period, and I did not record catches from these areas. The time at which fishers entered the water, the time at which they returned to shore, number of fishers, gear used and location fished were all recorded. During the study period all fishing on surveyed reefs was conducted with spearguns. Standard length (cm SL) was measured for all fish caught, and fishes were identified to species level where possible. Holocentridae (squirrel and soldierfish) were grouped at the family level. Published length-weight conversion factors were used as above to calculate CPUE in kg hr^{-1} for each fisher per trip.

Through discussion with community leaders I identified all fishers in each community who regularly fished on the fringing reefs, and then approached them for interviews. A few fishers were unavailable for interview, as they were visiting relatives elsewhere in Vanuatu. Of fishers who regularly fished in the areas studied, I interviewed 9 out of 11 fishers at Community 1, and 5 out of 6 at Community 2. I asked the following questions were asked of each fisher: how many times a week, and at what time did you fish? Where do you normally fish? What fishing gears do you use and how frequently do you use them? Which families of fishes do you normally catch and with which gear? Following Feary et al. (2011), when fishers were interviewed (while on land) they were asked to visually indicate the maximum distance at which they would shoot at an average-sized fish while holding their spear gun as they would in the water. They were then asked to place a stone at this distance and return to where they were originally standing. The distance between the stone and the fisher's face was estimated as the maximum effective range (MER) of spearguns, because it is likely fishes respond to the spearfisher, rather than the speargun (Chapter 2 & Januchowski-Hartley et al. 2012). The MER of spearguns across the study areas was 337 ± 9.5 cm (1 SE).

5.2.5 Data analysis

I assessed differences in FID, fish biomass and density, and benthic communities using three-way orthogonal analysis of variance (ANOVA), with community as a random factor, and management status (fished, PHC, NTR) and pre/post harvest status nested within management status as fixed effects. Tukey's post-hoc tests were used to identify where differences between management statuses occurred pre- and post-harvest. I assessed homogeneity of variances using Levene's test and normality of the data through histograms and normal probability plots. Biomass data were $\log(x + 1)$ transformed in order to meet assumptions where necessary (apart from Scaridae, which were $\log(x + 2)$ transformed). I used two-sample t-tests to compare the mean FID in each management type pre- and post-harvest with MER of spearguns for each family. I analysed CPUE data using a two-way ANOVA, comparing CPUE during regular fishing activities to CPUE during periodic harvests, with community as a random factor. I compared relative proportions of each focal family in the catch from normal fishing activities with catch from the periodic harvest using Chi-squared tests. All analyses were conducted in Minitab version 14.

5.3 RESULTS

5.3.1 Effects of periodically harvested closures on fish behaviour

Acanthuridae FID differed significantly between communities ($F_{1,140} = 18.36$, $P < 0.001$), with management status ($F_{2,140} = 32.19$, $P < 0.001$) and pre- versus post-harvest ($F_{3,140} = 5.08$, $P = 0.002$). Between communities, mean FID was lower in fished areas in Community 2 compared to Community 1. Post-hoc Tukey's test showed that pre-harvest, mean Acanthuridae FID inside NTRs and PHCs were similar (NTRs: 257.2 cm ± 11.5 [1 SE]; PHCs: 293.8 cm ± 13.0). Mean FID in both managed areas were significantly lower than mean FID in open fished areas (Fig. 5.2a). Post-harvest, mean Acanthuridae FID in PHCs was 374.0 cm ± 13.3, which was not significantly different to fished areas (387.5 cm ± 19.8). These were significantly higher than mean FID in NTRs (269.8 cm ± 20.3) (Fig. 5.2a). Scaridae FID also differed significantly between communities ($F_{1,140} = 9.40$, $P = 0.003$) and management status (Fig. 5.2b; $F_{2,140} = 46.93$, $P < 0.001$), but not pre- to post-harvest. Similar to Acanthuridae, mean FID of Scaridae in fished areas was generally lower in Community 2 than community 1. Mean Scaridae FID in NTRs was significantly lower than in PHCs, which in turn was significantly lower than in fished areas (Fig. 5.2b). Although there was a significant difference in FID between communities for these target families, the effects of management were consistent across both communities. There was no effect of

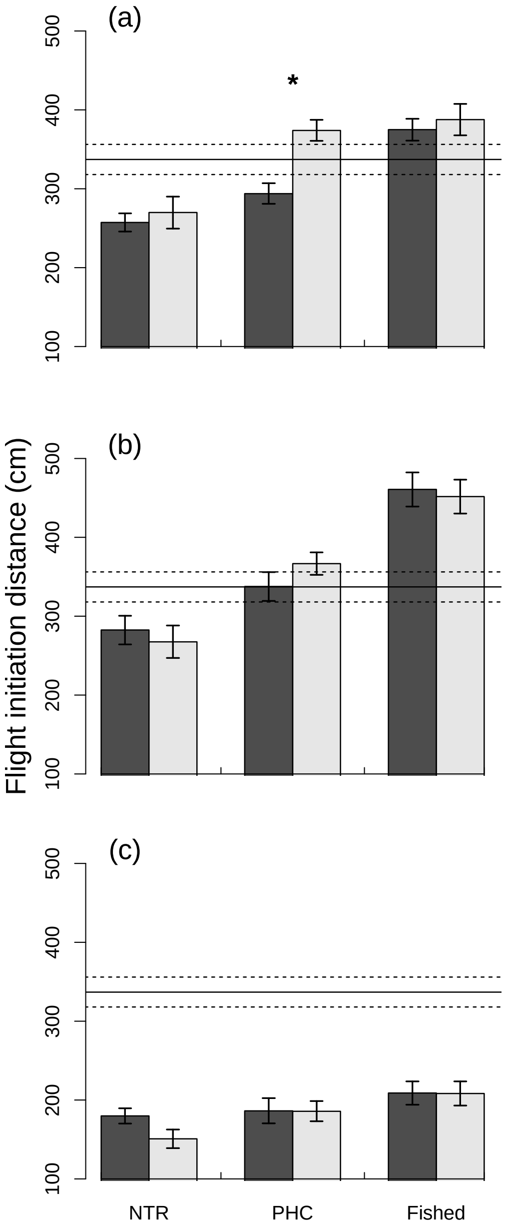

Figure 5.2 Pooled mean flight initiation distance pre-harvest (dark bars) and post-harvest (grey bars) for no-take reserves (NTR), periodically harvested closures (PHC) and fished areas. (a) – Acanthuridae; (b) – Scaridae; and (c) – Chaetodontidae. Error bars are ± 1 SE. The solid horizontal line indicates the mean maximum effective range of spearguns, and the dotted lines the 95% confidence intervals around the mean. Asterisks indicate significant changes in FID after harvest.

community or harvest on Chaetodontidae FID, but mean FID in NTRs was significantly lower than in fished areas (Fig. 5.2c; $F_{2,137} = 5.12$, $P = 0.007$). Mean FIDs of Scaridae and Chaetodontidae did not vary pre- versus post-harvest. For targeted families, mean FID in NTRs at all times was significantly less than MER; while in fished areas mean FID was significantly greater (Table 5.2). Acanthuridae mean FID in PHCs increased from less than MER pre-harvest to greater than MER post-harvest (Fig. 5.2a). Mean FID of Scaridae was not significantly different from MER either pre- or post-harvest in the PHCs (Fig. 5.2b).

Table 5.2 Results of 2-sample t-tests between mean FID and maximum effective range of speargun for target families at each village and management area combination, pre- and post-harvest.

Management area	*Pre/post harvest*	*Family*	*T-value*	*P*	*Relative to MER*
Fished	Pre	Acanthuridae	2.22	0.036	+
		Scaridae	5.22	< 0.001	+
	Post	Acanthuridae	2.26	0.032	+
		Scaridae	4.86	< 0.001	+
No-take reserve	Pre	Acanthuridae	5.40	< 0.001	-
		Scaridae	2.69	0.011	-
	Post	Acanthuridae	3.03	0.005	-
		Scaridae	3.10	0.005	-
Periodically harvested closure	Pre	Acanthuridae	2.73	0.012	-
		Scaridae	0.00	0.996	=
	Post	Acanthuridae	2.23	0.036	+
		Scaridae	1.69	0.104	=

5.3.2 Impact of periodically harvested closures on fish and benthic communities

Total biomass varied between communities ($F_{1,89} = 43.84$, $P < 0.001$), and with management status ($F_{2,89} = 17.73$, $P < 0.001$) but did not change pre- to post-harvest ($F_{3,89} = 1.86$, $P = 0.598$). Post-hoc Tukey's test demonstrated that total biomass was lower in fished areas than in NTRs and PHCs, which were not significantly different (Fig. 5.3a). Acanthuridae biomass showed differences in biomass between

