Predator-Prey Interactions in Coral Reef Fish:
The Implications of Predation Risk on the Behavior and Growth of Prey

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Abstract

Sublethal or nonlethal predator-prey interactions (predation risk) can influence prey species' behaviours and food web dynamics across a wide-range of ecological communities and diverse taxa. In this thesis, I explore the potential for predation risk to influence the behaviour and growth of marine animals. Local predation risk fluctuates greatly in space and time and anti-predator behaviour is expected to be selected over evolutionary times to optimise prey fitness. Flexibility in behavioural responses to predation risk is likely to be an evolutionary adaptation that mitigates the trade-offs between the costs of physical and chemical defences against predators and maximising growth and reproduction. In high-risk situations during the life of an animal, anti-predator behaviour maximising survival may reduce net energy intake by an individual and potentially its reproductive fitness relative to net energy intake and fitness in low risk situations. I identify major determinants of, and common prey responses to, predation risk in marine environments. I argue that nonlethal predator-prey interactions influence the behaviour of marine species and, because of the high phenotypic plasticity characteristic of these animals, are likely to affect life-history traits such as growth and size-at-maturity. These effects may be especially significant in speciose communities, such as coral reefs, where the number of nonlethal interactions is high.

I examine the anti-predator behaviour of juveniles and adults of a number of species of site-attached coral reef fishes. In order to test for a change in behaviour due to predation risk, I exposed these fishes to a caged Serranid predator, *Cephalopholis cyanostigma*, in laboratory aquaria. Seeking and associating with refuge was the most common antipredator response in diurnal species of the prey fish, *P. moluccensis* and *P. amboinensis*. Conversely, two nocturnal prey species (*Apogon fragilis* and

Cheilodipterus quinquelineatus) moved away from their refuge in the presence of the reef piscivore, presumably to avoid attacks from potential ambush predators. Both size-classes of the four species of prey examined reduced their foraging significantly in the presence of a predator. Vigilance, however, was primarily a role assumed by adults and not juveniles. Such differing ontogenetic behaviour and the associated selected advantages may help explain the persistence of mixed size-class groups, a common feature in social groups of coral reef fish planktivores. Moreover, anti-predator behaviour of individual coral reef fish may depend on the ecology of that species and the specific foraging of its ontogenetic stage.

I then examined, more closely, predator-induced modifications in foraging behaviour of a common tropical fish, *Pomacentrus moluccensis*, in groups of different size and at different ontogenetic stages on coral reefs in the Great Barrier Reef. Different group sizes of *P. moluccensis* were exposed to a potential predator or non-predator and changes in foraging behaviour of juveniles and adults were observed. In the presence of a predator, foraging effort, estimated by the number of bites taken and foraging distance away from shelter, was reduced whilst the presence of a non-predator caused an increase in foraging distance of *P. moluccensis*. In the presence of a predator, adults exhibited greater reduction in foraging than juveniles. Juveniles continued foraging even in the presence of predators which may help explain maintenance of high growth rates in young coral reef fishes. In contrast, reduced foraging in adults might reflect an emphasis on survival. Prey fish in large groups exposed to a predator displayed less reduction in foraging effort compared to fish in smaller groups. This was consistent with observational surveys that show a reduction in per capita vigilance with an increase in prey group size. Therefore, aggregating in coral reef fishes, a common phenomenon,

may serve to dilute predation risk and increase individual foraging effort in social groups of pomacentrids. These results suggest that nonlethal predator-prey interactions may have an important effect on food ingestion rates and therefore energy uptake of coral reef fish. These effects were mediated by prey group size and ontogeny.

Finally, I investigated the effects of non-fatal interactions on prey morphology and growth, and explored how intraspecifc density may influence these effects. Using experimental manipulations of group sizes of *Pomacentrus moluccensis*, and a system of artificial coral reefs and cages at Lizard Island on the Great Barrier Reef (GBR), I tested the prediction that predation risk would reduce foraging and growth in this species while grouping would dilute this risk and ameliorate some of these negative effects. Results indicated that the risk of predation affected the behaviour and reduced the growth rate of the prey and that these effects were most pronounced in small prey group sizes. Observational data collected from natural reefs in the immediate vicinity suggested that a reduction in per capita vigilance with increase in group size may explain the diminished individual costs of predation risk recorded in large groups. These results suggest that predators may significantly reduce the growth of a prey individual at low prey group size, but will have a smaller effect at higher prey group sizes due to a reduction in per capita vigilance. This suggests that social groups in coral reef fish systems may have evolved, in part, to optimise the trade-offs between survival and growth. Suppression of growth due to predation risk may affect population dynamics of adult coral reef fish by regulating the rate of individuals reaching reproductive maturity and/or by increasing the probability of size-selective mortality on juveniles.

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Chapter 1

General Introduction
Non and sublethal effects of predation on coral reef fishes

1.1 Background

Predation is a process of fundamental importance in the dynamics of many ecological systems (Taylor 1984). Predation has traditionally been distinguished from other forms of foraging in that it concludes with the eventual death and consumption of the prey (Curio 1976). Predator-prey theory examines the dynamics of predator searching (Tinbergan 1960), prey choice (Elner and Hughes 1978), prey switching (Murdoch and Oaten 1975), and evolution of predator ecology and morphology (Ehrlich 1975) but can also predict the effect of predators on the behaviour (Lima and Dill 1990), morphology, (Van Buskirk 2000), density (Hixon and Carr 1997), and dynamics of prey individuals and populations (Caley *et al.* 1996).

Classical predation theory examines the lethal effects of predators on prey and may predict diverse consequences of mortality on prey behaviour, morphology, and dynamics (Curio 1976; Taylor 1984). Some of these predictions include density dependent mortality and therefore predator-regulation of prey populations, evolution of specialised predator-avoidance strategies, and coexistence of competing prey (Curio 1976; Holt 1977; Zaret 1980; Hanski 1981; Caley 1995; Hixon and Carr 1997). Predator-induced mortality can also alter prey populations sufficiently to modify the interactions between species in a food web (Abrams 1987). Such interactions are referred to as density-mediated because the type and intensity of the interaction between two species may depend on the density of a third intermediate species (Schmitz 1998; Peacor and Werner 2000; Vonesh and Osenberg 2003).

Unlike predation, the *risk* of predation does not alter the density of prey individuals through immediate mortality but there may be significant modification of prey behaviour associated with the presence and threat of predators (Crowder *et al.* 1997; Krivan and Vrkoc 2000; Spieler 2003; Ward *et al.* 2000). The risk of predation can influence foraging behaviour, food accessibility and diet, habitat use, growth, and reproduction in many animals (Magnhagen 1991; Gerking 1994; Dahlgren and Eggleston 2000; Candolin and Voight 2003). In plastic life histories, extrinsic factors such as predation risk and competition can affect foraging and growth (Jones and McCormick 2002). Such effects may, in turn regulate body size, ontogenetic development, fecundity, and ultimately the reproductive success of individuals (Wootton 1992). Food web dynamics can also be affected as the type and intensity of interactions between two species may be mediated by the behaviour of a third intermediate species (Peacor and Werner 2000).

Optimal foraging theory predicts that prey will balance the positive and negative effects of foraging through modifications in behaviour (Lima and Dill 1990). There is a fundamental trade-off between growth and risk of predation that is mediated by foraging activity (Abrams 1990; Abrams 1991; Werner and Anholt 1993). More active individuals encounter food faster and grow faster but are at higher risk from predators than less active individuals (e.g. fish: Grant and Noakes 1987; tadpoles:

Skelly and Werner 1990). Increasing foraging activity and success can increase reproductive rate if there is a net energy gain (Abrams 1991) but may decrease survival as exposure and vulnerability to predators increases (Sih and Moore 1989). If predation risk declines with size, animals are predicted to increase foraging activity as they grow (Stein and Magnuson 1976; Werner and Anholt 1993), though the need for energy for maintenance and reproduction may also drive increased foraging in later-stage individuals. Because foraging activity is a trait that is also associated with competitive ability (Jones 1991), these trade-offs may be modified by prey group size. It is important, therefore, to characterise the mechanisms underlying these trade-offs in order to predict quantitatively their consequences and incorporate those consequences in population models (Werner and Anholt 1993).

1.2 Aim of this study

The primary aim of my study was to estimate the influence of predation risk on fish prey on coral reefs and infer the implications for any influence on fitness of those prey. Specifically, I aimed to determine whether predator presence and threat and stress of predation affects foraging and subsequent growth of common prey fish on coral reefs. I also investigated how such responses changed with ontogeny and group size of prey.

1.3 Research questions motivating the thesis

In the thesis I explore four main themes designed to elucidate the role of predation risk in coral reef fish communities:

1. <u>Nonlethal Effects in Marine Species</u>

A. What are some of the common behavioural responses of prey to predators in marine systems?

B. What factors may influence anti-predator behaviour in marine prey?

C. Why can predation risk play an important role in the life-history of marine organisms?

D. What are the potential implications of predation risk on fitness of prey individuals and population dynamics?

<u>2. Nonlethal Effects in Aquarium Experiments:</u>

Different Anti-Predator Behaviour in Coral Reef Fish Prey

A. How do some common prey species of social, aggregating, and site-attached, coral reef fish (*Pomacentrus moluccensis, Pomacentrus amboinensis*, *Apogon fragilis*, and *Cheilodipterus quinquelineatus*) modify their behaviour in the presence of non-lethal predation risk?

B. How does anti-predator behaviour change with diurnal or nocturnal foraging habit of prey fish?

<u>3. Nonlethal Effects in the Field</u>:

Behavioural Modifications in a Common Coral Reef Fish Prey

A. How does *P. moluccensis* modify foraging effort (distance from refuge and number of bites taken) in the presence of predators?

B. Is *P. moluccensis* sensitive to the level of ambient risk and will it respond accordingly with increased vigilance?

C. How do these changes in behaviour vary with life-history stage (juvenile or adult) and prey group size?

4. Demographic Consequences of Nonlethal Effects:

Potential Fitness Costs of Predation Risk in Coral Reef Fish Prey

A. Do predator-induced modifications in behaviour incur any costs in terms of fitness, such as change in growth, in coral reef prey fish?

B. Does group size influence the intensity of potential fitness costs?

1.4 Study System

Predators and prey

I used six species of reef fish in my experimental manipulations and field observations. Appropriate animals to use as prey were species that represented a substantial component of coral reef fish species (Randall *et al.* 1997), were common prey to many reef piscivores (Hiatt and Strasburg 1969; St. John 1995; Hixon and Carr 1997; Stewart 1998), and were plentiful and easy to collect. Diurnal and nocturnal activity may also influence the foraging ecology and anti-predator behaviour of prey fish and therefore it was important to select study species that covered a range of activity periods. Four species of prey that fitted these criteria were the diurnal damselfishes *Pomacentrus moluccensis* and *Pomacentrus amboinensis,* and the nocturnal cardinalfishes *Apogon fragilis* and *Cheilodipterus quinquelineatus*. These species occur in different sized groups (Mapstone 1988; Jones 1991; Marnane 2000; Marnane In Review), all are planktivorous with the exception of *Cheilodipterus quinquelineatus* (Jones 1991; Kerrigan 1994; Marnane and Bellwood 2002), and adults and juveniles are readily distinguishable (Jones 1991; Marnane and Bellwood 2002), facilitating easy examination of the role of group size and ontogeny in mediating any effects of predation risk.

I used two species of piscivores that are natural predators of the four chosen prey species (Sano *et al.* 1984; Westneat and Wainright 1989; Stewart 1998): the blue-spotted rockcod, *Cephalopholis cyanostigma*, and the slingjaw wrasse, *Epibulus insidiator,* in aquarium and field experiments. *C. cyanostigma* are benthic, ambush predators and *E. insidiator* are active, roving predators (Gottlieb 1992; Randall *et al.* 1997; Westneat and Wainright 1989; Stewart 1998). Thus, these species represent two major predator functional types characteristic of many coral reefs. Rockcods of the genus *Cephalopholis* are highly piscivorous in diet (Shpiegel and Fishelson 1989; Martin 1994; Stewart 1998) and are suitable for laboratory and field experimentation (Beukers and Jones 1997; Stewart 1998). The roving predator *E. insidiator* is a generalist predator of coral-dwelling invertebrates and fishes (Sano *et al.* 1984; Randall *et al.* 1997). Its relatively small size and its conspicuousness in the water column proved ideal for manipulative field experimentation.

Study site

All experiments and observations were conducted on reefs in the vicinity of Lizard Island and at the Lizard Island Research Station between April 1, 2001 and March 11,

2003. Lizard Island (14°40'S 145°28'E) is situated on the mid-shelf of the northern region of Australia's Great Barrier Reef, 30 kilometres from the Australian mainland and 19 kilometres from the outer barrier reefs that line the edge of the continental shelf and 270 km north of Cairns, Queensland. It is a continental island about 7 square kilometres in size, with three smaller islands nearby (Palfrey, South and Bird). Together these islands form the Lizard Island Group and their well-developed fringing reef encircles an extensive lagoon. Field observations and experiments were conducted at various locations around these islands.

1.5 Structure of the Thesis

This thesis consists of six chapters. Three data chapters (chapter 3, 4, and 5) follow the general introduction (chapter 1) and review of the literature (chapter 2). The final thesis chapter (6) is the general conclusions.

In chapter two, I present evidence from the literature to suggest that predation risk plays an important role in the dynamics of marine food webs. Using coral reefs as a case study, I illustrate the possible implications of nonlethal predatory effects on prey behaviour and fitness. I argue that certain ecological characteristics are necessary before non-lethal predation can play a significant role in the dynamics of individuals, populations, and communities. I outline characteristics of coral reef fish communities that make them likely to exhibit strong nonlethal effects of predation.

In chapter three, I describe laboratory experiments used to test the prediction that the presence of a predator would cause a significant modification in prey behaviour and to quantify how behavioural responses to this threat differed among prey species and between ontogenetic stages within species. Behavioural observations included measurements of shoaling and aggregation, foraging, vigilance, and refuge seeking in the presence and absence of predators. Feeding was reduced or interrupted in the presence of predators, animals reduced their foraging distance from their refuge, and vigilance was a behaviour of adults. Anti-predator behaviour varied, however, and may be associated with the specific foraging and diel activity of a prey species.

In chapter 4, I describe tests of the prediction that anti-predator behaviour translated into foraging reduction in the field, and I examine the extent to which this depends on group size. I used experimental introductions of captive *Epibulus insidiator* (Slingjaw wrasse) to test for effects of predator presence on foraging activity of different sized groups of *P. moluccensis*. Responses of adults and juveniles were video taped, and the video was subsequently analysed. Behavioural responses to the threat of predation appeared to be a reduction in foraging distance and number of bites taken. Adults displayed a higher reduction in foraging than juveniles did. In addition, social grouping appeared to reduce the effects of predator presence on foraging, as larger groups reduced foraging distance and bites less than smaller groups.

Having demonstrated that exposure to predators reduced foraging activity, I tested the prediction that such a behavioural response would cause a reduction in growth of prey. Group size and exposure to predation were manipulated on experimental artificial reefs. Results showed that growth of *P. moluccensis* was dependent on different levels of potential predation risk and group size. This study indicated that the reduction in foraging documented in chapter 4 could have a fitness cost for the coral associated planktivorous reef fish. This cost decreased with an increase in group size, possibly due to a reduction in per capita vigilance and associated increases in time available for foraging.

Chapter six draws general conclusions from the results in the context of predation, competition, foraging, and life-history theory. The threat of predation has been shown to modify the foraging behaviour of coral reef fishes and increase vigilance in adults. Effects on juveniles were less, but even smaller effects are large enough to lead to a reduction in growth in the presence of predators. This, in turn, may lead to delay in attaining the benefits of large size such as competitive dominance, fecundity, and reduced susceptibility to predators. At the population level, these effects are likely to lead to modifications in population size-structure and growth and resource consumption. Aggregating in groups appears to be correlated with dilution of some of the negative effects of predation risk and thus might constitute a defence strategy. Grouping in coral reef fishes may have evolved, at least in part, as a response to the threat of predation.