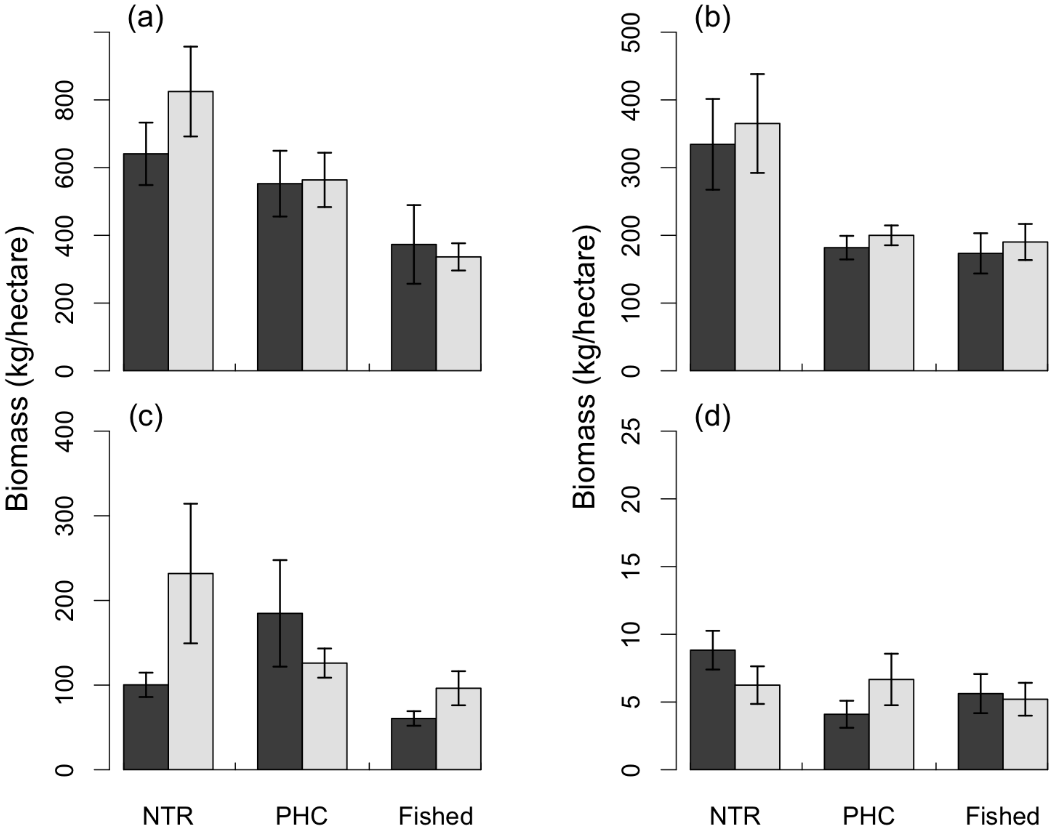

Figure 5.3 Pooled biomass of fishes pre-harvest (dark bars) and post-harvest (grey bars) at no-take reserves (NTR), periodically harvested closures (PHC), and open fished areas. (a) – all fishes; (b) – Acanthuridae; (c) – Scaridae; and (d) – Chaetodontidae. Error bars are ± 1 SE.

communities ($F_{1,89}$ = 33.06, $P < 0.001$), and with management status ($F_{2,89}$ = 11.05, $P < 0.001$) and was significantly higher in NTRs than either PHCs or fished areas, which had similar levels of biomass (Fig. 5.3b). Neither Scaridae nor Chaetodontidae showed any significant differences in biomass between communities, or management areas (Fig 5.3b,c). Abundance of fish only differed significantly between management areas for Acanthuridae, which showed higher abundance in the NTRs than fished areas both pre ($F_{2,44}$ = 6.23, P = 0.004) and post-harvest ($F_{2,44}$ = 6.96, P = 0.002). Differences between communities in total biomass were primarily attributable to reefs in one community having a significantly greater Acanthuridae abundance ($F_{1,44}$ = 6.32, P = 0.016). There was no effect of the harvest on biomass or abundance for any biomass category.

PHCs were significantly more rugose than fished areas ($F_{2,44}$ = 9.48, P < 0.001), but rugosity did not differ between communities. Benthic cover was dominated by crustose coralline algae and sediment-laden turf algae, which when combined accounted for 58.9 – 84.3% of benthic cover at all areas. The combined percent benthic cover of crustose coralline algae and sediment-laden turf algae did not differ either between management regime or community tenure. Turf algae cover was slightly higher in fished areas than NTRs ($F_{2,44}$ = 3.38, P = 0.043). There was higher hard coral cover in community 1 than in community 2 ($F_{1,44}$ = 18.31, P < 0.001), but hard coral cover was low in all areas, ranging between 1 and 7.5%. There were no differences found post-harvest for either rugosity or benthic composition.

5.4.3 Effects of periodically harvested closures on catch

Interviews with 14 out of the 17 regular fishers in the two communities indicated that during normal fishing activities there were 5.6 fishing trips/hectare/week to the fished area in community 1 (total number of trips/week = 84.5), while in community 2 there were 1.6 trips/hectare/week (total number of trips/week = 34.4) across both day and night. During the weeks of this study, less than the average number of trips to the fringing reef fishing grounds were observed, and several fishers indicated that this was due to community and family duties in the lead up to Christmas limiting opportunities for fishing. All fishers interviewed reported they primarily used spearguns on the reefs in this study; only one reported using a different gear (gill net), and then only once or twice a month. All fishing on the fringing reefs during the study period was conducted using spearguns. Primary target families were Acanthuridae (particularly *Naso* species) and Scaridae, although other families would be targeted opportunistically.

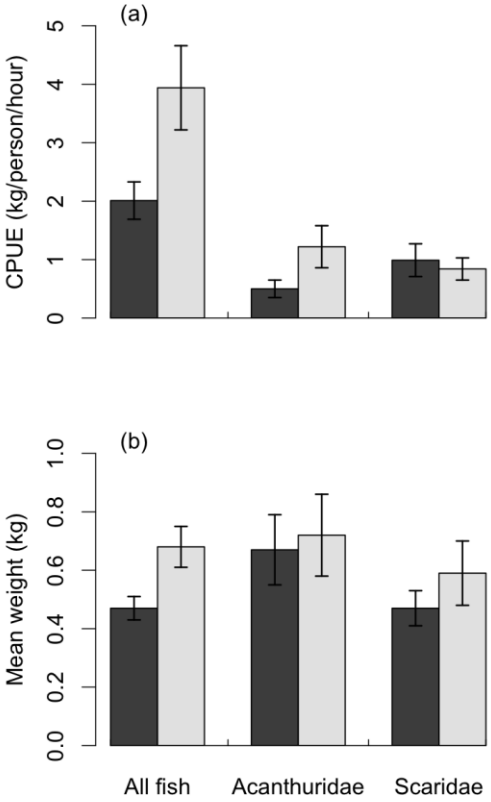

Figure 5.4 Catch data for normal and periodic harvest fishing trips. (a) Pooled catch per unit effort data (kg person-1 hour-1), and (b) average weight of individual fish (kg) in the catch from regular fishing trips (dark bars) and during period harvest trips (grey bars). Error bars are ± 1 SE.

A total of 153 fish consisting of 89 species from 20 families were caught by speargun during 16 fishing trips to open areas, and 122 fish from 12 fishing trips during the periodic harvest (Table 5.3). Twenty-two trips were conducted during daylight hours, and six at night. However, there was no significant difference in CPUE with time of day for either trips to the PHCs or normal fishing trips (2-way t-test, normal fishing: t = 0.96, P = 0.37; periodic harvest: t = 0.97, P = 0.40), and night-time and daytime fishing trips were pooled. CPUE (kg person^{-1} hour^{-1}) for all fishes differed significantly between regular fishing trips to open grounds, and fishing trips for the periodic harvest (two-way ANOVA; $F_{1,27}$ = 5.92, P = 0.022), with periodic harvest trips having a CPUE almost double that of regular fishing activities (Fig. 5.4a). Acanthuridae CPUE during periodic fishing harvests was almost 2.5 times greater than Acanthuridae CPUE during normal fishing trips ($F_{1,27} = 4.82$, $P = 0.038$). However, there was no difference in CPUE for Scaridae between normal fishing activities and harvest of the periodic closure. There was no effect of community on CPUE. The average size (kg) of individual fishes in catches from the PHCs was 45% greater than fishes from open areas (Fig 5.4b; $F_{1,272} = 16.28$, $P < 0.001$), and there was a significant difference in the average size of fishes in the catch between tenure areas ($F_{1,272} = 14.98$, $P < 0.001$). There was no significant difference in the average size of Acanthuridae in the catch (Fig. 5.4b). However, the average size of Scarids in the catch from PHCs was significantly greater (~ 26%) than in catch from open areas ($F_{1,96} = 7.66$, $P = 0.007$), and differed significantly between communities ($F_{1,96} = 10.62$, $P = 0.002$).

Table 5.3 Composition of catches by fish family during normal fishing activities and periodic closure harvests (n = number of fishing trips).

	Normal fishing			***Periodic harvest***		
Family	***Village 1*** *n = 12*	***Village 2*** *n = 7*	***Average (% Total Catch)***	***Village 1*** *n = 7*	***Village 2*** *n = 5*	***Average (% Total Catch)***
Acanthuridae	27	16	22.8	29	25	38.8
Balistidae	0	1	0.8	-	-	0
Caesonidae	2	-	0.8	2	-	1.4
Carangidae	1	2	1.9	2	1	2.15
Haemulidae	1	2	1.9	2	5	5.15
Holocentridae	26	3	12.8	3	2	3.6
Kyphosidae	1	3	2.7	7	2	6.35
Labridae	3	2	2.7	2	3	3.65
Lethrinidae	2	1	1.6	1	1	1.45
Lutjanidae	2	-	0.8	2	2	2.9
Monocanthidae	1	-	0.4	1	1	1.45
Mullidae	0	5	3.8	2	1	2.15
Scaridae	48	27	39.5	15	20	25
Serranidae	2	3	3.1	4	4	5.8
Siganidae	1	-	0.4	-	-	0
Sphyraenidae	1	-	0.4	-	-	0
Squid/ Cuttlefish	6	1	3.2	-	-	0
Total	***124***	***67***		***72***	***67***	

Acanthuridae and Scaridae dominated fish landings during both regular and periodically harvested closure fishing trips, combined accounting for 60 – 70% of all fishes caught. However, relative proportions of these families differed between regular fishing and periodic harvests at both communities, with Acanthuridae becoming more numerous in the catch during the periodic harvests, and the Scaridae less so (Table 5.3; χ^2 test: community 1, $\chi^2 = 24.35$, d.f. = 1, $P < 0.001$; community 2, $\chi^2 = 4.63$, d.f. = 1, $P = 0.031$).

5.4 DISCUSSION

A major obstacle to the success of co-management of near-shore artisanal fisheries is a mismatch in perceptions of benefits gained from measures such as marine protected areas (Gelcich et al. 2009; McClanahan et al. 2012). Despite this, because marine protected areas are known to be successful in increasing and maintaining fish biomass within their borders (Lester et al. 2009), as well as providing spillover of more catchable adults (Chapter 4 & Januchowski-Hartley et al. 2013b) and larval subsidy (Harrison et al. 2012) they are commonly implemented as a management tool. In this study, evidence is presented that lightly harvested PHCs are an alternative tool that can maintain similar levels of biomass to marine protected areas, while increasing fishing efficiency for at least one highly targeted family when opened for harvesting. This increase in efficiency appears to arise primarily through changes in the behaviour of fishery target reef fishes. This suggests that short-term openings of previously closed areas of fishing grounds can meet utilitarian goals of local communities (i.e., temporarily increasing fishing efficiency) through locally customary envisaged mechanisms (i.e., changing behaviour of fishes). PHCs can provide ecological benefits such as increased fish biomass, which in addition to providing fisheries benefit through adult and larval spillover (Halpern et al. 2009; Harrison et al. 2012) can aid in maintaining ecosystem functions such as herbivory. In addition, fishing efficiency may also be improved near PHCs through spillover of more catchable fishes (Chapter 4 & Januchowski-Hartley et al. 2013b) and these effects may help to ensure local support of conservation actions when placed within a co-management framework.

Prior to harvest, mean FID of Acanthuridae and Scaridae were lower in the PHCs than fished areas, while CPUE during harvest of the closures was almost double that of normal fishing activities. Importantly, the increase in mean fish size in the catch from periodic harvest would only account for less than 50% of the increase in CPUE for all fishes combined, and for only approximately 33% of the increase in CPUE for Acanthuridae. Notably, the Acanthuridae exhibited mean FID in PHCs that was considerably lower than MER of spearguns pre-harvest, strongly suggesting that the increase in CPUE was a result of increased catchability. Presuming that FID after the previous harvest events would be similar to that shown after this event, this implies that the reduction in FID and increase in catchability occurred over a relatively short temporal scale (~ 6 months), and more rapidly than biomass would be expected to increase in NTRs (McClanahan et al. 2007b). This is a considerably shorter duration of protection from fishing than reported in earlier studies that showing reductions in FID in areas under protection (Gotanda et al. 2009; Chapter 3 & Januchowski-Hartley et al. 2011). However, the time-scale for the full effect of protection to be realized may vary among families. For example, here the FID of Scaridae was still higher in PHCs than NTRs pre-harvest, whereas Acanthuridae FID did not differ. In general, Scaridae appear to be intrinsically more flighty than Acanthuridae, with higher FID than Acanthuridae at almost all levels of exploitation (Feary et al. 2011; Chapters 3, 4 & Januchowski-Hartley et al. 2011, 2013). This higher intrinsic wariness may dampen the effect of protection on FID, leading to changes in Scaridae behaviour taking longer to manifest.

The lack of post-harvest increase in Scaridae FID may be explained by substantial inter-family differences in FID. The pre-harvest mean FID of Acanthuridae in the PHCs was significantly below the MER of spearguns used on these reefs. In contrast, mean FID of Scaridae was at the limit of speargun MER. Therefore Acanthuridae may have attracted the majority of effort because Acanthurids were more likely to allow a closer approach by fishers than Scaridae, substantially increasing the likelihood of a successful shot. Change in the composition of the catch between regular harvesting and periodic closure harvesting support this theory. The increase in Acanthuridae as a proportion of the catch, while relative abundances of Acanthuridae and Scaridae between PHCs and fished areas pre-harvest did not vary, suggests fishers are taking advantage of differences in catchability. Similar changes in catch composition have been reported elsewhere after periodic harvests (Cinner et al. 2005). Significantly, post-harvest Acanthuridae FID increased to beyond MER of spearguns, even with the relatively low fishing intensity experience during the periodic closure harvest (~18 hours of fishing effort over ~18 hectares of reef).

The effects of protection on Acanthuridae behaviour were rapidly lost, and this has important implications for benefits from PHCs. First, if PHCs remained open to fishing for longer periods of time, fishers might start targeting Scaridae more frequently, and FID for this family would likely increase. Catch composition would then more closely resemble that of regular fishing activities. Second, reductions in FID are fragile, and potential benefits from changes in behaviour could be lost if there is low compliance with the periodic harvest schedule, or the boundaries of the area under protection are not well known. Third, this observed sensitivity to fishing of a popular fishery target family raises the possibility that FID can be used as a metric to assess compliance within protected areas, when compared to FID in nearby open fished areas (Chapter 3 & Januchowski-Hartley et al. 2011).

Relative to fished areas lightly fished periodically harvested areas can maintain higher total fish biomass, comparable to the effects of NTRs. FID related vulnerability might explain that while PHCs maintain similar total biomass to NTRs, they did not do so for Acanthuridae biomass. The lack of effect of either form of protection on Scaridae is possibly because the protected areas in this study were not large enough to protect the relatively vagile Scaridae (Welsh & Bellwood 2012). Both families are generally targeted by speargun (McClanahan & Cinner 2008), the primary gear used on these fringing reefs, while the total biomass category includes fish families which are not speargun targets in the region [e.g., Serranidae (McClanahan & Cinner 2008)], or where FID is generally greater than speargun MER [e.g., Lutjanidae (Chapter 3 & Januchowski-Hartley et al. 2011)]. This study highlights that behaviour may also play a critical role in how vulnerable fishes are to depletion. Unlike the more wary Scaridae, Acanthuridae appear to be vulnerable to pulse-fishing, or rotational harvesting events. For example, in harvests of previously closed areas in Fiji (Jupiter et al. 2012) and Papua New Guinea (Cinner et al. 2005), Acanthuridae were a major portion of the harvest and, similar to here, were a larger proportion of the catch than during normal fishing trips. Jupiter *et al.* (2012) speculate Acanthuridae schooling in the upper water column drove increased prevalence in the catch, because this behaviour resulted in fishes being immediately visible to spearfishers entering the water. While aggregating is known to increase vulnerability of fishes to artisanal fishing (Hamilton et al. 2012), and has been implemented in fisheries vulnerability assessments (Cheung et al. 2005), other behavioural based characteristics may also need to be considered, particularly in the context of small-scale artisanal fisheries.

There is ample evidence that unrestricted harvesting of a previously closed area can reduce biomass of fish to levels below that of normally fished areas, from which recovery may require several years (Russ & Alcala 2003; Jupiter et al. 2012). This study shows that even low and infrequent harvesting intensity may diminish some effects of protection, particularly for targeted families. The standing biomass of fishes is critically important for the maintenance of ecosystem states and processes, and although total fish biomass in the PHCs were at levels similar to NTRs, this level is below several thresholds leading to the loss of ecosystem processes for coral reefs in the Indian Ocean (McClanahan et al. 2011). If, as discussed above, there is a ratcheting down effect on biomass of frequent and intense harvests (Cohen & Foale 2012), thresholds at lower biomasses will be approached. At these lower levels of biomass, further small reductions may lead to several thresholds being crossed, and further degradation of ecosystem processes. A study in the Nguna-Pele Marine Protected Area network five years prior to this one, found similar relative proportions of no-take reserve and PHCs biomass (Bartlett et al. 2009). This implies that this low-intensity harvesting strategy, in this reserve network, is not leading to a ratcheting down effect. However, in PHCs, traditional taboos or other forms of management where harvesting is more intense or of longer duration (e.g., Cinner et al. 2005; Williams et al. 2006; Jupiter et al. 2012), biomass may be reduced below critical thresholds. Importantly, total biomass of fishes in fished areas in this network was found to be only slightly above the level of total biomass on Indian Ocean coral reefs below which thresholds leading to degraded ecosystem function are rapidly crossed (McClanahan et al. 2011). While threshold levels of biomass are unlikely to be exactly the same on Pacific Ocean coral reefs, given similarities between dominant species, functional groups and food webs, these thresholds are probably generally applicable. In both communities, the recent establishment of the NTRs, and the closure of additional reef to establish PHCs, have concentrated fishers on smaller areas of reef (< 50% the area pre-management), and potentially will result in total biomass in these areas dropping below the level of these thresholds in future years.

Although a number of studies have explored whether and how PHCs can provide social and ecological benefits (e.g., Cinner et al. 2005; Bartlett et al. 2009; Jupiter et al.

2012), their potential role in contemporary conservation has been questioned due to origins for other social and cultural purposes (Cinner and Aswani 2007; Foale et al. 2011). Periodically harvested fisheries closures are likely provide many of the benefits (spillover, recruitment subsidy) that are expected from permanent no-take areas because they maintain similar levels of biomass. This study demonstrates that periodic harvests can also be associated with a short-term increase in fishing efficiency, that this is likely due as much, if not more so, to behavioural change than to increases in fish size within PHCs. It is likely that similar strategies would result in similar outcomes through the same mechanisms in near shore artisanal fisheries in other parts of the world. Local context, including community involvement, strength of local institutions, economic and nutritional reliance on the resource, expectations from harvest events and integration with markets will all have a bearing on the success of customary PHCs (Brooks et al. 2012; Cinner et al. 2012). It should be emphasized that these benefits are documented only where harvesting is extremely light and considerable research is required to better understand the sustainable limits of PHCs.

5.5 ACKNOWLEDGEMENTS

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5.6 SUMMARY

- Periodically harvested fisheries closures are widely implemented across the South Pacific as a conservation and fisheries management tool. There is a lack of information on the mechanisms and effectiveness of this management system in meeting fisheries and ecosystem sustainability goals.

- A before-after-control-impact (BACI) pair design, was used to quantify flight initiation distance (FID), and biomass of two fishery-target (Acanthuridae and Scaridae) and one non-target (Chaetodontidae) families in two periodically harvested closures, two no-take marine reserves, and two open fished areas, prior to and after harvest of the periodically harvested closures. Creel surveys were used to quantify catch per unit effort (CPUE) in open fishing grounds, and during the periodic harvests.

- Prior to harvest, FID of targeted families was higher in fished areas than periodically harvested areas. Post-harvest, Acanthuridae FID increased significantly to beyond the maximum effective range of spearguns. Total biomass of fishes was lower in fished areas than areas under either type of management. Acanthuridae biomass in the periodically harvested closures was similar to fished areas, and lower than in the no-take reserves. There was no difference post-harvest for either total or Acanthuridae biomass.

- CPUE was higher for fishing trips inside the periodically harvested closures than regular fishing activities. Fishes were generally larger in catches from periodically harvested closures, but this was not sufficient to account for the increase in CPUE, particularly of the Acanthuridae, which were significantly more abundant in the harvest catch.

- When fishes are protected temporarily from fishing, their wariness decreases which makes them more easily catchable when fishing is reinstated. This study shows that fish behavioural change is an important and overlooked benefit of periodically harvested closures. However, differences in the magnitude of behavioural changes between fishery-target families may result in contrasting outcomes of periodically harvested management regimes.