Chapter 2

The Role of Predation Risk in Marine Systems

2.0 Abstract

Sublethal or nonlethal predator-prey interactions (predation risk) can influence prey species' behaviours and food web dynamics across a wide-range of ecological communities and diverse taxa. In this review, I explore the potential for predation risk to influence marine animals and population dynamics. Local predation risk fluctuates greatly in space and time and anti-predator behaviour is expected to be selected over evolutionary times to optimise prey fitness. Flexibility in behavioural responses to predation risk is likely to be an evolutionary adaptation that mitigates the trade-offs between the costs of physical and chemical defences against predators and maximising growth and reproduction. In high-risk situations during the life of an animal, anti-predator behaviour maximising survival may reduce net energy of an individual and potentially its reproductive fitness relative to net energy and fitness in low risk situations. I identify major determinants of, and common prey responses to, predation risk in marine environments. I argue that nonlethal predator-prey interactions influence the behaviour of marine species and, because of the high phenotypic plasticity characteristic of these animals, are likely to affect life-history traits such as growth and size-at-maturity. These effects may be especially significant in speciose communities where the number of nonlethal interactions is high. More studies are needed to understand the potential cascading effects of predation risk (such as delayed sexual maturity, interrupted mating, reduced progeny, and prey redistribution) on reproductive fitness and local population dynamics in marine systems.

2.1 Introduction

2.1.1 Predation

Modern interest in predation theory was inspired by the classic work of Lotka, Volterra, and Gause and its significance is widely recognised in most food webs (Taylor 1984; Sih 1985; Hixon 1991; Clutton-brock 1999; Sheaves 2001). Predation has often been cited as a strong selective force in evolution (e.g. Vermeij 1982; Sih 1987) and one with the ability to regulate diversity by mediating species coexistence (Paine 1966; Caswell 1978). The evolution of morphologies such as cryptic coloration, armour, and chemical defences has been attributed to selection for avoiding predation (Edmunds 1974; Ehrlich 1975; Harvey and Greenwood 1978). Sociality in animals (Bertram 1978; Clutton-brock *et al.* 1999; Spieler 2003) and certain reproductive strategies (Burke 1982; Magnhagen 1991) are thought to have evolved to decrease the probability of predation. Historically, predation has been seen as important only where predators consume prey (Lima 1998). The nonlethal effects of the mere presence of predators have received much less attention, but, recently, a number of authors have highlighted their potential importance (reviewed in Lima and Dill 1990).

2.1.2 Predation risk

Predators can have large impacts on prey communities, aside from actual mortality effects, because of the flexibility in prey behaviour (Lima 1998). For instance, predation risk may influence activities such as foraging, refuge-seeking, and mating, influencing such traits as growth and fecundity and therefore affecting individual fitness (Lima 1998) and seasonal or annual patterns in prey density (Downes 2001). Such direct behavioural effects of predators on prey can also have secondary indirect effects on other species interactions (Kerfoot and Sih 1987; Schmitz *et. al 2004*) and population growth (Sparrevik 1999) that may be positive or negative. Despite these potentially significant effects, behaviourally-mediated, nonlethal predator-prey interactions have not been considered important in food webs until recently, when a flurry of studies on terrestrial and freshwater systems has highlighted their important role (see reviews in Lima and Dill 1990; Lima 1998; Lima 2002; Schmitz *et al.* 2004).

Evolutionary adaptations only provide general defences against predators. During the life of an animal, however, the risk from predators can vary greatly with season, day, or from one minute to the next (Lima 1990; Helfman 1989). Animals, therefore, could derive advantages by responding to ambient risk levels by modifying their behaviour (Sih 1987). There is growing evidence that animals have the ability to assess their risk of being preyed upon and incorporate this information into their decision-making (Lima and Dill 1990). In ecological time then, individuals would trade off foraging and sheltering from predators (Sih 1997; see chapter 3 and 5), foraging individually and shoaling (Connell 2000; Hoare *et al.* 2000a; Hoare *et al.* 2000b; see chapter 4), immediate and future mating (Magnhagen 1991), or growth and survival (Werner and Anholt 1993; see chapter 5). Individuals' responses to environmental stimuli, such as predation risk, may increase or decrease survival and reproduction, and over evolutionary time certain behavioural responses will become more prevalent. Such context-dependent behaviour may reduce the need for an evolutionary compromise between morphologies (Endler 1987). The combination of morphological adaptations and flexible, behavioural decision-making maximises predator-evasion abilities and thus, presumably, fitness of an animal (Lima 1998).

2.1.3 Effects of predation risk

The capacity of predation risk to alter the behaviour of, and interaction between, species and individuals has been demonstrated for many different food webs (reviewed in Lima and Dill 1980; Lima 1998). Behavioural modifications in response to predation risk have been found in diverse habitats, including terrestrial, arboreal, and freshwater, and with species ranging from large savanna mammals to planktonic lake organisms (Clutton-brock 1999; Cai-Lin 2002). In all these cases, the hazard of predation has altered the behaviour of prey individuals sufficiently to influence daily activities (e.g. Kelly 2001; Spieler 2003) and in some cases reproductive fitness (Magnhagen 1990; Downes 2001). Such behavioural modifications include crypsis and refuge-seeking, foraging reduction, and increased vigilance. Trade-offs arising from such changes in behaviour typically include improved survival or reduced food intake and mating. Lima (1998) has suggested that anti-predator trade-offs are common in many different taxa and in many different contexts but an earlier review underscored the paucity of marine examples (Lima and Dill 1990).

In this chapter, I review accumulating evidence of the significant role of predation risk in marine environments. In the last decade, a variety of studies have been done that suggest that marine animals do modify their behaviour according to ambient risk. Such behavioural modifications exist in many marine habitats and I describe and examine trends between these diverse environments. I discuss a number of critical factors, such as group size, ontogeny, and reproductive activity, which appear to be major determinants of the level of predation risk and influence associated anti-predator behaviour. I argue that anti-predator behaviour and ensuing phenotypic changes are substantial and marine organisms in highly diverse systems may be especially prone to nonlethal predator effects. Consequently, I propose that predation risk may incur fitness costs on individuals in marine food webs and can affect the dynamics of prey populations. Finally, I identify gaps in existing theory and recommend avenues of future research.

2.2 Predator-induced behavioural modification in marine prey

Recent studies suggest that the primary and most conspicuous consequence of predation risk is a change in prey behaviour (see Table 1). The level of perceived risk and how individuals respond will be influenced by a number of factors (see section 2.3). Anti-predator behaviour of marine organisms reflects the 3-dimensional motility, resource accessibility, and refuge availability unique to aquatic habitats (Reese and Lighter 1978; Kerfoot and Sih 1987). General behavioural responses of marine prey to the presence of predators include crypsis (Endler 1987), reducing foraging space (Reese 1978), seeking refuge (Sih 1997), shifting habitat (Connell 2002), vigilance (Helfman 1989), shoaling (Connell 2000; Hoare 2000), and interrupting reproductive activity (Magnhagen 1990).

2.2.1 Foraging reduction, crypsis, and refuge-seeking

The costs and benefits associated with the activity levels of animals are key determinants of risk (Lima 1998). By adopting rapid and flexible responses to changing predation risk, potential prey can reduce the cost of unnecessary or excessive action (Hagen 2002). A reduction in general activity is a common response to the visual or chemical detection of marine predators (Appleton and Palmer 1988; Nicieza 1999; Downes 2001). In response to risk, prey typically reduce speed, frequency, and length of movement. For example, prey may reduce their time spent foraging (e.g. by spending more time hiding, Mittelbach and Chesson 1987), change the locations at which they forage (e.g. by foraging close to a refuge, Dill and Fraser 1985) or reduce their rate of resource consumption while foraging (e.g. through increased vigilance to detect predators, Prejs and Prejs 1987; Sih 1987; Sih 1997; Connell 2002). The seagrass shrimp, *Tozeuma caroliense*, reduces its movement in the presence of the pinfish *Logodon rhomboides* (Main 1987). The gastropod, *Thais lamellosa,* also exhibits such behaviour when exposed to chemical cues of crabs or injured conspecifics (Appleton and Palmer 1988). In benthic invertebrates such as the rose anemone, *Urticina piscivora*, individuals detach from the substrate and travel in response to the presence of predators (Houtman *et al*. 1997). Zooplankton also escape in the presence of the predatory copepod *Acanthocyclops vernalis* (Li and Li 1979). Some species of hermit crab increase their crypsis by increasing the number of anemones placed on their shells when they detect the presence of a predatory octopus (Brooks and Mariscal 1986). These changes in behaviour are likely to reduce the probability of being detected or encountered by a predator and therefore also reduce the probability of mortality. Such actions, however, may interrupt foraging and reduce total energy intake.

2.2.2 Reduction in reproductive activity

Anti-predator behaviour such as vigilance, defence, or escape can also interfere with reproduction (Sih 1980; Anholt and Werner 1995). The risk of predation can differ between sexes as a result of conspicuous mating behaviour by males to attract females (section 2.3.4). Reduced motility, manoeuvrability, and increased visibility of gravid and egg carrying females also may heighten the risk of predation. Courtship, mating, nest-building, and egg production can increase the susceptibility of individuals to predation and may be hindered by the presence of predators (Magnhagen 1991). Fuller and Berglund (1996) showed that male and female non-reproductive behaviours were not different under the risk of predation but that predation risk had a significant effect on the reproductive behaviours of both sexes. As the presence of predators increased, pipefish searched for mates less often and courted and copulated less frequently than when predators were uncommon (Fuller and Berglund 1996). Such suppression of breeding may have significant implications for prey populations (section 2.4.3).

2.2.3 Use and changes of habitat

Understanding the adaptive behaviour underlying habitat selection is critical to interpreting spatial and temporal dynamics of interacting species (Morris 2003).

Patches of habitat vary in terms of foraging profitability and predation risk (Lima, 1990). Anti-predator behaviour frequently involves habitat shifts as prey respond to local presence and abundance of predators (Gibson and Robb 1996; Gibson 1998; Hindell 2000; Heithaus 2001). Habitat-specific predation risk may be estimated by marine organisms, such as coral reef fish, through observation of predators, by direct experience of near lethal, failed predation events, or by observing predation on others (Warner 1997). It is sufficient for near lethal, unsuccessful predatory attacks to be high to influence prey behaviour and use of habitat (Lima 1998; Heithaus 2001). The strategy chosen to escape predators will vary. Cryptic species are more likely to reduce their movement compared with more conspicuous species that will favour rapid escape (Lima and Dill 1990). Furthermore, ontogenetic shifts in habitat, such as those observed for fishes moving from estuaries to reefs (eg. Gillanders and Kingsford 1996; Gillanders 1997) may be partially motivated by predation risk (Beck *et al.* 2001).

Gilliam and Fraser (1987) have argued that fitness (net reproductive output) is maximised by animals that select habitats where their ratio of mortality (u) to growth (g) is minimised. When the most energetically profitable habitat is also the most dangerous, animals must make decisions regarding the use of that space (Lima 1998). For instance, in the rose anemone, *Urticina piscivora*, individuals successful at acquiring food items were less likely to detach from the substrate in the presence of predators than those who had been unsuccessful (Houtman *et al.* 1997). Furthermore, De Robertis and others (2002) argued that food accessibility and optimal foraging habitat, two critical factors that affect life-history parameters of *Euphausia pacifica*

(Bollens and Frost 1991; Bollens *et al.* 1992), are dependent on levels of predation risk.

A key determinant of risk and the use of space in many vertebrates is the structure of a habitat which provides physical refuge (Caley and St. John 1996; Thorson 1998). For instance, habitat complexity is critical to the survival of red drum (*Sciaenops ocellutus*) recruits in seagrass (Rooker 1998). Primavara (1997) showed that the level of predation mortality experienced by juvenile tiger shrimp (*Penaeus monodon*) was reduced in the presence of mangrove pneumatophores, which it used as refuge. Two temperate gobiid fish species (*Pomatoschistus minutusi* and *Gobiid niger*) shifted to safer vegetated habitats (without food) in the presence of predators (Magnhagen 1988). This habitat shift was mediated by the nutritional condition of the gobiids. Hungrier individuals were less likely to make the shift into less profitable vegetated habitats. Patch-choice decision in juvenile black surfperch (*Embioto jacksoni*) is influenced by the interactions between food density, structural complexity, and the presence of the predatory kelp bass, *Paralabrax cathratus* (Schmitt and Holbrook 1985, Holbrook and Schmitt 1988a, 1998b). Marine species that are associated or highly dependent on structurally complex habitats, such as many coral reef fish, face an explicit choice between the refuge (and/or foraging) benefits of the habitat and the inability to flee if the threat of predation is high. Although post-recruitment habitat transition has been observed in some coral reef fish (McCormick and Mackey 1997), there is currently no evidence that this transition is driven by predation risk. Habitat obligates that are not highly vagile must therefore contend with the positional risk of predation and adjust other behavioural activities such as foraging distance from refuge (see chapter 4), social control of group membership and group size (Sale 1978;

Caraco *et. al* 1989; Almany 2003), and level of vigilance (see chapters 3 and 5) in response to changing exposure to predators.

Individuals can also choose where to feed within their habitat (Lima 1998). Increased predation risk in a microhabitat favours increased crypsis (Merilaita *et. al* 1999) and consequently a reduction in conspicuous foraging. In situations where minimising predation risk does not incur significant energetic costs, prey will choose a microhabitat with a lower probability of predator encounter and one that ensures better crypsis (Merilaita 1999). A caridean shrimp, *Tozeuma carolinense* moves to higher, less vulnerable positions on seagrass blades and reduces walking and feeding rates in the presence of pinfish, *Lagodon rhomboides* (Main 1987). Different individuals within a population may forage in different places because they respond to the growth / mortality risk trade-off differently. For example, the two sexes of *Idotea baltica,* a marine isopod that lives and feeds on the brown algae *Fucus vesiculosus,* responded to the threat of predation differently (Merilaita and Jormalainen 2000). Males displayed higher foraging and growth rates than females and were found on the light-coloured, apical parts of the algae, which were considered by the authors to be exposed, high-risk areas. Females occupied the more protected basal, darker coloured portion of the algae. This differentiation in habitat use may be due to reproductive success being strongly size-dependent in the males of this species and, consequently, they are driven to high foraging rates in high risk areas of the algae.

2.3 Factors influencing anti-predator behaviour in marine prey

Many environmental factors can mediate the level of risk that animals perceive and thereby influence their response to such risks. These factors may be broadly classified into extrinsic physical conditions such as light levels and habitat size and complexity, or ecological factors such as ontogenetic stage, group size and structure, and reproductive activity of potential prey. Such variables rarely operate independently but may demonstrate circumstance-dependent changes in relative importance. Below, I review the current knowledge with respect to how each of these factors can influence the perception of risk by potential prey in marine environments.

2.3.1 Diel patterns and light levels

Light levels can greatly influence foraging behaviour in many animals. Within a diel cycle, some periods are riskier than others due to variation in predator activity, abundance (Gibson 1996; Gibson 1998; Hindell *et. al* 2000), and environmental conditions. This is especially true during crepuscular periods, when levels of light and risk change quickly (Lima and Dill 1990). The qualitative relationship between light levels and predation risk may also be highly habitat-specific. Studies on coral reefs have suggested that crepuscular predators may pose the greatest threat to fish prey (Collette and Talbot 1972; Danilowicz and Sale 1999; Holbrook and Schmitt 2003) because of the rapid change in light levels. Clark and Levy (1988), however, suggested that pelagic planktivorous fish experience reduced risk during twilight (dim) conditions. Atlantic salmon can forage more easily during the day than at night, but the risk of predation to them is greater during the day (Metcalfe *et. al* 1998). Correlated with this change in risk, individuals become more diurnal when their risk of starvation, or their need to build energy reserves, increases (Metcalfe *et. al* 1998).

Observational studies suggest vertical migration patterns in pelagic fish (Gibson 1996; Gibson 1998; Hindell 2000) and zooplankton (Aksnes 1990; De Robertis 2002) are also driven by diel variation in predation risk. Models of zooplankton and fish predict that vulnerable prey should ascend to surface waters only in lower light intensities (Iwasa 1982). Similarly, young plaice migrate nocturnally into shallow seagrass habitats that are poor in food resources to feed, presumably because large predators are less abundant (Gibson 1998). Conversely, zooplankton in Saanich Inlet, British Columbia, migrate to deep, poorly illuminated and food-depauparate waters during the day to reduce the risk of attack by visual predators (De Robertis 2002). Norwegian herring, *Clupea harengus harengus*, also avoid shallow waters and aggregate in large schools at a depth of 150m-350m where light levels are low and where they cannot be efficiently hunted and consumed by their primary predators (Clark and Levy 1988**.** Although experimental data are scarce, Helfman (1989) showed that juvenile grunts (Haemulidae) adjust their diel migration times to the local abundance and simulated attack rates of the piscivorous lizardfish, *Synodus intermedius*.

2.3.2 Prey size and ontogeny

Ontogenetic changes in response to predation threat have been documented in many animals (Griffin *et al.* 2000; Blumstein 2002) including freshwater fish (Griffin *et al.* 2000; Brown *et al.* 2001, Brown *et al.* 2002). The developmental point at which juveniles change anti-predator strategies is phenotypically plastic and dependent on body morphology. Attaining a certain body depth may be the prerequisite for a change in anti-predator behaviour. A variety of factors may influence threat sensitive trade-offs and as a result the ontogenetic stage at which individuals change anti-predator responses. These factors include the form and intensity of predation and/or competition; the degree of habitat complexity; and the individual's nutritional condition or hunger level (Brown *et al.* 2001).   Under conditions of low predation risk (or low food availability), the relative benefits of antipredator behaviour (seeking refuge, crypsis, high vigilance) would be decreased in favour of foraging. Maintaining foraging may be selected for in smaller sizes and in nutritionally deprived individuals, where the need for foraging is higher and risk-taking may be more justified.

Differently sized marine animals employ different behavioural strategies in response to predation risk. Coral reef fish that are young and small face a higher risk of predation than larger, older conspecifics (Doherty and Sale 1985; Eckert 1987; Helfman 1989; Munday and Jones 1998). Smaller three-spot damselfish, *Stegastes planifrons*, showed stronger predator avoidance behaviour than did larger damselfish when exposed to model trumpetfish, *Aulostomus maculatus*. Young (2-3 yrs old) black gobies, *Gobius niger*, spawned in the absence of the predatory cod, *Gadus morhua*, but did not spawn in its presence (Magnhagen 1990). Older individuals of the same species (4-5 yrs old) appeared to be more tolerant and spawned in the absence and presence of their predator. These responses to predation risk are reversed in pelagic zooplankton. The zooplankton, *Euphausia pacifica* modifies its diel vertical migration in response to the rate of change of light intensity and the risk from visual predators. These modifications are body-size dependent (De Robertis 2002):

larger, more conspicuous copepods spend less time near surface waters than smaller copepods when exposed to visual predators (Fisken and Giske 1995).

Similarly, field observations and theoretical models of a pelagic planktivorous fish, *Maurolicus muelleri*, suggest that small individuals tolerate higher levels of predation risk than large individuals and experience higher growth rates as a result (Giske and Aksnes 1992). Small fish had consistently high feeding rates while the feeding rate of large, adult fish was very low in winter (Giske and Aksnes 1992). Large fish are dependent on seasonal changes in the environment where they minimise predation risk by reducing foraging (food intake) and do not reproduce in winter, while increasing foraging, rebuilding energy reserves, growing and reproducing in the summer. Maximising survival (and not growth) has been proposed as the optimal reproductive strategy for larger, older individuals that have reached sexual maturity and can only increase their fecundity by living longer (Aksnes and Giske 1990). If high growth rates lead to earlier maturity (Jones 1991) and increased fecundity (Rosland 1997), as in many phenotypically plastic marine fish, then the benefits from high growth may outweigh risk of mortality and the optimal strategy may be high foraging rate.

2.3.3 Prey group size, structure, and composition

Predation pressure is thought to have driven the evolution of a number of social phenomena in animals including social aggregation (Curio 1976; Taylor 1984; Heithaus 2001). Group size in fishes may be determined by the energy considerations of dominant individuals attempting to control membership to gain optimum resources such as food and refuge (Sale 1978), and subordinate individuals deciding whether to remain in the group and accept such dominant behaviour (Coates 1980; Caraco *et. al* 1989). Such costs of competing for resources may be alleviated by the benefits of being in a group. Group membership in aquatic vertebrates is likely to reduce an individual's risk of predation where increased group size may aid in social escape tactics, diluted predation risk, or enhanced vigilance and detection of predators (Hobson 1978; Lima and Dill 1990). While the emphasis in terrestrial aggregations may be on increasing awareness and detection of predators, aquatic aggregations may derive the most benefit from the confusion effect (Hobson 1978).

Increasing abundance of prey, however, may also increase per capita mortality (Stewart 1998; Hixon 1991; Hixon and Webster 2002). Larger group sizes are advantageous only when density-dependent predation (a tendency for predators to concentrate foraging effort on prey aggregations) is weak or absent (Connell 2000). In circumstances where predation on prey is strongly density-dependent, survivorship in large groups may be reduced to below that of small groups. Under such conditions group membership ceases to be an advantage. Larger school sizes in juvenile *Acanthochromis polyacanthus*, a coral reef fish, did not appear to offer higher protection from predation by large, transient predators but did against small, resident piscivores (Connell 2000). Group size in *A. polyacanthus*, therefore, may have evolved more in response to the benefit of increased protection from more enduring, resident predators (opportunistic, density-independent predation) despite a cost of being in a large group and vulnerable to sporadic transient predators (attracted to aggregations and exhibiting density-dependent predation). Similarly, Sandin and Pacala (2005) have shown that aggregation in *Chromis cyanea*, a dominant planktivore on continuous reefs of the Netherlands Antilles, minimises per capita risk of predation (density-independent predation). A potential explanation for the variation in predation patterns (density dependent versus density independent) in coral reef fish may stem from functional differences between patch and continuos reefs, and the resultant differences in community structure and availability of prey (Sandin and Pacala 2005).

Vigilance in social groups under predation risk is well studied in mammals and birds (e.g. Berger 1978; Dimond and Lazurus 1974; Wawra 1988; Lima 1987) but with the exception of pinnepids, it is not well-established in marine animals. From these studies, it is evident that vigilance is costly in terms of time and energy spent on active guarding and time and energy forgone as a result of not foraging. A decrease in vigilance is usually associated with an increase in group size (Lima and Dill 1990). In these circumstances, more eyes are able to detect predators more rapidly and group members can individually devote more time to foraging. Studies of freshwater fish suggest similar trends (Godin 1988; Hoare 2000). Anadromous juvenile coho salmon, *Oncorhynchus kisutch*, increase risky foraging (high predator exposure) when in groups, a response that may be due to increased group vigilance (although higher intraspecific competition is a plausible alternative explanation). Reef fishes may be one suite of taxa where early detection of predators and flight response is especially important and well developed (Hobson 1978). Although group composition and position within the group are important factors influencing vigilance and individual level of risk, such factors are poorly understood in many marine social groups (Coates 1980; Phelan 1987; Popp 1988; Hoare 2000).

Multi-species aggregations, such as shoals of coral reef fishes, can enhance the foraging of member species and individuals as compared to single-species shoals (Lukoschek and Mckormick 2002). Such aggregations may also increase efficiency of predator detection, as with Caribbean sea urchins (Parker and Shulman 1986). Although variation in the shape and behaviour of different species in a group may serve to confuse predators, it is not clear whether multi-species fish associations are better at diffusing predation risk than single-species shoals. Indeed, Wolf (1985) suggests that there are differences between individuals in protection derived from multi-species shoals, with odd individuals suffering higher predation risk. The "oddity effect" predicts that odd individuals in a group may suffer disproportionately high rates of predation and solitary individuals should join groups whose members are most similar to themselves in appearance (Krause and Godin 1994). If there is any partitioning of food resources between species, however, school members may compete less in a heterospecific school than they would in a monospecific school (Sackley and Kaufman 1996) unless some species are more efficient and general foragers than others (Mathis and Chivers 2003). When predation risk is high, the benefits of associating with more vulnerable species that may be more efficient foragers in a school may override the costs of the oddity effect and food competition (Mathis and Chivers 2003). Foraging advantages such as a diverse array of foraging morphologies and better access to food for all shoal members may outweigh the risks of being an atypical member and may explain the prominence of multi-species shoals in coral reef habitats (Lukoschek and McCormick 2002). These advantages are likely to be gained on a species or individual level.

2.3.4 Prey reproductive activity

The risk of predation may increase with reproductive activity of an individual (Lima and Dill 1990; Magnhagen 1991). Reproducing individuals may incur an energetic drain that will cause them to be more susceptible to predators and their mating strategies may increase their conspicuousness and reduce their vigilance. Signals used to attract mates may also attract searching predators. Males are usually more active than females in mate-acquisition and consequently are more likely to encounter and be vulnerable to predators. Few studies have directly addressed this phenomenon but work on male Baltic isopods, *Idothea baltica*, suggests that males will experience higher predation rates because they are more active than females during the day and during the breeding season (Jormalainen 1989). Sexual differences in colour morph frequencies, with a female biased sex ratio at the end of the breeding season, were attributed to male-biased predation (Jormalainen 1995) during the breeding season.

Males are not always the only gender under more risk of mating-associated predation. Acoustic, visual, or olfactory signalling for mates attracts predators to either gender of many different species (reviewed in Magnhagen 1991). Mating pairs in copulation or amplexus may move more slowly and be under higher predation risk than individuals (Ward 1986). A decrease in motility, however, could also prove beneficial as it can lead to an increase in camouflage or crypsis (Magnhagen 1991). Individuals carrying eggs may face higher predation hazard as a result of decreased mobility and higher conspicuousness (Magnhagen 1991). Reproducing females of the littoral prawn, *Paleamon adspersus*, are preyed upon more often by fish predators than non-reproducing females (Berglund and Rosenqvist 1986). Brooding males of the pipefish, *Nerophis ophidion*, are more susceptible to predators than non-brooders (Svensson 1988). Therefore, the heightened costs borne by males or females involved in parental care may increase risk of predation in marine animals (e.g. Ainley and Demaster 1980; Svensson 1988)

2.3.5 Predator behaviour and diversity

Different predators will have different nonlethal effects on potential prey (Lima 1998; Lima 2002). Most experimental studies examining the effects of predation risk in marine environments use one predator (see Table 1). Such experimental studies can be unrepresentative of field conditions, where the effect of multiple predators with different functional roles is evident in many systems (Hixon and Carr 1997; Sih *et. al* 1998). Not detecting a significant effect of predation risk in aquaria or field experiments may be due to the use of a single type of predator with a unique functional role or a non-threatening predator which renders the risk treatment inadequate. Prey may be unsusceptible or less vulnerable to certain predators and accumulate in areas where these predators aggregate, because these less dangerous predators may exclude (through interspecific competition) other, more dangerous predators (Lima 1998; also see section 2.4.3). Consequently, choosing treatment predators for experimental studies must address these issues.

The functional role of marine animals in a food web depends on their three-dimensional daily use of space for movement, foraging, and mating. Predator threat may come from above or below (Hixon and Carr 1997) and will depend on the specific foraging ecology of the predator (Curio 1976; Taylor 1984). The qualitative effect of multiple species of predators (as compared to effects of multiple individuals of a single predator species) on prey behaviour may be additive or multiplicative (Sih *et al.* 1998). Studies on coral reef fish prey show that transient roving piscivores (such as barracuda and trevally) or benthic resident predators (such as moray eels and groupers) alone do not exert significant predatory pressure on damselfish prey (Hixon and Carr 1997). Prey may perceive a significant threat only if both predators are present because transient piscivores will force them into their coral refuge while benthic predators may use the same coral refuge as a potential ambush site and render the coral structure unsafe.

Effective provision of protection and safety depends not only on refuge structure, type and quantity, but also on the behaviour of predators (Primavera 1997). Different predators can have qualitatively different effects on prey behaviour. For the greasyback burying shrimp, *Metapenaeus ensis*, it was predator type, not refuge size (sediment particle size) that affected the level of predation risk and the quality of refuge chosen (Primavera 1997). Counter intuitively, juvenile tiger shrimp, P*enaeus monodon*, respond more intensely towards sea bass which are aggressive chasers that kill few but consume whole individuals than toward snapper which are passive predators that kill many but consume only portions of individuals. Aggregation of juvenile *Acanthochromis polyacanthus* appears to be a successful strategy against predation from small predators (Hiatt and Strasburg 1960; Connell 1998), but not large ones (Connell 2000). Connell (2000) suggests that large piscivores sporadically gulp juvenile *A. polyacanthus* in large numbers, while smaller predators regularly target an individual in the school and are a more persistent threat. The intensity of the predator escape response by the threespot damselfish, *Stegastes planifrons*, was directly related to the size and threatening behaviour of the piscivorous Atlantic trumpet fish, *Aulostomus maculatus* (Helfman 1989). *S. planifrons* displayed progressively stronger predator-avoidance behaviour as predators moved closer and as predator profile oriented towards a striking pose. Furthermore, if prey selection changes with predator ontogeny, such as in the piscivorous coral trout, *Plectropomus leopardus* (St. John 1995), so may the risk effects on their prey. To date, such effects have not been demonstrated.

2.4 Potential implications of predation risk on energetics and dynamics of marine organisms

Separating the lethal effects of predators on prey from the nonlethal effects is difficult in the majority of food webs (Schmitz *et al*. 2004). However, marine systems are particularly under-represented in studies of non-lethal effects of predation on prey energetics, phenotypic changes, and demography (Lima and Dill 1990). This paucity in research may be due to the difficulty of tracing potential cascading effects of nonlethal predation in marine communities. Predation risk theory has thus far been developed for closed food webs, such as ponds and lakes, where fecundity and recruitment are tightly coupled and the impacts of anti-predator behaviour can be readily quantified (Werner *et al.* 1983; Mittelbach and Chesson 1987; Tonn *et al.* 1992; Persson *et al.* 1996; Peacor and Werner 2000). Although marine metapopulations are by definition reproductively closed, field studies of marine organisms have traditionally been conducted on local sub-populations (Caley *et al.* 1996) that are reproductively open (Connolly and Roughgarden 1999). Recruitment in marine sub-populations is sporadic and, as a result, age structure and density of local populations are highly variable (Warner 1997). In addition, post-settlement habitat transition of vagile predators and prey (coral reef fish, Stewart 1998; McKormick and Makey 1997; estuarine fish, Sheaves 2001), and migration between local populations (Zeller and Russ 1998) may conceal the mechanisms or effects of predation risk on prey populations in field observations (see section 2.4.3). Such conditions and the logistics associated with comprehensive field studies of marine organisms and food webs at multiple scales may render the study of nonlethal effects on prey demographics difficult. Nonetheless, some marine prey communities may be particularly prone to the nonlethal effects of their predators.

2.4.1 Susceptibility of marine food webs and animals to nonlethal predator-prey interactions

Highly diverse marine communities may be especially susceptible to the nonlethal effects of predators on prey. These food webs may be more connected than terrestrial and freshwater food webs because of the high number of species, lack of specialist predators, and large ontogenetic changes in size of many marine organisms (Link 2002). Therefore, if near-lethal attacks generally equal or outnumber lethal strikes by predators on their prey (Kerfoot and Sih 1987), many marine systems may be characterised by a higher number of nonlethal predator-prey interactions than are other ecosystems. Such behaviourally-mediated interactions may be numerous and significant in speciose communities (Schmitz 1998) that are characterised by distinct and discrete habitat units such as coral reefs where diversity and abundance of predators, prey foraging and refuge opportunities, and site fidelity are high. For coral reef fishes on the Great Barrier Reef, predation risk is likely to increase regionally toward the equator with an increase in diversity of predators (Caley 1995a; Caley

1995b; Beukers 1996). Prey in these conditions may be more vulnerable and respond to the majority of predators. Reef fishes appear to use space rigidly and occupy areas that are, at the least, an order of magnitude smaller than similar sized terrestrial vertebrates (Sale 1978). Consequently, they rely on hiding in coral refuge, a behaviour that hinders foraging, as their principal escape from predators (Reese 1978).