CHAPTER 6: VARIATION IN FISH FLIGHT INITIATION DISTANCE WITH PROTECTION ACROSS A GRADIENT OF FISHING PRESSURE

6.1 INTRODUCTION

Fishing is a major factor shaping the structure and function of coral reef fish communities globally (Pandolfi et al. 2003), and a number of studies have shown that biomass and density of targeted fishes, particularly high trophic level predatory species, decline along a gradient of fishing intensity (Jennings & Polunin 1996; Friedlander & DeMartini 2002). In contrast, the effects that fishing has on fish behaviour, and resulting implications for conservation and fisheries management have been largely overlooked. There is mounting evidence that fish inside marine reserves are less wary of humans, while outside reserves wariness increases with fishing pressure (Gotanda et al. 2009; Feary et al. 2011; Chapter 2, 3, 4 & Januchowski-Hartley et al. 2011, 2012, 2013). Importantly, these behavioural responses to fishing can potentially affect both fisheries yields and ecosystem functions. Fish can be less wary immediately outside marine reserves than in control areas further away, potentially increasing their catchability for gears such as spear guns (Chapter 4 & Januchowski-Hartley et al. 2013b). In addition, herbivorous fish with higher levels of wariness may spend more time near shelter or flee from predators earlier, reducing time spent grazing (Madin et al. 2010b).

Substantial research has shown the potential for marine reserves to help rebuild fish assemblages (Babcock et al. 2010), but their effects on behaviour are unknown. Knowing how wariness changes with protection and fishing pressure has important implications for both fisheries sustainability and the ability of fishes to perform key ecological functions (such as herbivory) that help sustain coral reefs. Here, I present the results of behavioural surveys of target fish families inside and outside marine reserves along a wide gradient of fishing intensity. I ask the following questions: 1) does fish wariness outside marine reserves change with increasing fishing pressure? And 2) does fish wariness inside marine reserves change with increasing fishing pressure in the surrounding seascape?

6.2 METHODS

6.2.1 Study sites

I estimated Acanthuridae (surgeonfish) and Scaridae (parrotfish) flight initiation distances (FID) at 13 areas where fishing was restricted through either permanent no-take reserves or traditional management practices (protected), and 10 open fished areas (fished) across four countries in the Indo-Pacific between 2009 and 2011 (Chagos - 3 large 'pristine' protected atolls; Papua New Guinea - 3 protected, 5 fished areas; Philippines - 3 protected, 3 fished; and Vanuatu - 4 protected, 2 fished). Protected areas were either remote (Chagos), or compliance with protection was considered to be high by communities in which areas were situated (FA Januchowski-Hartley, personal communication). FID was measured on both SCUBA and by free diving. Results from Chapter 2 (Januchowski-Hartley et al. 2012) showed no significant difference between FID recorded while free diving versus SCUBA, and I included data collected by observers using both of these techniques. The technique used to collect data while on SCUBA closely resembled the free diving methodology, including starting approaches from distances well beyond maximum recorded FID (> 10 m from the target fish), horizontal body position and steady speed approaches at the same depth as the fish (see Feary et al. 2011). In addition to fish species, size to the nearest centimetre total length and refuge availability (using reef complexity as a proxy), were recorded for all fishes, because both have been shown to be significantly associated with FID (Gotanda et al. 2009; Chapters 2, 3 & Januchowski-Hartley et al. 2011, 2012).

6.2.2 Fishing Pressure

I estimated fishing pressure as the number of fishers per kilometre of fringing reef. In the Philippines and Vanuatu, number of fishers within each fished area was estimated through key informant interviews with village leaders and chairmen of local fisher groups, conducted concurrently with estimates of FID. I asked interviewees how many fishers regularly (at least once per week) fished the fringing reefs in the fishing grounds. Where possible, I validated my results either through comparison with the number of fishers obtained by previous studies or with scientists and managers working independently in the same areas (R Weeks unpublished data; Abesamis & Russ 2006; Pascal 2011). For Papua New Guinea, estimates of number of fishers for each area were taken from household surveys at each area in 2009 (J Cinner, unpublished data), where respondents were asked the average number of days per week that each member of the household engaged in fishing. FID estimates were conducted concurrently with household surveys in two reserves and two fished areas in 2009, FID for the other four areas (1 unfished, 3 fished) were estimated in 2010, but at the same time of year (June-August) as the household surveys. I calculated the length of fringing reef in each fishing area, excluding fringing reef under protection, by digitally tracing the reef crest using Google Earth, using either known geographic features, or GPS co-ordinates to delineate the edges of the community fishing grounds.

6.2.1 Data analysis

Differences in FID between fished and unfished areas are well known and large and were not the subject of this study, so I analysed FID from fished and unfished sites separately because the large impact of protection (Feary et al. 2011; Chapter 2 & Januchowski-Hartley et al. 2012) is likely to obscure relationships between FID and other explanatory variables. I used linear mixed effect models to assess relationships between fish FID and the following explanatory variables: fish size, fishing pressure, substrate complexity and life-history stage (initial or terminal stage - parrotfishes only). I also included ecologically meaningful interactions between explanatory variables in the models if interactions were indicated in co-plots of the explanatory variables. Country and genus were included as random effects, and prior to finding the optimal fixed structure for each protection/family combination I first examined the random effect structure for a model with all explanatory variables as recommended by Zuur *et al*. (2009). This comparison was performed with restricted likelihood estimation within the lmer function of the lme4 package in R (R Development Core Team 2011). I selected the models with the lowest Akaike information criterion adjusted for small sample size (AIC_c). Variances of the full models (all explanatory variables) were found to be homogenous, and residuals normally distributed.

I found the optimal fixed structures for effects of explanatory variables by using likelihood ratio tests of nested models. Statistical significance was evaluated by testing -2 $\log_e$(likelihood) against the χ^2 distribution with 1 degree of freedom between each nested model and the full model (Zuur et al. 2009). I then dropped the explanatory variable with the lowest significant difference, and continued until all remaining explanatory variables were important in the model (likelihood ratio test $P < 0.05$). The 'best' set of models for each family/protection group were considered all those within 2 AIC_c units of the model with the lowest AIC_c score. These models were averaged to identify the effects of each explanatory variable on FID, and their normalised Akaike weight ($\boldsymbol{\omega_{ip}}$) for each predictor calculated. All analyses were performed within the lmer function of the lme4 and model.avg function of the MuMIn packages in R (R Development Core Team 2011). Variances of the full models (all explanatory variables) were found to be homogenous, and residuals normally distributed.

6.3 RESULTS

In general there was strong evidence for a relationship between FID and predictor variables, with four models representing more than 90% of the cumulative AIC$_c$ model weight in all family/protection combinations (Table 6.1). Fishing pressure was included in every model within the 90% AIC$_c$ model weight cut-off across all groups. Fish size and reef structural complexity were also well represented, but occurred less frequently than fishing pressure, while life-history stage was of variable importance between parrotfish subsets (Table 6.1). The interaction between fishing pressure and fish size was not important for surgeonfish FID in protected areas, but was in every other group.

Table 6.1. Ranked best sets of models predicting fish flight initiation distance in protected and fished areas for Acanthuridae and Scaridae.

	Fishing Pressure (FP)	Fish Size (FS)	Reef Complexity (RC)	Life-history stage	FP: RC	FP:FS
Protected						
Acanthuridae	0.251 ***	-0.043 ^{NS}	0.007 ^{NS}			
ω_{ip}	1.00	0.29	0.19			
Scaridae	0.704 ***	0.201 ***	-0.101 **	0.061 ^{NS}		-0.387 ***
ω_{ip}	1.00	1.00	1.00	0.64		1.00
Fished						
Acanthuridae	0.757 *	0.474 **	-0.381 **		0.501 ^{NS}	-0.420 ^{NS}
ω_{ip}	1.00	1.00	1.00		0.42	0.62
Scaridae	3.808 ***	0.761 ***	0.174 ^{NS}	0.022 ^{NS}	-2.793 ***	-0.855 ***
ω_{ip}	1.00	1.00	0.67	0.19	1.00	1.00

* $P < 0.05$, ** $P < 0.01$, $P < 0.001$

The interaction between fishing pressure and reef complexity was important for both parrotfish and surgeonfish in fished areas. The null model did not account for more than 0.001% of the cumulative model weight in any subset.

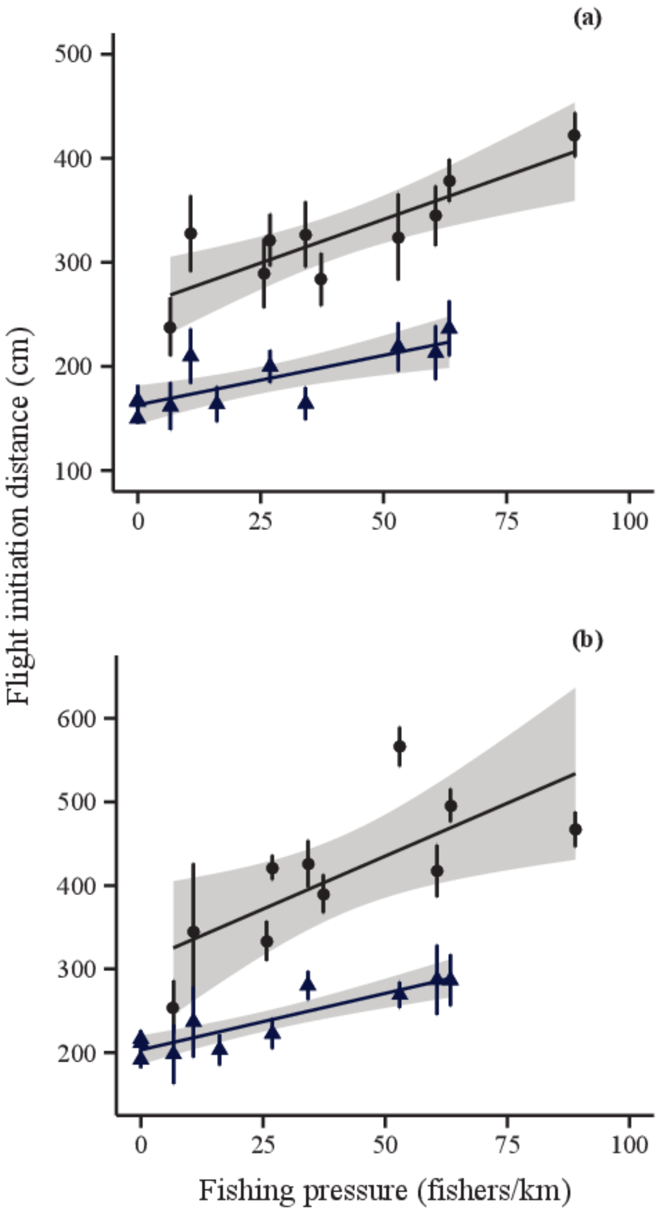

Figure 6.1 Flight intiation distance standardised by country in relation to fishing pressure. (a) Acanthuridae; (b) Scaridae. Blue triangles are protected areas, black circles are fished areas, error bars are 95% confidence intervals. Black lines are regression lines for the univariate relationship between adjusted FID and fishing pressure with 95% confidence intervals (grey shading).