Heterogenous environments, such as marine systems, favour the evolution of phenotypic plasticity (Schlichting 1989). In these environments, local conditions change dramatically through time and behavioural modifications are important and well-developed mechanisms by which organisms exhibit plastic responses to ambient conditions (Warner 1997). Phenotypic plasticity is likely to be widespread, especially in marine organisms that have bipartite life cycles with widely dispersing larvae that recruit to different habitats of varying levels of predation risk (Stearns 1989). Morphology, growth rate, and reproductive output are determined only after settlement when the adult habitat is reached and when local conditions may be assessed. Predator-induced phenotypic changes may be especially common in aquatic animals that live in species-rich groups (Dodson 1989) such as coral reef food webs.

2.4.2 Risk effects on prey energetics

Many marine animals are phenotypically plastic in that genetically identical organisms reared under different environmental conditions display distinct traits (Stearns 1989). Predation risk can be one of these environmental conditions for which phenotype changes as a function of ambient risk (Dodson 1989). It is clear that the primary fitness benefit of behavioural modifications under predation risk is a reduction in immediate and future mortality (Curio 1976; Taylor 1984). The risk of predation, however, may cause modifications in behaviour that lead to energetic costs and phenotypic variation in life-history traits such as growth rate or age-at-maturity (Dodson 1989; Turner 2004) and can lead to fitness costs as total reproductive potential of an individual may be reduced (Schlichting 1989)

A reduction in foraging is a common response to predation risk (Sih 1980; see section 2.2.1) and one that will lead to an overall decrease in energy intake compared to that which would occur in the absence of such risks. This reduced intake may cause a reduction in growth, if energy expenditure saved by not foraging is less than the reduction in intake (*sensu* "submergent behaviour" Maiorana 1976; Skelly and Werner 1990; Werner and Anholt 1993; Peacor and Werner 2000). Slower growth can also result from shifts to resource-poor but safer habitats due to the presence of a predator in more profitable and preferred habitats (Connell 2002). Studies of the life-history of a coral reef prey fish, *P. moluccensis* show latitudinal variation in growth rates and associated size at maturity (Bray 2001) that may be partly due to variation in local predation risk (Caley 1995**;** Beukers 1996). Reduced growth may incur a substantial fitness cost for adults as it may lead to a reduction in long-term survival (Lima 1998) and life-time fecundity.

Individuals of the Baltic isopod *Idotea baltica*, choose avoidance of predators over foraging increasingly with age (Merilaita and Jormalainen 2000), indicating that survival becomes more important than growth. Individuals may be restricted to more vulnerable small size-classes for longer than normal and thus experience high size-selective mortality (Persson *et al.* 1996; Jones 1991; Jones and McCormick 2002) when predation risk induces reduced foraging. Other long-term, non-lethal effects may include reduced body condition (Hik 1995; Sinclair and Arcese 1995) which may lead to lower fecundity and egg viability in females and a decrease in competitive ability in males (Lima 1998). In animals with plastic growth rates and size-dependent fecundity, smaller individuals will be less fecund than larger ones (Kirkpatrick 1984). Where greater predation risk results in diminished body size at a given age because of slower growth, individuals will mature either later or at a smaller size and their overall reproductive potential and output is likely to be depressed.

Changes in fecundity and mortality rates may be byproducts of the costs of predator-induced morphological defences (Harvell 1986; Stearns 1989; Dodson 1989). Organisms may protect themselves by assuming shapes, structures, and / or sizes that reduce mortality (Dodson 1989). Overall efficiency of energy allocation to such predator defences is probably maximised by induced responses that allow animals to divert energy only when needed (Young 1997). In the rocky intertidal zone, thin-shelled snails, *Thais lamellosa*, are more vulnerable to the crab predator, *Cancer productus*, than are thick-shelled snails (Palmer 1985). The presence of these predators induces thicker shells in snails and this energy investment correlates negatively with growth and reproduction (Stearns 1989). Bryozoans in the subtidal zone develop spines in the presence of a specialised predator nudibranch (Harvell 1986). These spines are correlated with reduced rates of growth and smaller individuals produce fewer sexual propagules. Such phenotypic changes are likely to be widespread in marine organisms, as life-history traits are often dependent on local conditions (Stearns 1989). Predator-induced phenotypic changes are likely and may be particularly beneficial where predator abundance fluctuates over space and time, prey can reliably detect the presence of predators, resources are limited, and prey are aquatic animals that live in species-rich groups (Dodson 1989).

While predation risk has been cited as a necessary cost of reproduction in many species (Magnhagen 1991; see section 2.2.2), there is accumulating evidence to suggest that predation risk interferes with mating, reproduction, and nest building in some marine animals (Magnhagen 1990; Fuller and Berglund 1996; Svensson 1988). Predation risk can influence mating behaviour and strategies of terrestrial and freshwater animals (e.g. frogs: Ryan 1985; freshwater guppies: Breden and Stoner 1987; waterstriders Sih *et al.* 1990). Breeding suppression due to the presence of weasel predators has been seen in Fennoscandian vole populations where reproductive activity was substantially restricted when the risk was high (Ylonen 1994). Few marine studies have examined such predator-induced interruptions in mating (e.g. Endler 1980; Endler 1987; Forsgren 1992) and monitored the associated potential consequences to individuals' reproductive output and life-time fecundity. In the temperate black goby, young individuals refrain from nest building and do not spawn in the presence of predators. Older conspecifics, however, engage in reproduction in the same circumstances, which suggests that higher risk taken by older gobies may reflect a lower probability of future reproduction as fecundity wanes with age (Magnhagen 1990). Alternatively, these older and larger individuals may also be facing a lower perceived risk due to larger size or more predator-avoidance experience (Gerking 1994; Brown and Warburton 1997; Warner 1997; Persson 1988). In marine coastal habitats, Fuller and Berglund (1996) showed that the *non-reproductive* behaviour of pipefish was similar under the risk of predation. However, predation risk had a significant effect on the reproductive behaviours of both sexes. As the level of predation risk increased, pipefish searched for conspecifics (mates) less often and courted and copulated less frequently (Fuller and Berglund 1996). Breeding suppression due to predator presence is not well investigated in other marine animals but may have significant implications for individual reproductive output and population fluctuations.

2.4.3 Community and population effects

The effect of predation risk on local populations may be most readily detected by examining individuals' use and change of space (see section 2.2.3). Prey habitat use is likely to contribute, at least partially, to the density and dispersion of individuals over larger spatial scales (Lima 1998, Morris 2003). The physical structure of the habitat (Caley and St. John 1996) is an important link between microhabitat selection and local population density of prey (Beukers and Jones 1997; Anderson 2001; Jones and McCormick 2002; Morris 2003). Refuge size, abundance, and quality, which are necessary to alleviate the risk of predation, may indirectly structure assemblages of tropical reef fishes (Caley and St. John 1996) and regulate their local abundance (Beukers and Jones 1997). Habitat and microhabitat shifts are a common response to the presence of predators. For example, individuals of the temperate reef-fish, *Cheilodactylus nigripes*, avoid habitats where a seal predator abounds (Connell 2002). The likelihood that marine animals will shift habitat will depend on characteristics of the ecology of the animal. Highly mobile prey with a low affinity or association with physical habitat will be more likely to move to a different habitat. Large scale migrations in some marine mammals, such as pregnant female baleen whales, into low-latitude waters are thought to be motivated by the risk of calf-predation by killer whales, *Orcinus orca,* at higher latitudes (Corkeron 1999). Killer whale abundance is substantially greater in high latitude waters compared with low latitude waters and they do not appear to migrate with baleen whales.

Nonlethal predator-induced effects may be restricted to local scales where the presence of predators results in rearrangement of prey among microhabitat patches or local stocks but does not change the overall density of the population. For instance, competitive bottlenecks have been demonstrated in closed systems such as lakes as a result of prey redistribution (Werner *et al.* 1983). Prey faced limited and dwindling resources and experienced lower than normal growth when safety of habitat forced large numbers to occupy shallow, predator-inaccessible water. Persson *et al.* (1996) suggest that such behavioural modifications can start a cascade of events through an entire population. Juvenile crucian carp, *Carassius carassius,* in lakes experienced a similar, competitive bottleneck and subsequently failed recruitment into adult life stages after the introduction of the predatory perch, *Perca fluviatilis* (Tonn *et. al* 1992). Such growth inhibition due to increased competition may also occur in marine communities, such as coral reefs, where prey are constrained to refuge areas of high structural complexity within a reef to avoid predation.

Negative reproductive effects of predator-induced behaviour modifications on populations have been documented in terrestrial and freshwater systems (Scrimgeour and Culp1994; Ylonen 1994; Hik 1995; Sinclair and Arcese 1995) but have not been discussed in the marine literature. For instance, although the dominant predation effect driving the classic lynx-hare cycle was lethal, predator-induced microhabitat shifts in the hares led to lowered female body condition (Hik 1995). The consequent reduction in reproductive output hastened the decline and lengthened the recovery phase of the hare cycle. Breeding suppression due to high predator presence may also hasten crash phases in vole populations and their weasel predators (Ylonen 1994). Consequently, such antipredator behaviour may reduce or exacerbate the oscillatory dynamics inherent in model predator-prey systems (Ives and Dobson 1987).

There are numerous theoretical models examining prey mortality due to predators whose assumptions are inconsistent with the adaptive anti-predator behaviour of prey (Abrams 1993; Lima 1998). Recently, a growing number of theoretical studies have begun to consider behavioural modifications and predator-induced decision-making in terrestrial and freshwater settings (Abrams 1993; Ives and Dobson 1987; Mittelbach and Chesson 1987; Proctor 2003; Ruxton 1995; Peacor and Werner 2000; Ward 2000; Winder 2001). Few models, however, exist that are tailored to marine contexts and explicitly incorporate oceanographic and biological parameters unique to them, such as complex life cycles (larvae, juveniles, and adults), plastic growth rate and fecundity, and wide dispersal to distinct habitats (but see De Robertis 2002). Consequently, theoretical inferences about the nonlethal effects of predators on marine prey are generally lacking and can not readily be tested.

2.5 Conclusions and future research

Characteristics of marine animals, and the highly species rich food webs in which some participate, suggest that nonlethal predator-prey interactions may play a significant role in modifying phenotype and demography. Empirical studies of how marine animals change their behaviour due to perceived risk of predation have gained momentum in the last decade. Predation risk has been documented to modify prey activity and motility, foraging distance and effort, habitat and patch choice, reproductive activity, morphology, and migration patterns. External factors such as light conditions, prey group size and structure, or predator diversity may influence these behavioural modifications. Internal factors such as prey size, gender, and reproductive activity also play an important role in influencing anti-predator behaviour. Such changes in behaviour will have energetic costs and may cause phenotypic variation in life-history traits. If local predator abundance or diversity induces prey redistribution or a reduction in prey reproductive output, nonlethal predator-prey interactions may have larger scale, community and population-level effects.

The results of marine studies on predation risk have raised more questions than provided answers. The small scale at which many experiments are conducted may not be appropriate for extrapolating to larger spatial scales at which population dynamics are expressed. Lima (1998), however, argues that small-scale studies are necessary to provide insight into local population level phenomena and serve as a useful starting point for large-scale experiments. Ideally, small-scale behavioural observations of individuals or functional groups should be coupled with larger scale manipulations of predator densities and diversity.

Unlike terrestrial (e.g. Downes 2001) and freshwater systems (reviewed in Stearns 1989; Peckarsky and McIntosh 1998), the influence of predation risk on long term life history, fecundity, and reproduction of marine animals is largely unstudied (some intertidal organisms are an exception, see Dodson 1989). Specifically, the effect of predation risk on modifying reproductive behaviour and strategies, the implications of reduced growth and poor condition on fecundity and reproductive potential of individuals, and the condition of offspring born under such conditions have not been explored. In circumstances where predator-induced responses of reproductively active animals are examined, it is also important to be able to differentiate between reductions of growth due to a cost of reproduction or due to reduced foraging as a result of predation risk.

Most theoretical and empirical studies of behavioural predator-prey interactions do not consider the adaptive behaviour of predators in response to evasive behaviour of prey (Lima 2002). Furthermore, studies in marine systems using multiple marine predators as potentially complementary sources of risk are also lacking. Studies have examined the effect of multiple predators on density-dependent mortality of prey (e.g. Hixon and Carr 1997) but there are few studies on the synergistic effects of concurrent threats from multiple species of predators (e.g. Peckarsky and McIntosh 1998) and none that have been done in marine habitats. The nonlethal effects of a diversity of predators, their ontogenetic stage, and their abundance should be examined in studies of predation risk. Finally, predator-induced redistribution of prey may be an important determinant of local population size for vagile marine organisms. Few studies have explored these potential effects, specifically in larger marine animals such as dolphins, manatees, dugongs, and whales that may modify such large scale behaviour as migratory patterns in response to localised or spatially extant pockets of high predation risk.

Nonlethal predator-prey interactions clearly have significant effects on many species in different food webs. Predator-induced behavioural effects however, must cause significant change in energetic investments of an individual (that may manifest as morphological modifications or changes in reproductive output) before they can have consequences on local prey population dynamics. In this thesis, I chose coral reef fish communities as a likely food web candidate for studies of such emergent effects of predation risk. In the following chapter, I describe the behavioural responses of some common prey fish to coral reef piscivores. I then explore the factors that may affect these responses and the mechanisms by which a common coral reef fish prey reduces its foraging (Chapter 4), and finally I quantify the potential fitness cost of reduced prey growth due to predation risk (Chapter 5).

Table 1. Representative examples of nonlethal predator-prey interactions illustrating prey behavioural responses to predators and the factors influencing these responses.

Marine System	Predator-prey Species	Prey Response /Cost	Mediating factor	Reference
Coastal				
Littoral	Baltic Isopod, *Idothea baltica*	Differential microhabitat choice between sexes; increase in suboptimum feeding time with age	Gender, micro habitat	(Merilaita 2000)
	Littoral prawn, *Palaemon adspersus*	Increased predation sensitivity	Gender and reproductive state, non-reproducing females are less susceptible	(Berglund 1986)
Mangrove	White shrimp, *Penaeus merguiensis*; tiger shrimp, *Penaeus monodon* - Sea bass, *Lates calcarifer*; Mangrove snapper, *Lutjanus argentimaculatus*	Increased mortality	Refuge availability and density, pneumatophores of the mangrove *Sonneratia griffithii*	(Primavera 1997)
	Greasyback shrimp, *Metapenaeus ensis* - Sea bass, *Lates calcarifer*; Mangrove snapper, *Lutjanus argentimaculatus*	Increased mortality	Predator type	(Primavera 1997)
Tropical Sandy, Seagrass	Code Goby, *Gobiosoma robustum* , Clown Goby, *Microgobius gulosus* - Gulf Toadfish, *Opsanus beta*	Shift to suboptimal nonstructured sand habitat	Interspecific competition and predator presence	(Schofield 2003)
	Longnose killifish, *Fundulus majalis* - Sand seatrout, *Cynoscion arenarius*	Elevated plasma cortisol, increase rate of oxygen consumption	Level of exposure to predator (full, partial, none) and presence of artificial vegetation	(Woodley 2003)
Temperate, sandy, seagrass	Black goby, *Gobius niger* - cod, *Gadus morhua*	Reduction in nest building and spawning	Size/age of prey	(Magnhagen 1990)