Table 6.2 Ranked best sets of models predicting fish flight initiation distance in protected and fished areas for Acanthuridae and Scaridae.

Model Rank	Fishing pressure (FP)	Fish size (FS)	Reef Complexity (RC)	Life-history stage	FP: FS	FP: RC	df	ΔAICc	ωAICc	Cumulative ωAICc
PROTECTED										
Acanthuridae										
1	■			X		X	5	0.0	0.451	0.451
2	■	■		X		X	6	1.2	0.252	0.703
3	■		■	X		X	6	2.0	0.166	0.869
4	■	■	■	X		X	7	3.2	0.092	0.961
NULL							4	19.0	<0.001	1.000
Scaridae										
1	■	■	■	■	■	X	8	0.0	0.627	0.627
2	■	■	■		■	X	7	1.2	0.352	0.979
NULL							3	66.1	<0.001	0.999
FISHED										
Acanthuridae										
1	■	■	■	X	■		8	0.0	0.338	0.338
2	■	■	■	X	■	■	9	0.3	0.287	0.625
3	■	■	■	X			7	0.7	0.238	0.863
4	■	■	■	X		■	8	1.8	0.137	0.999
NULL							4	110.4	<0.001	1.000
Scaridae										
1	■	■	■		■	■	8	0.0	0.418	0.418
2	■	■			■	■	7	0.7	0.295	0.713
3	■	■	■	■	■	■	9	1.8	0.169	0.882
4	■	■		■	■	■	8	2.5	0.117	0.999

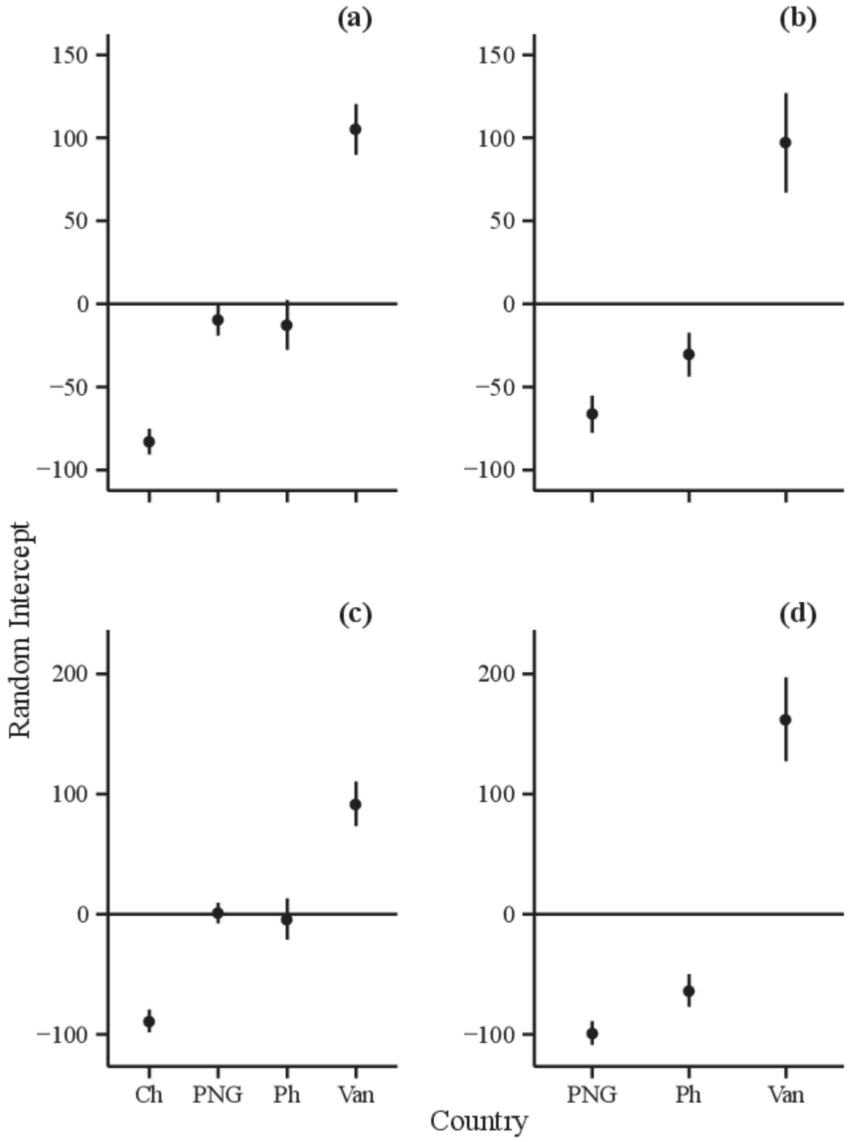

Figure 6.2. Random intercept coefficients by Country for: A) Acanthuridae protected; B) Acanthuridae fished; C) Scaridae protected; and D) Scaridae fished. Ch: Chagos, PNG: Papua New Guinea, Ph: Philippines, Van: Vanuatu. Error bars are 95% CI.

The averaged models indicate fishing pressure had moderate to strong positive relationships with FID for both parrotfish and surgeonfish in fished and protected areas (Fig. 6.1, Table 6.2). Fish size similarly showed a moderate and positive relationship with FID except for surgeonfish in protected areas while reef complexity primarily exhibited a weak negative relationship with FID for two of the groups (Table 6.2). Life-history stage only showed weak effects on FID.

Country explained between 50 and 75% of the variance within groups, while genus accounted for less than 15%. Examination of the random coefficients for country indicated that fishes in Chagos will generally have a considerably lower FID than any other country, while in Vanuatu will have a higher FID (Fig. 6.2).

6.4 DISCUSSION

My study demonstrates that fishing pressure was positively related to FID in key fishery-target families. A key and surprising finding is that this same relationship held inside protected marine reserves as well, despite all these areas having high levels of compliance. Specifically, fish inside well-protected managed areas (both no-take reserves and periodically harvested closures) became more wary of humans as fishing pressure in the surrounding seascape became more intense. These results reinforce other work indicating that behavioural responses to predation (in this case fishing) are scaled to overall levels of chronic predation risk in the wider landscape, but higher where predation risk is more acute (Stankowich & Blumstein 2005; Madin et al. 2010a, b; Holmes & McCormick 2011). This agrees with reviews of FID in other taxa, which showed increased FID during hunting seasons and with prey experience (Walther 1969; de Boer et al. 2004; Theil et al. 2007; Stankowich 2008). Additionally, I show that fish size and reef complexity, while important in predicting FID, have less of an effect than predation risk. These findings have potentially important implications for the role of marine reserves in conserving key functions of coral reefs. Specifically, parrotfishes and surgeonfishes are herbivores that play an important role in maintaining reef functions (Bellwood et al. 2004). Studies on indirect fishing effects show that where predation risk is high, foraging effort by herbivores becomes patchy (Madin et al. 2010b), and my results imply higher fishing pressure is likely to evoke similar responses.

Behaviour in fishes has a distinct genetic component (Giles & Huntingford 1984; Sutter et al. 2013). My results imply that in addition to influencing size, growth rates and reproductive schedules (Enberg et al. 2009), fishing selective pressure has the potential to influence fish behaviour. If fishing preferentially removes less-wary fishes from a population, the average fish that succeeds in reproducing will have higher levels of intrinsic (i.e., unlearned) wariness than fishes from an unfished population. This theory could explain the lower FID of fishes in Chagos, because fishes recruiting to Chagossian atolls originate from an isolated, unfished population (Graham & McClanahan 2013), unlike the rest of protected areas in this study. However, this is somewhat contradicted by results from Vanuatu, where fishes had greater than expected FID despite relatively low fishing pressure. It should be noted that my fishing pressure estimates are from reefs immediately adjacent to marine reserves, while the natal reefs of fishes can be up to 200 km from the reefs to which they recruit (Hogan et al. 2011).

An alternative explanation for this pattern is the import of learned responses to predation into the reserves from fished populations (Holmes & McCormick 2011; Chapter 4 & Januchowski-Hartley et al. 2013b). Frequent exposure to acute predation events and presence of olfactory alarm cues in the water are likely to lead to visual association by fish of divers with predation (Brown 2003). Increases in FID inside protected areas could subsequently result through social transmission of anti-predator behaviour to fishes in low-risk environments by fishes habituated to higher-risk environments (Brown et al. 1999; Brown 2003). Most reserves in this study are small (< 25 hectares) and in reserves or wilderness areas many times larger than target species home ranges, social transmission of behaviour could be limited to a zone near the reserve borders.

The relative influence of the above potential mechanisms influencing fish behaviour could be important for the function of marine reserves. If social transmission is the dominant mechanism, small reserves may be effective at lower fishing pressures, but offer fewer benefits for reef health at higher fishing intensities due to potential inhibition of herbivore foraging under higher predation regimes (Madin et al. 2010a,b). Importantly, in the developing country context most marine reserves are small, and occupy a small proportion of a larger fished seascape (Wood et al. 2008). If genetically based intrinsic wariness is dominant, reserve size is unlikely to matter when considering behavioural effects of fishing. To accurately account for behaviourally mediated impacts on coral reef ecosystems, research is needed to assess learning capability of coral reef fishes, and how grazing fluctuates with protection and fishing intensity. My results show that conservation practitioners and scientists need to be aware of the influence of local external factors (such as adjacent fishing pressure) to marine reserve function when planning new reserves or assessing reserve success.