	Male straightnose pipefish, *Nerophis ophidion*	Increased mortality	Male parental care (egg carrying)	(Svensson 1988)
	Pipefish, *Syngnathus typhle* - cod, *Gadus morhua*	Less frequent searching for mates, courtship, and copulation,	Reproductive status of individuals, strength of predation cue	(Fuller 1996)
Estuarine	Decapod shrimp-*Dyopedos monacanthus* (benthic shrimp-amphipod)	Reduced activity of gravid females	Breeding season	(Thiel 1998)
	Predatory fish-prey fish *Eg. Gadus morhua-Pleuronectus platessa* (cod-juvenile plaice)	Reduction in extended parental care, increased pelagic movements	Water temperature effects local abundance of predators	(Gibson 1996;Gibson 1998; Hindell 2000)
	Galeocerdo cuvier - *Chelonia mydas* and *Caretta caretta* (Tiger Shark-Green and Loggerhead turtles)	Habitat shift/diel migration Escape swimming	Diel/tidal cycle	(Heithaus 2002a, 2002b)
	Grass shrimp, *Palaemonetes pugio* - various finfish predators	Habitat (depth) shift / diel migration	Light conditions	(Clark 2003)
	Pinfish -Caridean shrimp *Lagodon rhomboides* - *Tozeuma carolinense*	Habitat shift, reduced walking and feeding rates	Prey speed and gender	(Main 1987)
Kelp				
	Anarhichas lupus/ Cancer pagurus-*Strongylocentrotus droebachiensis* (Atlantic wolfish / Edible crab-green sea urchin)	Avoidance and movement reversal, site attachment	Strength of predatory chemical cue	(Hagen 2002)
Reef *Tropical*	Stoplight parrotfish, *Sparisoma viride*-	Abandoning multi-species	Oddity, # of conspecifics in group	(Wolf 1985)

coral	trumpetfish, *Aulostomus maculatus*	foraging shoal, loss of foraging advantage		
	Threespot damselfish, Stegastes planifrons - trumpetfish, *Aulostomus maculatus*	Predator avoidance, curtailed feeding and territorial defence	Prey size/ontogeny; distance of predator; predator pose	(Helfman 1989)
Temperate rocky	Seal-Fish	Shift to safer habitat, less food	Nutritional condition of individual	(Connell 2002)
Pelagic	(Norwegian fjords) *Calanus finmarchicus, Paracalanus parvus* (copepods)	Ontogenetic and daily vertical migration	Ontogeny, depth/temperature	(Aksnes 1990; Aksnes and Magnesen 1988)
	Copepod, *Eurytemora* - Threespined Stickleback, Gasterosteus aculeatus	Vertical migration; Increased predator preference	Gender and reproductive status/parental care: egg carrying in females increases predation risk	(Vuorinen 1983)
Deep *Sublittoral*	*Saduria entomon-Monoporeia affinis* (Isopod-Amphipod)	Reduced swimming; increase hiding; reduced foraging; reduced growth rate; reduced recruitment		(Sparrevik and Leonardsson 1995; Sparrevik 1999)

Chapter 3

Species- and Ontogeny-specific Anti-predator Behaviour of Coral Reef Fish Prey: an Experimental Evaluation

3.0 Abstract

The risk of predation causes many animals to modify their behaviour at an energetic cost. Understanding these modifications is important as such responses may have large-scale consequences for prey fitness and population dynamics. In this chapter, I examine the anti-predator behaviour of juveniles and adults of a number of species of site-attached coral reef fishes. In order to test for a change in behaviour due to predation risk, I exposed these fishes to a caged Serranid predator, *Cephalopholis cyanostigma,* in laboratory aquaria. Seeking and associating with shelter was the most common antipredator response in diurnal species of the prey fish, *P. moluccensis* and *P. amboinensis*. Conversely, two nocturnal prey species (*Apogon fragilis* and *Cheilodipterus quinquelineatus*) moved away from their refuge in the presence of the reef piscivore, presumably to avoid attacks from potential ambush predators sheltering within the habitat. Both size-classes, juveniles and adults, of the four species of prey examined reduced their foraging activity significantly in the presence of a predator. Vigilance, however, was primarily a role assumed by adults not juveniles. Ontogenetic differences in behaviour and associated selective advantages may help explain the persistence of mixed size-class groups, a common feature in social groups of coral reef fish planktivores. Moreover, anti-predator behaviour of individual coral reef fish may depend on the ecology of that species and the specific foraging of its ontogenetic stage.

3.1 Introduction

The size of an organism is generally considered one of its most important life history traits (Stearns 1992) and is an important factor that affects its interactions in ecological systems (Werner and Gilliam 1984; Munday and Jones 1998; Claessen *et al*. 2000; Claessen and Dieckmann 2002). Size can influence energy demands, foraging capacity, food processing abilities, competitive interactions, and predator-evasion abilities of animals (Persson 1988; Werner 1988; Hjelm and Persson 2001; Munday 2001). Many animals exhibit marked changes in their behaviour with ontogenetic development and growth (Werner and Gilliam 1984; Nicieza 1999; Claessen and Dieckmann 2002; de Roos *et al.* 2002; Jones *et al.* 2003). Changes in food intake, required by increased metabolic needs of larger bodies and associated changes in activity patterns, may lead to changes in feeding strategies and therefore changes in anti-predator responses. Larger individuals tend to be faster, less vulnerable to gape-limited predators, and can access a larger size range of food items than smaller individuals (Persson 1988; Gerking 1994; Olson *et al.* 1995; Hjelm and Persson 2001). Subsequently, these individuals are expected to have higher feeding rates and longer foraging excursions, both in time and distance, than smaller individuals (Gerking 1994). Furthermore, the onset of specific defence strategies in fish prey may correspond to the developmental stages of sensory capabilities (Gallego and Heath 1994). As young recruits, fish larvae probably depend on inconspicuousness due to small size and transparency to escape visual predators (Persson 1988; Wootton 1992; Gerking 1994). As they grow older and more conspicuous, other strategies, such as schooling, vigilance, or fast escape, may become necessary to escape predation (Gallego and Heath 1994; Persson 1988).

Improved peripheral vision and perception of movement due to the development of cones and rods in the eyes may also play an important role in predator avoidance (Blaxtor and Jones 1967; Hunter and Coyne 1982).

3.1.1 Trade-offs between foraging and hiding in coral reef fish prey

Typical reef fish are demersal, sedentary, strongly site-attached animals (Ehrlich 1975; Sale 1978). Many small planktivorous fishes, a large component of coral reef fishes and common prey of coral reef piscivores (Hiatt and Strasburg 1960; Goldman and Talbot 1976; Randall *et al.* 1997), are closely associated with discrete sites from which they derive refuge and where they can forage nearby in the water column (Davis and Birdsong 1973; Hobson and Chess 1976; Beukers and Jones 1997; Caley and St. John 1996; Marnane 2000). Planktivorous fishes maintain particularly advantageous positions in space so as to maximise encounter rates with unevenly distributed patches of plankton (Reese 1978). In the absence of predators, food intake depends on the group size, social rank of group member (Coates 1980), distances travelled from the refuge (to encounter planktonic food items), the amount of space that is searched (Reese 1978; Sackley and Kaufman 1996), as well as the number of bites taken in a specific location (chapter 4). In the presence of a predator, individuals retreat into the reef structure and hide until the threat passes (Sackley and Kaufman 1996). Foraging stops while they hide, or is significantly reduced, because prey individuals lose their advantageous feeding positions in the water column. In particular, predation risk is likely to alter the size of prey foraging space as individuals reduce the distance of their foraging excursions and the number of bites they take on each excursion (chapter 4).

On a daily basis, planktivorous reef fish must balance the benefits of foraging against the costs of anti-predator behaviour, most notably seeking refuge (Forrester 1990). A simple conceptual model of trade-offs between foraging and hiding characteristic of site-attached prey fish on coral reefs is presented in Figure 3.1. At small sizes, the foraging capacity of an organism will be small due to gape limitation and low search capacity (Noakes and Godin 1988). Therefore, as size approaches 0 (in the pelagic larvae or egg stage) the probability of foraging activity, f, decreases and approaches 0 (in both high, P+, and low, P-, risk conditions). As size decreases the probability of seeking refuge, r, increases because vulnerability to predators may be higher at smaller sizes than larger sizes in planktivorous coral reef fish (Coates 1980; Doherty 1985, Eckert 1987; Shulman and Ogden 1987; Hixon 1991; Munday and Jones 1998). Indeed, coral reef fishes often settle to high complexity habitats (Shulman 1984; Ohman *et al.* 1998) and small size classes are often found in habitats that offer the most protection from predation (Sale 1971; Jones 1984, 1988; Sih 1992). Conversely, larger individuals have a higher consumptive capacity and need (Werner 1988) and can consume a larger size-range of food items as compared to smaller individuals (Olson *et al*. 1995). Therefore as size increases, f increases and approaches f_{max} and r decreases and approaches r_{min}.

In high-risk circumstances, individuals are more likely to hide rather than forage, as compared with low risk situations (Sih 1997). In the presence of predators, small or young individuals may be more likely to maintain a close association with refuge and may not modify their behaviour substantially (difference between the lines in Figure 3.1). As size increases, prey fish are better able to respond to ambient risk because of higher speed (Persson 1988) and better ability to detect predators (Hunter and Coyne 1982; Blaxter 1986). Thus, adults may display greater flexibility of behaviour than juveniles. Consequently, a large individual under high predation risk, S_2, may feed and hide at the same rate as a smaller, and more vulnerable, individual under low risk of predation, S_1. Such size-dependent behaviour, however, will depend on the size-scaling of foraging rate and metabolic demands (Werner 1988, Hjelm and Persson 2001). Therefore, the model predicts that (1) f/r should increase with size for both P+ and P-, although the precise shape of the response (linear, saturating, or accelerating) is not known; and (2) that f/r should be lower in the presence of predators than in their absence for all prey sizes, but (3) whether the response is larger in (small) juveniles than (larger) adults, or vice-versa, is not entirely clear.

Some reef fishes including species of Serranidae, Labridae, and Apogonidae , exhibit ontogenetic behavioural changes in feeding and diet (Grutter 2000; St. John 1999), swimming ability (Fulton and Bellwood 2002), and habitat use (Finn and Kingsford 1996; Green 1996; Lirman 1994). For most coral reef fishes, size changes dramatically with ontogeny and is a major correlate of predation risk within and among species (Munday and Jones 1998). Therefore, differences in anti-predator behaviour between ontogenetic stages within species should be evident. Few studies have explicitly examined anti-predator behavioural responses of coral reef fish (but see Helfman 1989). To date, no studies have examined how such behavioural changes are related to the foraging ecology and ontogeny. In this chapter I examine behaviour in response to the perceived risk of predation using juvenile and adult coral reef fish from two distinct but abundant prey families exposed to a benthic predator. Specifically, I tested the predictions that under the threat of predation (a) coral reef fish will trade-off foraging with seeking refuge in physical structure; (b) that large adults will be more likely to forage and less likely to seek refuge as compared to smaller juveniles; and (c) there will be a larger reduction in the probability of foraging and a larger increase in the probability of hiding in adults when compared with juveniles. Overall, greater behavioural flexibility is predicted for larger, adult individuals.

3.2 Methods

In order to examine potential antipredator strategies of coral reef fishes and investigate the influence of ontogeny on these behaviours, four species of prey and one species of piscivore were used in a series of laboratory experiments. All fishes were collected from reefs in the immediate vicinity of Lizard Island, Great Barrier Reef and all experimental trials were conducted at the Lizard Island Research Station. The blue-spotted rockcod, *Cephalopholis cyanostigma* (family Serranidae, Randall *et al.* 1997), is an abundant, common predator on these reefs (Stewart 1998). *C. cyanostigma* were collected by divers on SCUBA using underwater fishing with pilchard baited hooks. The relatively small size of *C. cyanostigma*, its piscivorous diet (Shpiegel and Fishelson 1989; Martin 1994), territoriality (Shpiegel and Fishelson 1991; Mackie 1993), and proven suitability for laboratory and field experimentation (Mackie 1993; Martin 1994; Beukers and Jones 1997; Stewart 1998) made it an ideal predator for these aquarium-based experiments.

The prey species used included two diurnally active damselfish, the lemon damselfish (*Pomacentrus moluccensis*) and the ambon damselfish (*Pomacentrus amboinensis*), and two nocturnally active cardinalfish, the fragile cardinalfish (*Apogon fragilis*) and the five-lined cardinalfish (*Cheilodipterus quinquelineatus*). These species were chosen to provide a representative sample of small diurnal and nocturnal coral reef fish species and all species are common prey of *C. cyanostigma* (Stewart 1998). All species were collected from coral colonies of *Pocillopora damicornis* and the branching coral *Porites cylindrica* using a clove oil solution of approximately 6:1 ethanol to clove oil (Munday and Wilson 1997), placed in clear plastic bags, and transported to the laboratory in aerated plastic bins. Individuals were categorised as juveniles (*P. moluccensis* <25mm SL, *P. amboinensis* < 45mm SL, *A. fragilis* < 20mm, *C. quinquelineatus* <50 mm SL) or adults following the size criteria of Jones (1986), Kerrigan (1994), and Marnane (unpublished data). Adults and juveniles of each species were separated and held in 300 L tanks and allowed to acclimate to laboratory conditions for 24 hours. *C. cyanostigma* were separated from all other species and held in a 2000 L tank and allowed to acclimate for 48 hours.

3.2.1 Experimental design

Four experiments were conducted: one for each of the prey fish species. A 2 x 2 factorial design replicated in 4 aquaria was used for each of the four species to compare the responses of adult and juvenile prey fish (factor B) in the presence or absence of caged *C. cyanostigma* (factor A; Figure 3.2). Each of the four experiments used sixteen rectangular aquaria filled with 80 litres of seawater. As the prey species used naturally exist in groups, each aquarium received 5 juveniles or 5 adults, randomly selected individuals, of one of the prey species. A density of five individuals in this volume of water was within the range of densities observed in the field (Chapter 4 results). For trials designed to mimic high predation risk, a rockcod was placed in a pen on the far-side of aquaria containing adult or juvenile prey and separated from the prey fishes with a plastic mesh fence. The fence was constructed from a PVC frame with plastic mesh with 1-cm diagonal openings and fences were placed in all aquaria, including those that did not contain rockcods. The rockcod was clearly visible through the mesh but could not access the prey. Rockcods were fed 1 fish a day (Stewart 1998) and introduced one day after the introduction of the prey. Prey were exposed to the continuous presence of the rockcod because the commonly used protocol of exposing foragers to a single pulse of heightened risk tends to overestimate typical investment in anti-predator behaviour (Hamilton and Heithaus 2001). Trials without predators were run in exactly the same way but without a rockcod. This experiment was repeated with each of the 4 species and each experiment was conducted for two days.

Each 80-L aquarium was supplied with a continuous flow of filtered seawater, supplied from a common reservoir, and 2 air stones for aeration. Water temperatures fluctuated between 23 and 25.7^{o} C in all aquaria. To standardise habitat complexity and refuge availability across all treatments and avoid confounding of habitat variables with treatments or species, I placed one half-section of 20cm diameter PVC pipe 25cm long into each aquarium as refuge for the prey. The PVC refuge was placed close to a 50-cm vertical outflow PVC pipe, which prey also used as refuge.

In order to mimic field conditions where plankton is patchy and scarce (Noda *et al.* 1992; Kerrigan 1994), two separate trials were conducted using this design in which individuals were observed with and without food. Observations in the absence of food were possible because the continuous flow of seawater was filtered to remove plankton. In the feeding trials, cubes of frozen pilchard and squid were placed on feeding trays attached to the mesh separating prey from the rockcods (where present) and the melting cubes ensured slow food release into the aquaria. Any remaining food was removed after 30 minutes if not consumed.

3.2.2 Behavioural observations

Prey behaviour was observed for 15 seconds in each aquarium every 15 minutes over a period of 4 hours and quantified by recording the number of fish engaging in each of five behaviours (i.e. scan sampling, Altman 1973). Each experiment ran for two days. In the feeding trials, the number of individuals feeding or seeking refuge was observed every 30 seconds for 5 minutes during daily feeding. This procedure was repeated on two successive days for each experimental prey species. Observations of *P. moluccensis* and *P. amboinensis* were made during the day and *A. fragilis* and *C. quinquelineatus* were observed at night using red light to minimise disruption of the behaviour of the fish. Five categories of prey behaviour (Table 3.1) were scored during each trial: schooling or aggregation; distance from shelter; foraging; diurnal or nocturnal vigilance; and refuge-seeking (Karplus and Tuvia 1979; Karplus *et al.* 1982; Helfman 1989; Sackley and Kaufman 1996).

3.2.3 Statistical Analyses

Levene's test of equality of variances was used to examine the homogeneity of variances in the different behaviour categories. For each of the four prey species separate two-way ANOVAs were used to test for differences among treatments (presence or absence of predator, adults or juveniles) in mean number of individuals engaging in a certain behavioural activity, mean diameter of aggregations, and foraging distance from refuge. All 2-day observations of each aquarium were summed within each treatment, i.e. proportions were calculated for each observation and then averaged. As the number of individuals exhibiting certain behaviours in an aquarium was constrained by initial treatment densities (i.e., 5 individuals) I used proportions of individuals engaging in activities to reflect the probability of that behaviour occurring. Proportions were calculated as the number of individuals engaged in the behaviour being observed divided by the total number of individuals in the aquarium (eg. 2 of 5 individuals displaying behaviour is 0.40). Proportions were transformed to $\sqrt{x}$. If necessary, data for "aggregation diameter" and "distance from refuge" were transformed to $\log_{10}(x+1)$ to meet the assumptions of equal variances in ANOVA.

3.3 Results:

In the presence of a predator, all four species of coral reef fish significantly modified their association with the refuge in the aquaria (Tables 3.2 and 3.3), with *P. moluccensis* and *P. amboinensis* increasing refuge association (Figures 3.3a, b and 3.5

a, b) and *A. fragilis* and *C. quinquelineatus* decreasing association with refuge (Figures 3.3c, d and Figures 3.5c, d). Both adults and juveniles of all species experienced a reduction in the probability of foraging in the presence of a rockcod (19%-77%, Figure 3.5a-d and Table 3.3).

P. moluccensis, *A. fragilis,* and *C. quinquelineatus* all significantly modified the diameters of their aggregations in different ways when exposed to a rockcod (Figure 3.4a, c, and d; Table 3.2). For *P. moluccensis*, there was a significant interaction (Table 3.2) with juveniles decreasing diameter of aggregation under predator exposure, but adults showing little if any change (Figure 3.4a). *A. fragilis* increased the size of their aggregations (adults from ~29cm to ~45cm and juveniles ~28cm to ~36cm, respectively) but *C. quinquelineatus* decreased the size of their aggregations (adults from ~30 to ~17cm and juveniles ~13cm to ~7 cm) in the presence of a rockcod (Figure 3.4c and d; Table 3.2). For *P. amboinensis*, no significant response of aggregation diameter was detected (Figure 3.4b, Table 3.2).

There were significant interactions between predator exposure and ontogenetic stage for *P. moluccensis*, *P. amboinensis*, and *C. quinquelineatus* but not *A. fragilis* (Table 3.2). Visual inspection of results suggests that the interactions were the result of adults increasing vigilance strongly when exposed to predators but juveniles showing little or no response (Figure 3.3; Table 3.2). Vigilance by both adult and juvenile *A. fragilis* however, increased when exposed to a rockcod (Figure 3.3c; Table 3.2). Adults of all species were ~28% more vigilant than juveniles. Adult *P. moluccensis* displayed the highest probability of vigilance (~0.82; Figure 3.3a and Table 3.2), with adult *C. quinquelineatus*, *A. fragilis*, and *P. amboinensis* displaying lower but similar levels (~0.55, ~0.53, and ~0.42, respectively).

The diurnal and nocturnal coral reef fish I examined all displayed significant anti-predator behaviour in regard to refuge-seeking (Table 3.2 and 3.3). In the presence of a predator, the diurnal *P. moluccensis* and *P. amboinensis* associated significantly more (~65%) with available refuge while the nocturnal *A. fragilis* and *C. quinquelineatus* associated significantly less (~41.2%) with available refuge (Figure 3.3 and 3.5; Table 3.2 and 3.3). Predation risk had a significant but different effect on the distance *P. moluccensis* and *A. fragilis* individuals positioned themselves from available refuge (Figure 3.4a and c and Table 3.2). While *P. moluccensis* moved closer to refuge in the presence of a predator, *A. fragilis* increased their distance. *P. amboinensis* and *C. quinquelineatus* showed little or no response.

There was a significant interaction between predator exposure and ontogenetic stage for *P. moluccensis* in aggregation diameter (Table 3.2). Visual inspection of the results suggests that the interaction was a result of juveniles decreasing the size of their aggregation while adults showed little response (Figure 3.4a). Adult *A. fragilis* and *C. quinquelineatus*, the nocturnal species, displayed significantly larger aggregation diameters than juveniles (Table 3.2; Figure 3.4c and d). Adult aggregation diameters of *A. fragilis* measured ~40 cm and juvenile aggregations measured ~29 cm. Similarly, adult aggregation sizes were larger (~23 cm) in *C. quinquelineatus* as compared to juveniles (~12 cm).

Ontogeny had a significant but different effect on refuge seeking in diurnal *P. amboinensis* and nocturnal *C. quinquelineatus* (Table 3.2). In the presence of a predator, both size classes of *P. amboinensis* increased refuge seeking while both classes of *C. quinquelineatus* decreased refuge seeking (Figure 3.3b and d). There was a higher probability of juvenile *P. moluccensis* (0.55) and *P. amboinensis* (0.30) to seek refuge as compared to adults (PM: 0.22, PA: 0.18), but the effect was only statistically significant for *P. moluccensis* in the presence of food (Table 3.3) and *P. amboinensis* in the absence of food (Table 3.2). Conversely, there was a lower probability of juvenile *A. fragilis* (0.20) and *C. quinquelineatus* (0.17) to seek refuge as compared to adults (AF: 0.35; CQ: 0.30). This was statistically significant in *C. quinquelineatus* in the absence (Table 3.2) and presence of food (Table 3.3), but only statistically significant for *A. fragilis* in the presence of food (Table 3.3). Distance away from refuge in *P. moluccensis* was significantly modified by ontogeny, with juveniles foraging closer to the refuge than adults (Figure 3.4a). Indeed, adults were positioned at approximately the same distance (~37cm) in the presence of predators as juveniles did in the absence of predators (~36.5cm). Distance away from refuge was also modified by ontogeny in *C. quinquelineatus,* although juveniles positioning themselves farther from refuge (~25 cm) than adults (~15 cm).

3.4 Discussion

These results strongly suggest that anti-predator behaviour in coral reef fish may depend on ontogeny, as well as the foraging ecology of the species. These diurnal coral reef fish prey trade-off foraging against seeking refuge in the presence of a predator. The same may not be true for nocturnal prey fish. Although all four species were less likely to forage when exposed to a predator, diurnal species sought physical refuge while nocturnal fish avoided physical refuge in the presence of a benthic ambush predator. Adults were less likely to seek refuge than juveniles of the diurnal species, regardless of predation risk. Furthermore, adult *P. moluccensis* foraged farther from cover than did juveniles and in the presence of a predator, adults were positioned at approximately the same distance away from refuge as juveniles were in the absence of a predator. Other anti-predatory behaviour such as vigilance was evident in adults and not juveniles of all species examined except *A. fragilis*. In this species, juveniles were also vigilant but less so than adults. Aggregation in response to a predator was species- and ontogeny- specific

3.4.1 Anti-predator behaviour of diurnal fish is different from their nocturnal counterparts

As predicted, the two pomacentrids species studied here associated more closely with refuge in the presence of the piscivorous rockcod than in its absence. When exposed to a predator, *P. moluccensis* was more likely to seek refuge than *P. amboinensis* (see Figure 3.3a and 3.3b). This lower refuge dependence of *P. amboinensis* may be related to their opportunistic foraging behaviour and more generalised feeding ecology (Jones 1991). This species is a planktivorous and benthic omnivore (Jones 1991; Kerrigan 1994). Individuals will actively search over a wider area and not depend, as does *P. moluccensis*, on planktonic particles carried in the current and floating past their home coral. Indeed, foraging distance, which is a measure of distance travelled away from refuge, was larger in *P. amboinensis* compared to *P. moluccensis*. Furthermore, in the wild *P. amboinensis* associate more closely with coral rubble and bottom relief, and not with one species of live coral as does *P. moluccensis* (Jones 1991; Ohman *et al.* 1998). In the field, *Pomacentrus moluccensis* are often found in association with discrete live *Pocillopora damicornis* colonies. Such species specific habitat preferences may have evolved to minimise risk of predation while complimenting particular foraging behaviour of different fish species (Jones 1991).

Compared to the two diurnal species of pomacentrids, the two apogonid species I studied here displayed strikingly different behaviours in the presence of a predator. Contrary to my predictions, the two species of cardinal fish, *A. fragilis* and *C. quinquelineatus*, did not increase their association with physical refuge in the presence of a predator. Rather, *A. fragilis* and *C. quinquelineatus* increased their distance from it. These differences between diurnal and nocturnal species may be related to the different food capture strategies of nocturnal versus diurnal species and different predator-evasion behaviour. Most species of apogonids are nocturnal, feeding on a range of plankton, benthic invertebrates, and small fishes from a variety of reef microhabitats (Vivien 1975). During the day, most apogonid species reside in caves or in the interbranch spaces of branching corals, often in multi-species aggregations (Marnane 2000; Marnane and Bellwood 2002; Marnane in review). The majority of apogonids forage in habitats different from their diurnal resting sites and there is a strong horizontal and vertical separation between species distributions when active (Marnane and Bellwood 2002). Nevertheless, nightly foraging migration, vertical segregation, and niche partitioning of different apogonid species have not been examined in context of predation and anti-predator behaviour.

The high densities, species overlap in resting locations, site fidelity, and short lives suggest that apogonids represent a predictable and significant source of prey for reef predators (Marnane 2000; Marnane and Bellwood 2000; Marnane in review). Structural complexity can provide the greatest refuge from diurnal predators (Hixon and Beets 1993; Caley and St. John 1996). Therefore, the common observation of multi-species aggregations of apogonids sheltering in colonies of branching *Porites* is consistent with them using this habitat for shelter from predation. These same topographically complex coral patches may also serve as ambush sites for crepuscular and nocturnal predators such as *Cephalopholis* spp. and muraenid eels (Hixon and Carr 1997; Stewart 1998). *C. cyanostigma* in particular are often seen in association with schools of Apogonids (Marnane pers. com., Abdulla pers. obs). In gut analysis of *C. cyanostigma*, fifty-one percent of its diet was comprised of apogonids with more than 60% identified as *A. fragilis* and *C. quinquelineatus* (Stewart 1998). This observation of high predation rates may explain the larger foraging distances from refuge that were observed when *C. cyanostigma* were present in experimental trials. In the field, nightly foraging excursions of apogonids may also serve to distance them from ambush predators, toward the relative safety of the water column, when the majority of predators, which are diurnal, are no longer active (Goldman and Talbot 1976). In the wild, such predator-evasion behaviour may not incur a foraging cost for nocturnal, planktivorous species such as *A. fragilis* that feed in the water column.

Disassociation from structural refuge and dispersion of individuals were more pronounced in the smaller, planktivorous *A. fragilis* than in the larger, carnivorous *C. quinquelineatus* (see Figure 3.4c). Such behaviour may serve to maximise foraging space, minimise competitive interactions, and increase scatter and confusion effects.

In contrast, *C. quinquelineatus* spends most of its time close to coral in order to hunt amongst its branches. This behaviour is diminished when it perceives a potential predator, such as *C. cyanostigma,* that may utilise coral branches for ambush. *C. quinquelineatus* displayed classical aggregation behaviour (Pulliam 1973, Hoare *et al.* 2000; Treves 2001) by reducing adult and juvenile aggregation size in the presence of a predator (see Figure 3.4d).

3.4.2 Ontogenetic changes in anti-predator behaviour

Refuge seeking was a clear response of both juvenile and adult *P. moluccensis* in the presence of a predator. However, adults were more likely to forage and feed at locations further away from the refuge than juveniles (Figures 3.4 and 3.5). In the presence of a predator, both size classes decreased their foraging with adults still more likely to forage and feed at locations further from shelter than the juveniles. However, the costs of lost foraging space or opportunities may be low as juveniles feed mainly on small plankton carried by currents that is initially encountered and ignored by larger conspecifics (Coates 1980) and smaller individuals may have lower metabolic needs than larger ones (Werner 1988). Larger individuals in social damselfish are dominant to smaller ones and have access to larger and more nutritious prey (Coates 1980). Furthermore, larger individuals can swim faster and are better able to detect and escape predators (Persson 1988). These individuals can forage further from the refuge as they have outgrown a higher proportion of gape-limited predators by increasing their body depth (Persson 1988; Gerking 1994). Therefore, growing energetic demands and declining vulnerability to predators or perception of risk may cause an ontogenetic shift in anti-predator behaviour (Wahle 1992; Persson

1988). Young *P. moluccensis* may shift from highly refuge-associated foraging to less conservative foraging when energy demands exceed the nearby food supply and the perceived danger from predators is not enough to induce a refuge-seeking response.

Other anti-predator strategies appear to be prominent at different phases of the development of the fish examined. Juvenile *P. moluccensis* appear to form tighter aggregations (Figure 3.4, Table 3.2) as an adaptation to reduce vulnerability to predators and, as small young vertebrates, are more likely to seek refuge (Sih 1987; Lima and Dill 1990). As they grow older and larger, individuals of the four species may use vigilance and active scouting as alternative anti-predator strategies. Although the importance of vigilance is clear, it can be a costly activity because an animal may forfeit feeding, resting, or searching for mates (Treves 2000). Per capita cost of vigilance decreases if individuals aggregate in groups (Pulliam 1973; Roberts 1996; Treves 2000). Cooperative behaviour between members such as abrupt changes in speed and direction when one or a few members detect a predator can also reduce per capita vigilance (Huntingford *et al.*1994). While adult coral reef fish spend more time being vigilant for predators, juveniles may rely on adult behaviour as warning for predators thereby allowing them to dedicate a larger portion of their time to foraging. Such size-dependent behaviours within these social groups may help explain the high growth rates characteristic of juvenile temperate and coral reef fish (Tzioumis and Kingsford 1999; Meekan *et al.* 2001; Schwamborn and Ferreira 2002). Furthermore, such differing behaviours may help explain the persistence of mixed-size groups characteristic of coral reef fishes. Although small members in a group will feed on larger and higher quality plankton if larger individuals are experimentally removed (Coated 1980), they may derive the advantages of enhanced predator detection due to increased vigilance in the presence of adults. Additionally, larger and older members can derive an advantage from the presence of juveniles as all members should experience a decrease in per capita risk due to the dilution and confusion effects associated with groups (Pulliam 1973).

Both species of cardinal fish in this study displayed less association with their refuge (in comparison to *P. moluccensis* and *P. amboinensis*) in the presence of the rockcod, with adult *A. fragilis* doing so considerably more than adult *C. quinquelineatus*. Such behaviour may reflect the different foraging ecologies and morphological protection of the two species. *A. fragilis* are small fish that feed on plankton in the water column, while adult *C. quinquelineatus* are larger, camouflaged fish that are carnivorous and must forage close to the reef matrix. Juveniles of both species were less likely than adults to associate with refuge in the presence of predators and that may reflect higher vulnerability of small individuals as compared to larger ones and an increased avoidance of potential ambush from the refuge. Adult *C. quinquelineatus* were more likely to associate with refuge than juveniles and this difference in habitat association may reflect the ontogenetic changes in diet. Juvenile *C. quinquelineatus* are more dependent on plankton and as they grow older become more carnivorous (Marnane and Bellwood 2002) and therefore need to stay closer to corals to facilitate foraging.

3.5 Conclusion

Coral reef fish studied here displayed diverse anti-predator behaviour that was ontogeny and species-specific. They evidently rely on behavioural strategies beyond simple refugee-seeking, such as vigilance, aggregation, and ambush avoidance, to diffuse predation risk. For the two species of diurnal pomacentrids, seeking refuge in a physical structure was the main form of defence when threatened by a predator. For these fishes, there was a clear trade-off between foraging and hiding. The conceptual model presented here assumes that these two behaviours are the main trade-offs, and therefore is initially supported by the behaviour of the pomacentrids I examined. The model also predicts that adults under threat will forage and hide at the same rate as juveniles free of predation threat. This was also supported by results from *P. moluccensis*. It is not clear from the results of this chapter whether adults modify their behaviour more than juveniles in the presence of predators, another prediction of the model. Furthermore, species from the family Apoginadae, disassociated from physical structure in the presence of a predator, and therefore refuge-seeking may not be a cost of predation risk, and the model may not apply to these species.

Although this chapter has shown that foraging reduction and vigilance are significant behavioural response of coral reef fish prey to predation risk, the mechanisms underlying such behaviours and the factors affecting them are still not well understood. In Chapter 4, I explore predator-induced foraging reduction and vigilance in more detail and factors such as prey ontogeny and group size that may influence them. Finally I will revisit size-class dependent flexibility in anti-predator behavioural response in order to test the validity of the final assumption of the conceptual model: that adults will modify their behaviour more than juveniles will when exposed to the risk of predation.