6.5 ACKNOWLEDGEMENTS

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6.6 SUMMARY

- Fishing is a major factor that shapes fish communities, changing species composition, biomass and influencing fish behaviour.
- Behaviour can play an important role in mediating ecosystem functions, highlighting the need to identify behavioural responses of fishes to increasing fishing intensity.
- I collected fish flight initiation distance (FID) in fished areas and protected across four countries (Chagos, Papua New Guinea, Philippines and Vanuatue) and a wide gradient of fishing intensity from near-pristine sites to heavily fished areas.
- Using linear mixed effect models and model averaging, I assessed the support for fishing pressure, fish size, reef rugosity and life-history stage (Scaridae only) determining FID of Acanthuridae and Scaridae .
- Fishing pressure had the strongest support for explaining FID for both families in both fished and protected areas embedded within fished seascapes, with increasing fishing pressure predicting increases in FID.
- Body size and rugosity both had moderate support for explaining FID, but operated in different directions; larger fishes have higher FID, but in more rugose areas FID decreases. There was no effect of life-history stage on FID.
- These results show that fishing effects such as increases in wariness can be imported into marine reserves, and supports predictions of increases in FID with increased predation risk and reproductive value.
- The import of fishery effects into protected areas may occur through either population level increases in wariness through fishery preference for non-wary

fishes, or through import of learned behaviours, and provides further evidence that large marine reserves maximise benefits from protection more so than smaller reserves.

CHAPTER 7: GENERAL DISCUSSION

Fishing is one of the major sources of mortality of large-bodied, adult coral reef fishes, particularly within the Indo-Pacific (Newton et al. 2007). The majority of studies on how fisheries affect coral reef function and processes concentrate on the influence of fisheries on density and/or biomass of key functional groups, in addition to the direct effect of fisheries on coral reef fish communities (e.g., McClanahan et al. 2011;Mumby et al. 2012). However, processes that can be impacted by anthropogenic exploitation can go beyond those mediated by density and biomass or changes in abundance of key functional species (Peckarsky et al. 2008; Madin et al. 2010b). The results of this thesis suggest that both fishing and protection from fishing can have significant effects on the behaviour of some coral reef fishes (Chapter 3), which not only improve fishing efficiency (Chapter 5), but also provide unexpected benefits from no-take marine reserves (NTRs) (Chapter 4). There are also indications that no-take reserves are porous to behavioural changes caused by fishing. As fishing pressure increases, fishes within NTRs that are embedded within the fished seascape show higher levels of wariness (Chapter 6). This brings into question how ecosystem processes such as herbivory are maintained in NTRs because foraging can often be constrained by perceived risk in the environment (Madin et al. 2010a). This present chapter aims to 1) discuss how the results of this thesis contribute to and fit within our current knowledge of predator escape behaviour, 2) discuss the implications of fisher-escape behaviour for reef management and conservation, and 3) propose future directions of research on fish behaviour to provide insights into mechanisms, functions and consequences of fishing.

7.1 PREDATOR ESCAPE BEHAVIOUR

How human disturbance impacts animal behaviour is an important topic in the management of animal populations (Weston et al. 2012; Cromsigt et al. 2013). In human dominated systems, the effects of human activities on animal behaviour can exceed that of natural predators or environmental conditions, potentially carrying a considerable fitness penalty (Ciuti et al. 2012). There is a plethora of theoretical, observational and experimental evidence underlying predator-escape behaviour in terrestrial systems, but the field is somewhat less developed in the marine realm. Chapters 2, 3 and 6 explore the effects of predator characteristics (Chapter 2), levels of predation risk and prey and environmental conditions (Chapters 3 & 6) on predictions made by optimal and economic theories of flight initiation distance (FID) in regard to marine fishes, and provide important insights into the ecology of predator escape behaviour as it relates to human exploitation.

As the danger posed by a predator increases, FID should also increase (Cooper & Frederick 2009). However, flight from a predator comes with associated costs (Ydenberg & Dill 1986; Cooper & Frederick 2007), so prey may consider certain cues (i.e., indications that the predator is satiated, or that it is otherwise not a threat) in deciding whether to flee. The particular factors that are important in a given predator encounter may vary, because prey are likely to have imperfect knowledge of environmental and predator conditions, and may use 'rules of thumb' to assess costs and benefits and make flight decisions (Bouskila & Blumstein 1992). There is some evidence that mammals are able to discriminate between potential predatory species that pose different levels of threat (e.g., lions versus hyenas, or humans versus wolves), and make decisions accordingly (Walther 1969; Proffitt et al. 2009). Experimental studies have confirmed that fishes use visual cues based on predator behaviour to determine intent (Murphy & Pitcher 1997; Smith & Belk 2001), can distinguish between piscivorous and non-piscivorous species (Coates 1980), between sympatric species (Gerlai 1993) and may use distance between eyes and the shape of the mouth to identify predatory species (Karplus & Algom 1981). The ability to discriminate intent, or at least cues that may indicate intent, extends in some taxa to human ‘predators’. For example, both birds and iguanas will respond to directness of gaze of an intruding human showing lower FID if gaze is averted or obscured (Burger & Gochfield 1993; Bateman & Fleming 2011).

Despite this potential ability of fishes to discriminate subtle predator characteristics, and evidence of such from other taxa, I found little evidence that coral reef fishes respond to key predator characteristics that determine intent of human predators. Neither the presence/absence of a simulated spear gun, nor that of observers using SCUBA versus free diving resulted in a significant influence on FID for parrotfishes (Chapter 2 & Januchowski-Hartley et al. 2012). Other studies conducted on SCUBA (Gotanda et al. 2009; Feary et al. 2011) show FID values within the range of those collected while free diving during this thesis, as does Miller et al. (2011) which was conducted by free-diving (although only within a NTR). The response of fishes to SCUBA apparatus is not clear, with a number of studies showing attraction (Chapman et al. 1974; Cole et al. 2006), while some show repulsion when compared to observers on snorkel/re-breathers (Dearden et al. 2010; Welsh & Bellwood 2012). It has been hypothesised that movement rather than shape is a primary visual cue for threat assessment (Wisenden & Harter 2001), and these results, where an approaching large intruder initiates flight irrespective of whether it is displaying benign/malign intent supports this hypothesis. It is further evidence that selection favours paying attention to a limited set of factors to increase the speed of decision-making (Bouskila & Blumstein 1992; Bernays & Wcislo 1994), which may result in flight from non-threatening stimuli (such as a recreational SCUBA diver) when in an environment where similar sized predators are present (Thiel et al. 2007; Chapter 2 & Januchowski-Hartley et al. 2012). However, in Chapter 4 I show that in NTRs with high levels of non-predatory human disturbance (tourism), FID is still significantly lower than in fished areas, indicating that fishes can alter their response to potential predators depending on knowledge of local predation risk on relatively small spatial scales (Chapter 4 & Januchowski-Hartley et al. 2013b).

The degree of exposure to predation influences the degree to which prey animals perceive danger in their environment. In areas where predator density is relatively high (i.e., an encounter with a predator is more likely), the majority of studies show decreased FID compared to low-density areas (reviewed in Stankowich & Blumstein 2005). This counter-intuitive result may be because the majority of studies that have investigated predator density used humans as a surrogate predator, with the potentially problematic assumption that animals would respond to humans as they would to other types of predators (Frid & Dill 2002). In contrast, I studied reef fisheries, where humans are key predators, and my research showed that FID increases with fishing pressure (increasing density of predators) across a wide gradient (Chapter 3, 6 & Januchowski-Hartley et al. 2011). This agrees with results from other studies that show that FID is greater in areas where animals are hunted by humans, compared to those areas where they are not (Walther 1969; de Boer et al. 2004; Matson et al. 2005; Thiel et al. 2007; Reimers et al. 2009; Gotanda et al. 2009; Feary et al. 2011). However, coral reef fishes do not exhibit perfect knowledge of the local risk environment, with FID being depressed immediately around NTRs (Chapter 4 & Januchowski-Hartley et al. 2013b), and significant evidence that predation in the surrounding seascape can have effects on FID within NTRs (Chapter 6). Furthermore, the ability of fishes to recall appropriate responses to predators, previously demonstrated in minnows in laboratory conditions (Magurran 1990) is here confirmed in fished species on coral reefs (Chapter 5 & Januchowski-Hartley et al. 2013a).

While experience of predation is the predominant factor influencing FID of coral reef fishes, physical/reproductive condition and natural history traits have significant influences on flight decisions and FID (Gotanda et al. 2009; Chapters 2, 3, 6 & Januchowski-Hartley et al. 2011; 2012). In fishes, the size of individuals is often closely related to reproductive value (Warner 1998). Larger individuals are therefore likely to flee earlier due to the lower potential benefits of remaining relative to their probable higher individual fitness (Stankowich & Blumstein 2005; Cooper & Frederick 2007, 2010) Parrotfishes are protogynous hermaphrodites, many species of which exhibit a harem system of reproduction, where large terminal phase males will mate with several initial phase females (Choat & Robertson 1975). If initial fitness is a significant determinant of FID, terminal phase parrotfishes and larger fishes should flee earlier (show higher FID) than smaller fishes or fishes with lower initial fitness with access to the same potential benefits (Cooper & Frederick 2007, 2010).FID could potentially decrease, or plateau at larger sizes if an individual attaining a large enough body size escapes predation by other fishes (Gill 2003), particularly with the reduction in the abundance of large predators on coral reefs (Graham & McClanahan 2013). Interestingly, parrotfish reproductive stage shows little predictive effect on FID in response to fishers (Chapter 3, 6 & Januchowski-Hartley et al. 2011), while fishes that are large enough to be targeted by fishers show a significant increase in FID with size, and this is consistent across fish families (Cole 1994; Gotanda et al. 2009; Miller et al. 2011; Chapters 2, 3, 6 & Januchowski-Hartley et al. 2011, 2012; but see Feary et al. 2011). Moreover, in fished areas, this relationship tends to be stronger (Gotanda et al. 2009; Chapters 2, 6 & Januchowski-Hartley et al. 2011). This may indicate either lower levels of predation on smaller parrotfishes as the fishery has removed their predators, or larger parrotfishes being unable to escape human predation.

While the effect of reproductive value on FID cannot be ruled out, because size is often linked to reproductive value in fishes, it is likely that other mechanisms, such as the energetic costs of escape are playing a role (Miller et al. 2011). In order to achieve sufficient speed to escape predators, smaller parrotfishes tend to use body and caudal fin locomotion, which is less energetically efficient than pectoral fin locomotion used by larger fishes (Drucker 1996; Domenici 2010). While the costly swimming motion of smaller fishes induces a lower FID, a more efficient but slower gait may increase the attraction of fleeing early and spending less energy (Miller et al. 2011). Fishes in NTRs tend to be larger (Lester et al. 2009), and with size and protection exhibiting different effects on FID, it is essential to include both size and fishery status as covariates in studies of FID (Gotanda et al. 2009).

In contrast to these effects seen for non-predatory families such as Acanthuridae and Scaridae, predatory fish such as the Epinephelinae (groupers), Lutjanidae (Feary et al. 2011; Chapter 3 & Januchowksi-Hartley et al. 2011) or Sparidae (Cole 1994) show little evidence of altering FID due to increased fishing pressure. Carnivorous animals are hypothesized to be more flighty due to high levels of attention to their environment, a result seen among birds (Blumstein 2006), but my results indicate this may not be consistent among fishes. Lutjanidae tend to be significantly more wary than all other families studied, and are less common as a spearfisher target family (Kaly 2005; McClanahan & Cinner 2008), potentially due to remaining beyond the effective range of spear guns (Feary et al. 2011; Chapter 3 & Januchowski-Hartley et al. 2011). In contrast, neither Sparids nor groupers are particularly flighty, and groupers often inspect intruders (Cole 1994; Chapter 3 & Januchowski-Hartley et al. 2011), potentially due to higher levels of territoriality than non-territorial fishes.

The quality of the territory in which a fish forages and spawns, and the availability of refuge within that territory are hypothesised to have significant influence on FID. However, only the latter quality (availability of refuge) is considered to have a ubiquitous and significant effect on FID (Stankowich & Blumstein 2005). Gotanda et al. (2009) and Miller et al. (2011) demonstrated that the distance to the nearest visual relief can have significant predictive influence on FID, a result driven predominantly by fishes that took refuge in holes in the reef. This contrasts to my results that indicate mixed evidence of refuge importance on predictions of FID, both inside and outside marine reserves (Chapter 6). However, where refuge availability was found to be important, the general trend was for increased availability of refugia to be associated with declines in FID [similar to findings of Gotanda et al. (2009) and Miller et al. (2011)]. In the context of coral reef fisheries this is a difficult metric to measure, because deep water can also provide a refuge from human predation – two-thirds of the fish used distance or deep water as a refuge in Miller et al. (2011) - and the reef structure may not be utilised as a refuge, particularly in fished areas (Guidetti et al. 2008). The role that patch quality (food/mating availability) may play is yet to be assessed.

Studies on terrestrial taxa, and two on coral reef fishes, have shown increases in FID with hunting, a result confirmed here for coral reef fishes and spearfishing. The results here suggest that as predicted by theory, FID is significantly influenced by experience of predation, as well as some prey conditional and environmental factors. In contrast, little evidence was found that FID was influenced by other factors such as predator type or group size. In general, I found that the level of predation risk in the environment tends to have the largest effect on FID, while predator characteristics showed little to no effect on FID (Chapters 2 & Januchowski-Hartley et al. 2012). Prey condition and environmental variables had small but significant effects (Chapters 3, 5, 6 & Januchowski-Hartley et al. 2013b). Prey fishes' response to predation threat varied significantly between fish families, and is likely to be mediated by life-history and other traits, or intrinsic levels of wariness (Chapter 3 & Januchowski-Hartley et al. 2011).

7.2 IMPLICATIONS FOR MANAGEMENT

This thesis has advanced our knowledge about the importance of changes in fish behaviour to the vulnerability of fishes to fishing, and how fish can be expected to respond to management actions. This has important implications for local fisher buy-in for NTR implementation, for the design of marine protected areas, for species-specific vulnerability assessments (particularly at the local level) and for the effects of periodically harvested closures (PHCs) on coral reef ecosystems. While fishery-induced changes in behavioural traits have generally been overlooked (Alós et al. 2012), links between behaviour and selectivity of fishing gears have often been noted (Kallayil et al. 2003; Suski & Philipp 2004; Allendorf & Hard 2009). Research on behavioural shifts within fished populations has often concentrated on susceptibility to fishing of particular behavioural phenotypes (Suski & Philipp 2004; Uusi-Heikkilä et al. 2008; Alós et al. 2012), and does not take account of potential changes in behaviour that may take place at the level of the individual fish. The work in this thesis demonstrates behavioural change that can occur due to management tools and within a relatively short time frame may influence how management of fisheries can increase catchability of fishes, and has implications for the vulnerability of different species to fishing. Both fishery and ecosystem benefits of NTRs and PHCs may be influenced by changes in fish escape behaviour across limited temporal and spatial scales (Chapters 4, 5 & Januchowski-Hartley et al. 2013a,b).

Climate change, overfishing and other anthropogenic impacts on coral reefs have led to loss of biodiversity (Hughes et al. 2003) and exploitation of reef resources beyond that considered sustainable (Newton et al. 2007). Subsequently, there have been considerable efforts to place significant proportions of reef area under protection (e.g., US Coral Reef Task Force 2003; Coral Triangle Initiative 2008). One of the most commonly proposed tools to protect coral reef systems are NTRs, with PHCs often recommended as an alternative in areas where NTRs may not be culturally appropriate (Govan 2009). Both of these types of management can have significant ecological benefits (McClanahan et al. 2006; Lester 2009; Bartlett et al. 2009), and are expected to contribute towards both fishery sustainability and conservation. NTRs, through the preservation of large, fecund individuals can replenish local reefs through larval export (Harrison et al. 2012), and adjacent reefs through density-dependent spillover of adult fish biomass (Russ 2002). Chapters 3 and 5 (Januchowski-Hartley et al. 2011; 2013a) of this thesis show that in NTRs and PHCs flightiness of reef fishes can be greatly reduced after only a few months, and potentially this behaviour can be exported outside NTRs (Chapter 4 & Januchowski-Hartley et al. 2013b). This provision of fish that are potentially more catchable to reefs surrounding a NTR or PHC represents a benefit to local fishers that has previously not been demonstrated. It is a conceptually simple mechanism that agrees with local expectations of outcomes of protection in some areas (Macintyre & Foale 2004; Feary et al. 2011), and can be easily explained and demonstrated (spearfishers will notice being able to approach a target fish more easily). This may aid in engendering support for NTRs, and increasing compliance. However, the spatial scale at which this occurs is relatively small, and undesirable results, such as increased fishing the line near NTR boundaries may result in penetration of fishing effects further into a reserve (Kellner et al. 2007; Chapter 6), and on smaller reserves the possible loss of any potential enhancement of biomass (Claudet et al. 2008).

Chapter 6 further demonstrates the permeability of reserve boundaries to behaviour with fishes in protected areas in a heavily fished seascape (~ 80 fishers km^{-1} reef front) demonstrating similar FID to fish in fished areas at low (< 5 fishers km^{-1} reef front) levels of fishing. This difference in behaviour may mean that fishes in NTRs surrounded by heavily fished areas may change foraging behaviour, with potential impacts on cover of algae (Madin et al. 2010b). There is evidence suggesting that fishing can preferentially remove fishes demonstrating less-wary behaviours (Suski & Philipp 2004), with the result that fish populations recruiting within a heavily fished seascape could be intrinsically more flighty. Alternatively, socially transmitted behaviour from fishes that have experienced fishing may be penetrating fully into the protected areas (Pitcher et al. 1986; Chapter 4 & Januchowski-Hartley et al. 2013b), which are all relatively (< 1 km reef front) small. If this latter hypothesis is the mechanism that is at work, it provides further evidence that larger marine reserves are required in order for full benefits of protection to be realised (Claudet et al. 2008).

Temporal and spatial variability in FID implies that catchability of fishes also varies both temporally and spatially. Furthermore, differences between fish families in intrinsic wariness and temporal change in behaviour may result in some families having considerably higher vulnerability to fishing than others (Alós et al. 2012). In the context of PHCs, this may mean that even if overall fish biomass appears relatively high, certain families that are significantly more catchable due to PHCs may be disproportionately low in biomass when compared to NTRs (Chapter 5 & Januchowski-Hartley et al. 2013a). This has primarily been seen for Acanthuridae, which appear particularly vulnerable to spearfishing after opening of a PHC, potentially due to behavioural characteristics, including reduced FID (Jupiter et al. 2012; Chapter 5 & Januchowski-Hartley et al. 2013a). However, in PHCs that have experienced several opening/closing cycles, Acanthuridae showed a significant increase in FID to above the mean effective range of spear guns in just three days of low fishing intensity (Chapter 5 & Januchowski-Hartley et al. 2013a). Other families such as groupers, which show little change in behaviour with fishing pressure (Chapter 3 & Januchowski-Hartley et al. 2011)), may not be able to respond as quickly to fishing events may be more at risk. This is particularly concerning for groups or species of fish that may play a key role in the trophic structure of some coral reefs such as *Bolobometapon muricatum* and large predatory species (Dulvy et al. 2004). Fishing on top level predators such as groupers may lead to increases in mesoconsumer abundance leading to reductions in abundance of targeted species (Heithaus et al. 2008) or reef degradation through release of crown of thorns starfish (Dulvy et al. 2004) or eroding urchins (McClanahan & Muthiga 1988; McClanahan et al. 1995). These results have important implications for using catch data to examine the condition of a fishery. Hyperstability, where catch rates remain high even as abundance declines (Hilborn & Walters 1992) has been shown for aggregating species (Erisman et al. 2011). Similar patterns may be present for species that show slow changes in behaviour, particularly groupers, which due to the reliability of the spatial location and timing of aggregations are already potentially highly vulnerable to fishers (Hamilton et al. 2012). Hyperstability may also occur in fished areas that receive an influx of fishes from unfished populations (e.g., through spillover), where high catch rates in fishing grounds near NTRs may mask both local depletion, and slower than expected build-up of biomass within the reserve, if fishes crossing reserve boundaries are highly catchable.