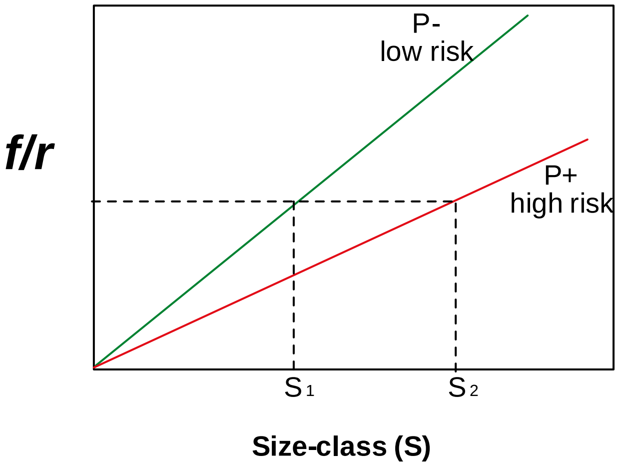

Figure 3.1 Conceptual model of behavioural trade-offs characteristic of site attached, planktivorous, coral reef fish prey. ***f*** is the probability of an individual foraging and ***r*** is the probability an individual seeking refuge. **P+** is the probability of a certain behaviour under high predation risk, and **P-** is under low predation risk. **S** indicates the size class of a prey individual. The horizontal dashed line indicates that the probability of foraging / refuge seeking for a large individual, $\mathbf{S_2}$, under high predation risk may be the same as that for a smaller individual, $\mathbf{S_1}$, under low predation risk.

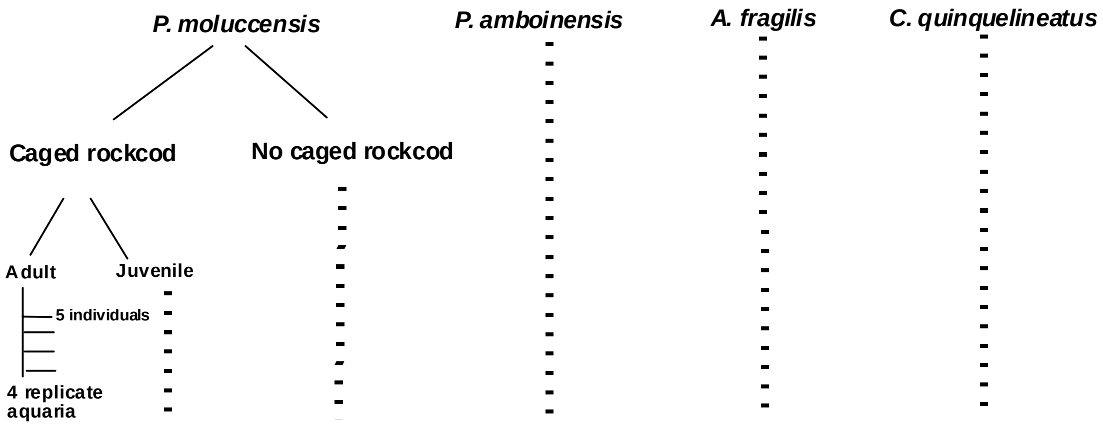

Figure 3.2 The experimental design featured four species with two factors per species: Caged rockcod / No caged rockcod crossed with Adult / Juvenile prey. Each treatment was replicated in four aquaria where every aquarium contained five individuals of each prey species.

Table 3.1 Definitions of the five behavioural categories scored in the experiments presented

Behavioural category	Defining characteristics to observe
Distance from refuge	Distance between the individual furthest from shelter and the shelter itself.
Aggregation size	Distance between the two individuals furthest apart in the aggregation
Foraging	Proportion of individuals actively searching for food, picking at substrata, or feeding from tray
Vigilance (diurnal)	Proportion of individuals scanning the environment, on alert, displaying sudden swim and stop "jerky" movements, or appeared to be scouting
Vigilance (nocturnal)	Proportion of individuals that do not move from position (to increase crypsis) but change orientation on one axis to visually scan their environment and to examine possible threat from different angles
Refuge-seeking	Number of individuals within or immediately adjacent to refuge

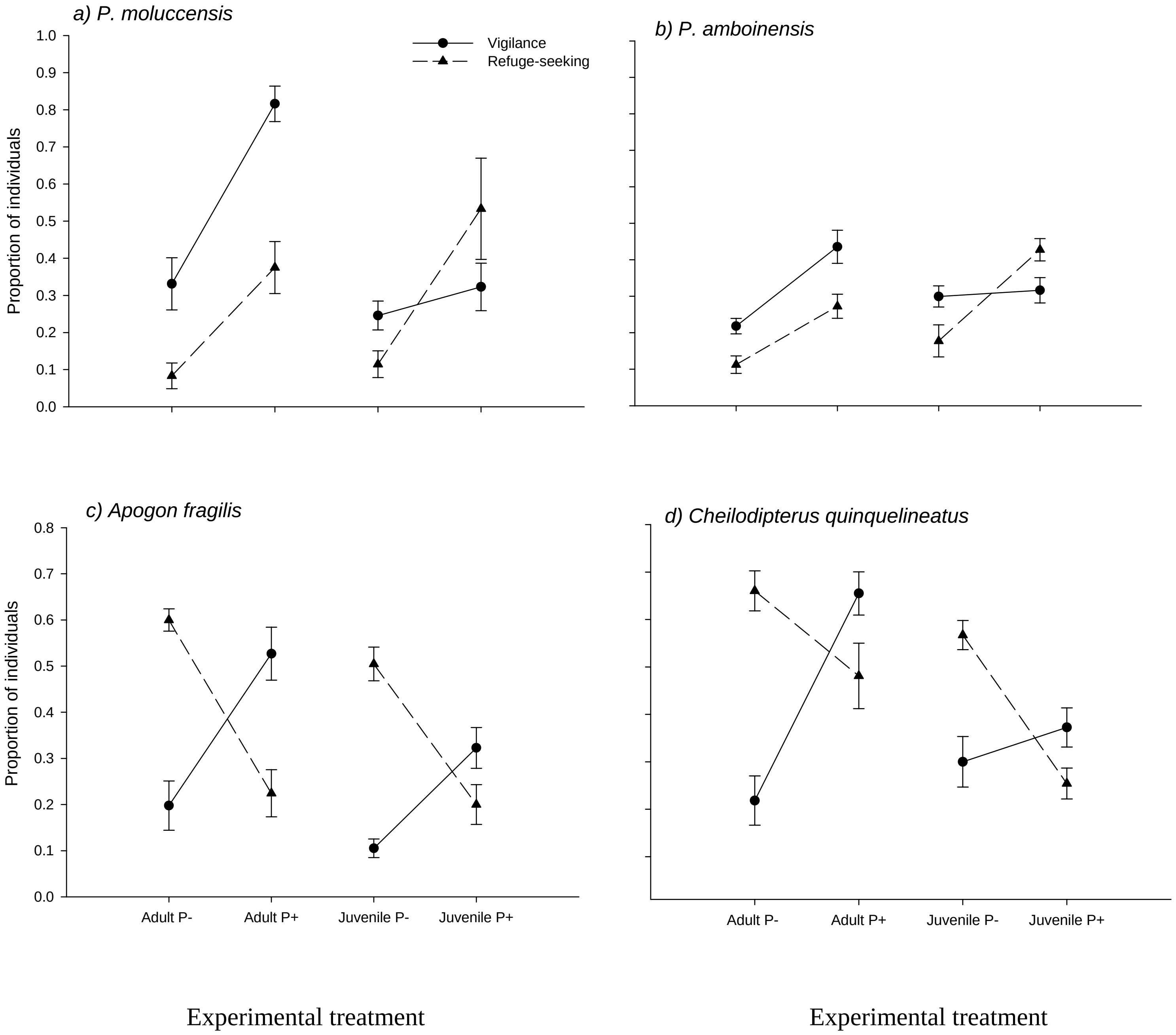

Figure 3.3 Behaviour of four species of coral reef fishes in the absence of food. Vigilance (●) and refuge-seeking (▲) of adults and juveniles were observed the presence (P+) and absence (P-) of a caged predator. Error bars indicate one SE.

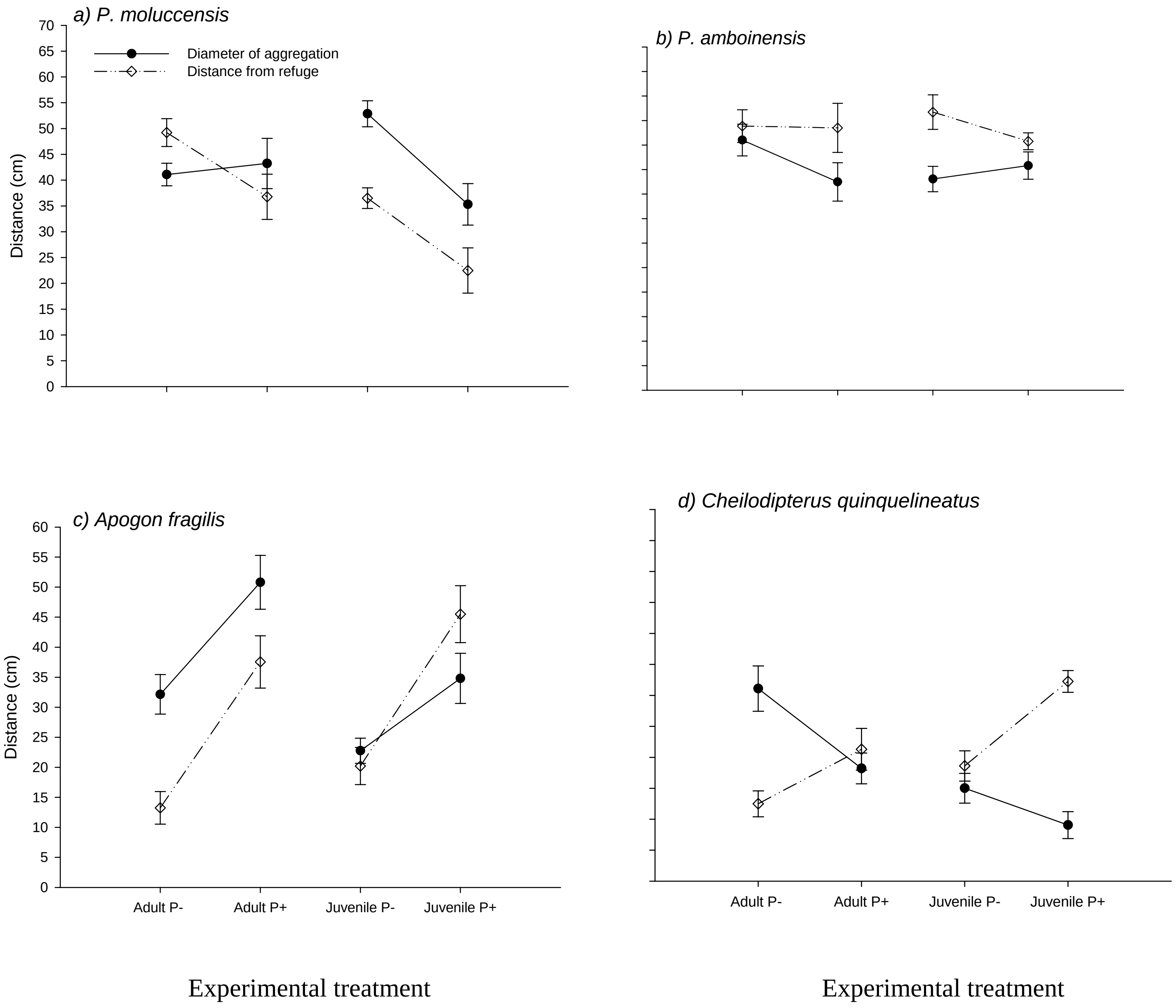

Figure 3.4 Diameter of the aggregation (●, distance between the two individuals furthest apart) and the distance from refuge (◇) of the furthest individual were observed for four species of coral reef fishes in the absence of food. The two behavioural categories were observed in adults and juveniles and in the presence (P+) and absence (P-) of a caged predator. Error bars indicate one SE.

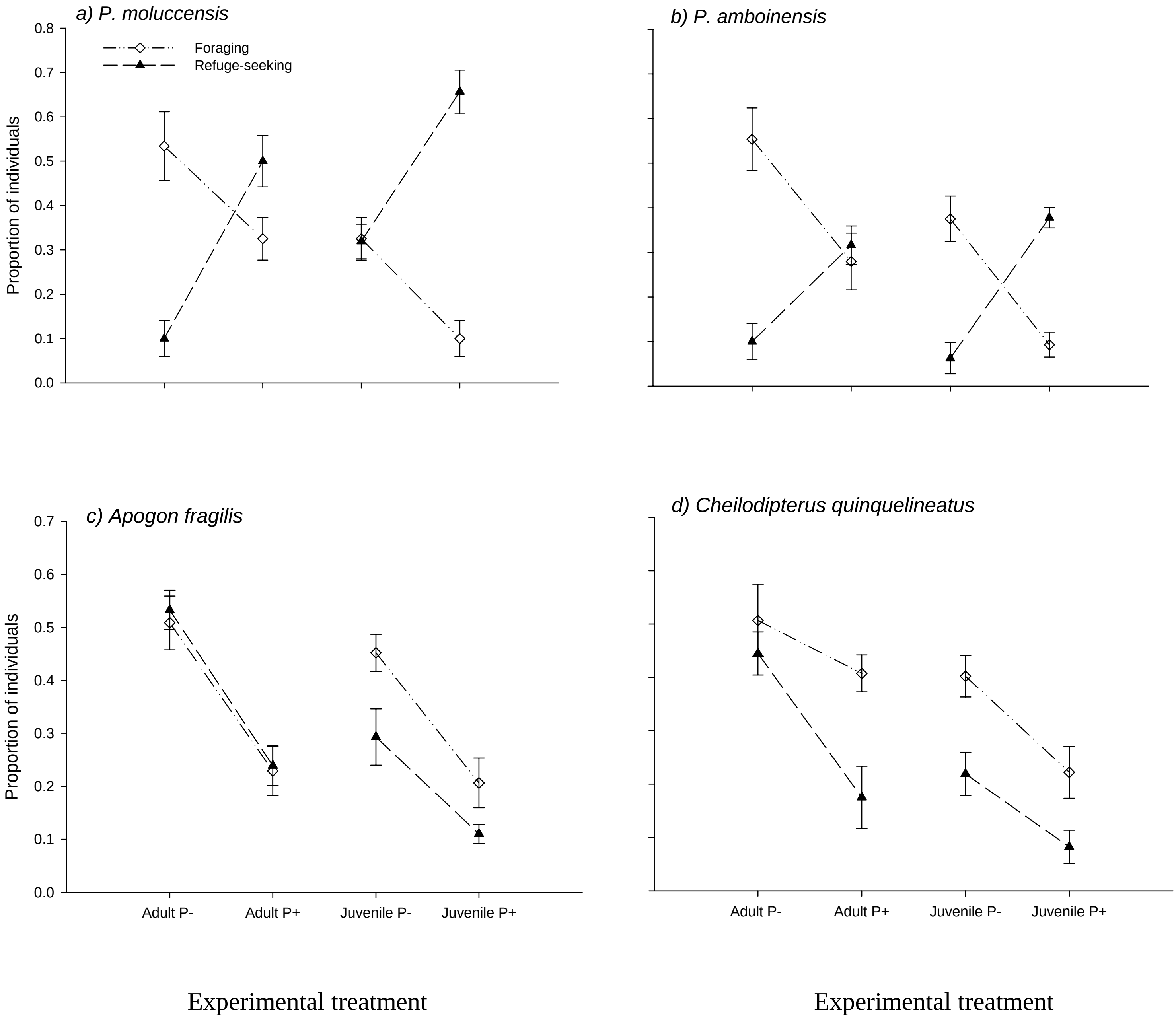

Figure 3.5 Behaviour of four species of coral reef fishes in the presence of food. Feeding (◇) and refuge-seeking (▲) of adults and juveniles were observed the presence (P+) and absence (P-) of a caged predator. Error bars indicate one SE.