7.3 FUTURE RESEARCH DIRECTIONS

The role of fish behaviour in ecosystem processes, conservation and management of coral reef fisheries is becoming increasingly recognised (Madin et al. 2010a, b; Hamilton et al. 2012; Chapters 4, 5 & Januchowski-Hartley et al. 2013b, in press). There are many avenues for future research directions that have become apparent during my thesis and will likely prove fruitful. In the remainder of this chapter I will highlight four of these potential avenues, elaborating on their value to research and how they build upon work in this thesis.

Firstly, from a behavioural perspective, two aspects of research that may be fruitful: species-specific traits, and further investigation of environmental factors that influence flight decisions. The applied and observational nature and focus of this thesis on assessing behavioural changes of coral reef fish on fished reefs within a management framework limited my ability to accurately assess some important factors that may influence FID. Due to the limited spatial extent of areas over which much of the research was conducted, I was unable to estimate FID for fishes at the species level without potentially violating independence of samples, or sampling the same fish on more than one occasion. This required grouping fishes at the family level, despite life-history traits having been shown to be important in other taxa (e.g., birds - Stankowich 2006), and differences in FID between species within families having been observed (over 100 cm difference in mean FID between *Scarus niger* and *Chlorurus sordidus* in fished areas – Feary et al. 2011). Further work on species-specific differences in flight response, potentially looking at life-history traits and other behaviours such as pre-flight behaviour or refuge choice would be important to fill out our theoretical knowledge of FID in the marine environment, identify which species are likely to be vulnerable on the basis of their behaviour and relate this to current knowledge of fishery vulnerability.

While patch quality, territoriality and mating opportunities have shown relatively weak overall predictive ability for FID in terrestrial animals (Stankowich & Blumstein 2005), coral reef fishes proved a potential model system to investigate some of these factors. The relative flightiness of animals is likely to be somewhat dependent on activity, and resource availability. To control for activity, I specifically avoided fishes that were engaged in territorial aggression or spawning/mating, which may reduce FID of a prey animal (Walther 1969; Ydenberg & Dill 1986; Cooper 2003b; Cooper et al. 2003, 2009). Hypothetically, in broadcast spawning coral reef fishes it is possible that total lifetime benefits are increased if a mating opportunity is taken, even if it results in death, because it results in the production of offspring that do not require parental care (Cooper & Frederick 2007). In this thesis I did not assess patch quality, with the exception of refuge availability. While the evidence for significant effects of refuge availability on FID of coral reef fishes is suggestive if inconsistent (see above), I am not aware of any work that has been conducted on other aspects of patch quality such as food availability for reef fishes, leaving this a good candidate for further research.

A second potentially fruitful avenue of research would be into the potential of FID as a tool to measure compliance within NTRs and other areas under protection. The effect of protection on FID is significant (Chapters 2, 3, 5, 6 & Januchowski-Hartley et al. 2011, 2012, in press) and is consistent between NTRs and adjacent fished areas at even very low fishing pressures (Chapter 6). Moreover, it shows relatively low instantaneous variation or variation between observers, unlike underwater visual census of reef fish communities (McClanahan et al. 2007a), and differences in FID between fished and well-protected areas potentially can develop within months of protection (Chapter 5 & Januchowski-Hartley et al. 2013a) rather than years as documented for fish abundance and biomass (Alcala et al. 2005). FID has also been shown to be relatively sensitive with significant changes after only a few days of low intensity fishing (Chapter 5 & Januchowski-Hartley et al. 2013a). Furthermore, detection of FID should be relatively easy to teach to community monitors of protected areas, who are often spearfishers, can be conducted rapidly with no specialised gear (~ 12-15 measurements can be made in one hour by an experienced observer, and power analysis suggests this is a sufficient number of replicates per area to detect an effect (Chapters 2, 5 & Januchowski-Hartley et al. 2011, in press) and requires little post-data collection analysis. Two major caveats to the use of FID as a compliance indicator are: 1) FID can vary substantially by family and with natural history traits, therefore selection of focal families is important; and 2) FID will not show significant differences between NTRs and fished areas if poachers are concentrating on a group that does not vary in FID with fishing pressure (e.g., groupers) or are using a gear which does not select for low FID fishes or provide a stimulus for flight (e.g., hook and line). In this study I selected areas that I had reason to believe were well protected. In order to properly implement or assess FID as a tool to assess compliance, future research on how FID is influenced in NTRs with low compliance, as well as further refining the techniques to assess to what degree known covariates such as fish size and refuge availability are required.

The third potential avenue for research would be to assess how changing fish behaviours interact with fishing gears other than spear guns and management strategies. Other active gears, such as drive nets may have similar effects on FID as spearfishers, but possibly trigger flight through different cues, for example sound (Parrish 1999). If changes in behaviour (for example, loss of wariness due to protection) can make fish temporarily more susceptible to fishing gears, it is important to know which gears take advantage of these changes, and how these influence the vulnerability of fishes to fishing and the sustainability of coral reef fisheries. During this thesis, I found that where spear guns were often a secondary or tertiary gear, significant changes in FID compared to inside NTRs were still recorded (Chapter 4 & Januchowski-Hartley et al. 2013b). It is well established that selection by fishing gears other than spear guns is likely to have a behavioural component; experimental fishing of captive bred populations has indicated that large-mouth bass (*Micropteres salmoides*) that are more aggressive when defending nests are more likely to be caught when using hook and line (Suski & Philipp 2004) and fishes that show higher levels of activity are more likely to be caught by passive gears such as gill nets (Alós et al. 2012; Olsen et al. 2012). The use of management tools or fisheries strategies on coral reefs that take advantage of behaviour can result in dramatic declines in the abundance of some species and exceptionally high effectiveness of some fishery gears (Hamilton et al. 2012; Jupiter et al. 2012). Research on how observed differences between fish families in behavioural responses to management and fishing (Feary et al. 2011; Chapters 3, 5 & Januchowski-Hartley et al. 2011 in press), and gears may be important in assessing vulnerability to overexploitation and in forming sustainable management plans on local scales.

Finally, the fourth avenue is to investigate whether changes in fish flight behaviour in and surrounding NTRs result in trophic effects. The decline in abundance of higher-level marine predators, particularly on coral reefs, has led to a call for research on behaviourally mediated consequences of fishing (Heithaus et al. 2008). We know that trophic cascades through overfishing higher trophic level species on coral reefs can result in mesoconsumer release and ecosystem degradation (McClanahan et al. 1995; McClanahan 2000). However, there is evidence from the Caribbean that protection can result in desirable cascades, with increased grazing of macroalgae due to higher abundance of grazers facilitating coral recruitment (Mumby et al. 2007). Fishery induced trophic cascades have been observed on coral reefs (McClanahan & Muthiga 1988; Dulvy et al. 2004), but are far from ubiquitous (Mumby et al. 2006; Newman et al. 2006, Bruno et al. 2009), and the mechanisms by which fishing influences ecosystem processes such as grazing are generally less well understood in the species-rich Indo-Pacific (Mumby et al. 2013). Alterations in predation risk due to human removal or reintroduction of predators can influence spatial distribution of prey foraging and per capita consumption rates (e.g., Ripple et al. 2001, Schmitz et al. 2004; Madin et al. 2010b). Importantly, these non-consumptive effects of predators can be independent of any numerical changes in the prey species while playing a key role in driving observed patterns in predator-prey interactions (Dill et al. 2003; Heithaus et al. 2008; Peckarsky et al. 2008).

Recent research in the Line Islands identified fear-release of herbivorous fishes when predator biomass was reduced through fishing, leading to herbivores foraging for longer and further from shelter (Madin et al. 2010a). Ecosystem mediated consequences of changes in behaviour have been identified in in other ecosystems within the marine realm (Dill et al. 2003; Heithaus et al. 2008). For example, in Alaska changes in the diet preferences of killer whales reduced the abundance and distribution of sea-otters (which would move shoreward), reducing predation pressure on urchins, which increase in abundance, giving rise to urchin barrens (Peckarsky et al. 2008). While changes in density of otters certainly decreased predation on urchins, non-consumptive effects on otter behaviour is likely to have increased the magnitude of the trophic cascade on kelp forests (Peckarsky et al. 2008). Changes in fish behaviour driven by fishing could similarly influence the ecosystem consequences of fishing (Dill et al. 2003; Madin et al. 2010b). Future research on the behavioural consequences of fishing for processes such as grazing, coral predation and bioerosion is necessary to uncover the potential consequences for the wider ecosystem. Changes in abundances and sizes of organisms can influence the magnitude of ecosystem processes on coral reefs (Bellwood et al. 2012), but an understanding of how behavioural changes further influence alterations in ecosystem processes is poorly understood.

7.4 CONCLUDING REMARKS

This study has shown that coral reef fishes targeted by subsistence fishers will change their flight behaviour significantly in response to protection from fishing. While agreeing with many of the predictions of FID theory about influential factors such as fish size and refuge availability, previous experience of fishing and the intensity of fishing had the strongest effects on FID (Chapters 2 & 3). Furthermore, I showed that there are several management implications from this work, including local accessibility of benefits from NTRs (Chapter 4), increased fishing efficiency in the immediate days following opening of a periodically closed area (Chapter 5), potential differences in vulnerability of different families of fishes to fishing driven by behaviour (Chapters 3 & 5) and possible effects of fishing on behaviour that may intrude into small NTRs (Chapter 6). These results indicate that behavioural responses to both protection and fishing will have influence across ecological, fisheries management and conservation disciplines. Furthermore, they highlight the need for more research on the drivers and consequences of behavioural change to predict future trajectories of coral reef health.

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APPENDIX A: OTHER PEER-REVIEWED ARTICLES PUBLISHED DURING MY CANDIDATURE

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