Table 3.2 Summary of two-way ANOVAs of means for the behaviour of adults and juveniles in the presence and absence of a rockcod for each of four study species. These observations were recorded in the absence of food. Observations of number of individuals engaged in a certain behavioural activity were converted to proportions. To meet the assumption of homogeneity of variances in ANOVA, proportional data were transformed to $\sqrt{x}$. Data for aggregation diameter and distance from refuge were transformed to $\log_{10}(x+1)$. Bold indicates values that are statistically significant. *indicates a significant p value < 0.05, ** indicates a significant p value of $p < 0.01$.

		P. moluccensis		***P. amboinensis***		***A. fragilis***		***C. quinquelineatus***	
Factor	*Dep. Var.*	*MS*	*F*	*MS*	*F*	*MS*	*F*	*MS*	*F*
Predation Risk	Aggregation Diameter	237.67	**4.66***	33.713	0.837	943.00	**17.882****	0.299	**35.033****
	Distance from refuge	700.04	**14.05****	39.848	0.771	2458.631	**42.174****	0.0003	0.026
	Vigilance	0.316	**24.61****	0.0549	**12.113****	0.299	**35.033****	0.259	**27.871****
	Refuge-seeking	0.505	**19.40****	0.168	**37.287****	0.463	**72.279****	0.242	**28.38****
Ontogenetic Stage	Aggregation Diameter	14.855	0.291	21.218	0.527	642.834	**12.19****	0.088	**10.31****
	Distance from refuge	727.88	**14.61****	0.0156	0	221.923	3.807	0.083	**8.317***
	Vigilance	0.335	**26.09****	0.0014	0.318	0.0805	**10.313****	0.043	4.336
	Refuge-seeking	0.036	1.382	0.0484	**10.736****	0.0143	2.237	0.102	**11.993****
P. Risk x O. Stage	Aggregation Diameter	387.60	**7.603***	127.079	3.157	43.615	0.827	0.013	1.46
	Distance from refuge	2.444	0.049	31.174	0.603	0.988	0.017	0.0006	0.059
	Vigilance	0.166	**12.96****	0.0431	**8.897***	0.0124	0.146	0.133	**14.267****
	Refuge-seeking	0.016	0.621	0.0081	1.797	0.005	0.784	0.018	2.093
Error	Aggregation Diameter	50.982		40.259		52.734		0.009	
	Distance from refuge	49.828		51.661		58.297		0.010	
	Vigilance	0.0128		0.0045		0.0085		0.009	
	Refuge-seeking	0.026		0.0045		0.006		0.009	

Table 3.3 Summary of two-way ANOVAs of means for the different behavioural categories of adults and juveniles in the presence and absence of a rockcod for each of the study species. These observations were recorded in the presence of food. Observations of number of individuals engaged in a certain behavioural activity were converted to proportions. To meet the assumption of homogeneity of variances in ANOVA, proportional data were transformed to √x. Bold indicates values that are statistically significant. *indicates a significant p value < 0.05, ** indicates a highly significant p value of p < 0.01.

		P. moluccensis		***P. amboinensis***		***A. fragilis***		***C. quinquelineatus***	
Factor	*Dep. Var.*	*MS*	*F*	*MS*	*F*	*MS*	*F*	*MS*	*F*
Predation Risk	Foraging	0.188	**15.351****	0.31	**25.07****	1.948	**238.48****	0.078	**8.17***
	Refuge-seeking	0.544	**61.4****	0.283	**53.63****	1.38	**232.67****	0.165	**21.63****
Ontogenetic Stage	Foraging	0.188	**15.351****	0.133	**10.80****	0.0627	0.768	0.084	**8.792***
	Refuge-seeking	0.141	**15.944****	0.0006	0.112	0.136	**22.9****	0.102	**13.299****
Risk x O. Stage	Foraging	0.0003	0.021	0.00007	0.006	0.001	0.140	0.007	0.686
	Refuge-seeking	0.004	0.438	0.01	1.859	0.0123	2.07	0.018	2.301
Error	Foraging	0.012		0.0012		0.008		0.010	
	Refuge-seeking	0.009		0.005		0.006		0.008	

Chapter 4

The effect of predation risk, group size, and ontogeny on foraging of planktivorous coral reef fish

4.0 Abstract

Chapter 3 demonstrated that coral reef fish prey modify their behaviour in a number of different ways in response to predation risk. In this chapter I examine predator-induced modifications in foraging behaviour of a common tropical fish, *Pomacentrus moluccensis*, in groups of different size and at different ontogenetic stages on coral reefs in the Great Barrier Reef. Different group sizes of *P. moluccensis* were exposed to a potential predator or non-predator and changes in foraging behaviour of juveniles and adults were observed. In the presence of a predator, foraging effort, estimated by the number of bites taken and foraging distance away from shelter, was reduced whilst the presence of a non-predator caused an increase in foraging distance of *P. moluccensis*. In the presence of a predator, adults exhibited greater reduction in foraging than juveniles. Juveniles continued foraging even in the presence of predators which may help explain maintenance of high growth rates in young coral reef fishes. In contrast, reduced foraging in adults might reflect an emphasis on survival. Prey fish in large groups exposed to a predator displayed less reduction in foraging effort compared to fish in smaller groups. This was consistent with observational surveys that show a reduction in per capita vigilance with an increase in prey group size. Therefore, aggregating in coral reef fishes, a common phenomenon, may serve to dilute predation risk and increase individual foraging effort in social groups of pomacentrids. These results suggest that nonlethal predator-prey interactions may have an important effect on food ingestion rates and therefore energy uptake of coral reef fish. These effects are mediated by prey group size and ontogeny.

4.1 Introduction

Physiological needs and physical abilities of an individual will influence the magnitude of the responses to predation risk (Persson 1988; Jones and McKormick 2002). For example, ontogenetic stage may greatly affect how animals respond to the risk of predation (Munday and Jones 1988; Dahlgren and Eggleston 2000; Brown *et al.* 2001; Brown *et al*. 2002). Different size-classes may occupy different habitats and access different refuges that change with growth of the organism (Hobson 1991; Munday and Jones 1998; Dahlgren and Eggleston 2000). Feeding behaviour will also change as physiological needs change and food choice and accessibility change with increases in gape size (Coates 1980; St. John 1999; Brown *et al.* 2001; Hjelm and Persson 2001) and physical performance (Persson 1988). Vulnerability decreases as larger individuals approach the gape-limitation of some of their predators (Werner and Gilliam 1984; Werner *et al.* 1993). Changes in foraging over ontogeny in response to interactions with predators and conspecifics, however, has received little attention in social marine animals.

Coral-reef associated fishes are an ideal model system for the study of site-attached, social prey that face daily trade-offs between survival and growth. A large majority of coral reef fishes are planktivorous, recruit to preferred coral species, and occur in a wide range of group sizes. Often group densities are high and many animals within these groups tend to forage away from conspecific competitors while exhibiting high site-fidelity to the specific coral colonies shared by the group as shelter. Competition for resources between members in such groups occurs and can be intense (Jones 1986, 1987, 1991) as available plankton is spatially patchy, temporally unpredictable, and infrequent (Noda *et al.* 1992). A high proportion of planktivorous fish have empty stomachs when examined (Noda *et al.* 1992) and exhibit physiological conditions symptomatic of starved individuals (Kerrigan 1994). Even with high levels of competition, social groups are relatively stable and are frequently governed by size-class dominance hierarchies (Coates 1980; Forrester 1990).

So what then are the advantages of group membership? One possibility is that individuals in groups are less susceptible to the direct or indirect effects of predators than solitary individuals. Accordingly, group membership would be expected to dilute the individual risk of mortality due to predation because of the greater number of available target individuals and the confusion effects of many moving prey which do not allow a predator to develop search images (Pulliam 1973). Group vigilance may also increase with group size while the per capita time spent being vigilant may decrease (Roberts 1996; Treves 2000). Therefore, the size of groups may have implications for the response and behaviour of individuals in the presence of a predator (Forrester 1990). Few studies have experimentally assessed such potential benefits of social groups in marine fish (but see Connell 2000).

Most studies examining predation on marine fish have emphasised mortality and numerical responses of prey but have not addressed the effects of nonlethal species interactions such as competition and predation risk (Jones and McCormick 2002). Juvenile mortality due to predation is thought to be high in coral reef fish (Doherty and Sale 1985; Caley 1996) and prey body condition (McCormick and Hoey 2004), predator diversity (Caley 1995), and habitat complexity (Caley and St. John 1996;

Beukers and Jones 1997) can mediate mortality rate. The effects of ontogeny and group size in mediating the risk of predation, however, have yet to be examined.

I conducted field observations and an experiment on the planktivorous yellow damselfish, *Pomacentrus moluccensis*, designed to elucidate potential anti-predatory benefits acquired by juvenile and adult coral reef fish from group aggregations. Specifically, I explored the hypotheses that: (a) individuals will reduce foraging effort (distance and bite rate) in the presence of a potential predator and not in the presence of other non-predatory fish; (b) these responses will be larger in smaller groups than in larger groups because larger aggregations may dilute the risk of predation; and (c) more vulnerable juveniles will exhibit lower foraging rates and greater reductions in foraging in the presence of predators than conspecific adults.

4.2 Methods:

4.2.1 Study Site and Species

The experiment and observational surveys were done on the fringing reefs associated with the Lizard Island Group in the Cairns section of the Great Barrier Reef (Figure 4.1). All sampling was done by divers on SCUBA during October 2001. *P. moluccensis* was used because it is a benthic-habitat associated fish, occurs in different sized groups containing adults and juveniles, and feeding distance from shelter foraging effort can be readily observed and easily quantified. The Slingjaw wrasse, *Epibulus insidiator*, was used in the experiment to increase predation risk faced by foraging damselfish because it is a common, diurnal, stalking predator that feeds on fish and invertebrates (Westneat and Wainwright 1989) including *P.*

moluccensis (Gottlieb 1992). A third species, *Chaetodon rainfordi,* a benthic invertivore / corallivore was used as a benign non-predator control.

4.2.2 Experimental design

A 3 x 3 x 2 factorial design was used for the experiment (Figure 4.2) where the predator exposure treatment and two treatment controls (exposure to benign corallivore and exposure to equipment only) were crossed with three prey fish densities and two prey size-classes (adults and juveniles). Fifty-four groups of *P. moluccensis*, ranging in size from 1 to 14 individuals, were selected at random for the experiment. Groups were allocated to three categories: 2-3; 4-8; or 9+ members. I assumed that plankton densities were equal or randomly varying across groups, meaning that these group categories represented (relatively) low, medium, and high levels of intraspecific competition. To exclude habitat size and complexity as a confounding variable and to standardise refuge "quality", all chosen groups occupied a coral colony of *P. damicornis,* a preferred habitat of *P. moluccensis,* of approximately equal size, 0.25m^3 (Eckert 1987; Jones 1991; Ohman *et al.* 1998). Each group of *P. moluccensis* occupied a distinct coral colony that was separate from any other group. Each combination of treatments was replicated 6 times. The behaviour of juveniles and adults within each group was scored separately.

Each group was exposed to either the predator treatment or the two controls in random order for five minutes approximately two hours before or two hours after high tide, when current flow was strongest. Exposure to the predator or the corallivore involved placing an individual of *E. insidiator* or *C. rainfordi* in a clear plastic bag filled with seawater with a bubble of air to maintain positive buoyancy. In the second control treatment, an empty bag identical in all other aspects was presented. These “balloons” were placed 50 cm away from, and level with, the *P. moluccensis* group (Figure 4.3). Approximately 3-5 minutes of acclimation to the intrusion of placing the balloon were allowed for the return of normal behaviour before any video recording was done. The behaviours of individuals in each group were recorded using an underwater video camera (Sony CCD) for 5 minutes and for an additional 5 minutes after exposure to a "balloon" treatment. The footage was taken perpendicular to the direction of the current in order to measure foraging distance “up current” from the colony. The 10-min observation period was determined from pilot studies to be the most cost-effective duration in terms of SCUBA bottom time for observing a large number of fish groups while ensuring representative and natural behaviour. Before any exposure to treatment or controls, a plastic stake marked with 10-cm graduations was placed approximately 1 meter away from the colony and within the frame of the video camera. This measurement stake allowed distance to be calibrated, in each image frame sampled from the video footage.

4.2.3 Image Analysis

The video footage was digitised to AVI and MPEG formatted files and Display Analyser was used to analyse the frames. Display Analyser superimposes a cartesian coordinate plane on to a video image or frame from an AVI file. I used this overlay to track the position of different individuals and their movement over the duration of the five-minute sample of each colony under exposure to either the predation risk treatment or each of the two control treatments. The social and foraging behaviour of individuals were clearly visible in the video samples. From these video frames the position of individuals in relation to their coral refuge, the number of bites taken, and the size class of the individual were estimated.

Using the centre of a coral colony as the point of origin, the coordinates of different locations at which an individual foraged or hovered above its habitat could be estimated. Distances between foraging or hovering locations and the origin were measured using 2-dimensional Euclidean space on the coordinate plane. In the first 30-60 seconds, group size and size class composition was recorded. Three types of behaviour were observed and five different observations were made. Firstly, the first frame to show all individuals was used to record locations of all group members with reference to their coral refuge. This was repeated six times in the next minute and the observations averaged. This was done 3 times in the first five minutes prior to exposure to treatments and 3 times post-exposure. Two focal observations were also done and each one involved recording, every ten seconds for one minute, the number of bites an individual took and the position at which these bites were taken. This was conducted once for an adult and once for a juvenile, with each subject chosen haphazardly for each set of observations.

4.2.4 Data Analysis

Three behavioural responses were analysed statistically: mean distance away from the refuge, change in mean foraging distance, and change in mean number of bites taken. Change in mean foraging distance (or bite-rate) was calculated as the difference between the mean foraging distance (or bite-rate) of individuals in a size class “After” and “Before” exposure to the predator treatment and two controls. The Kolmogorov-Smirnov test was used to compare (the distribution of) foraging distances of *P. moluccensis* before and after treatments. A Repeated Measures ANOVA was used to examine the effects of treatments on the change in foraging distance and bite-rate. In this design the “Between Subjects” factors were exposure treatment (including controls) and group size and the “Within Subjects” (i.e. repeated measures) factor was ontogenetic stage**.** Data were log transformed, log x + lowest value in range + 0.01 (Quinn and Keough 2002), and normality of data was examined with histograms and quantile-quantile (Q-Q) plots. Homogeneity of variances was tested with Levene's test.

4.2.5 Observational Surveys

In order to ascertain whether modifications in foraging behaviour observed during experimental trails were consistent with natural conditions and behaviour, observational studies of prey vigilance behaviour were conducted. Nine locations around the Lizard Island Group were chosen based on pilot observations and past studies (eg. Stewart 1998) to represent a wide range of piscivore densities (Figure 4.1). In each location three sites were chosen and in each site five 50m x 5 m (250 m^2) observational transects were conducted. Transects were laid haphazardly along the reef slope within a depth range of 4-9 meters. Transects were a minimum of 4 meters apart. Two fish counters counting predators and prey behaviour separately swam side by side along each transect and all fish 2.5 m on either side of the measuring tape delineating the transect were observed. I conducted a scan sample (Altman 1973) to measure group vigilance, which is defined as the number of prey individuals in a group that were scanning, inspecting, scouting, and not feeding. Individuals who were vigilant often display characteristic stop-jerk swimming behaviour and dorsal fin extensions (Chapter 3). I also used focal animal sampling (Altman 1973) to measure individual vigilance, which is defined as the total number of seconds the focal animal displayed vigilant behaviour in a 3 minute sample. Behavioural artefacts due to the presence of the observer were minimised by a cautious approach and discreet observation. Although such bias could not be eliminated due to the nature of the sampling regime, it was consistent throughout the samples. For analysis, data from the observational surveys of prey vigilance behaviour and piscivore densities were (separately) pooled across surveys within sites (Stewart 1998). Vigilance behaviour data were regressed against prey group size and piscivore density.

4.3 Results

The three treatments were characterised by different behavioural responses. Individuals were similarly distributed before and after the introduction of the empty plastic bag (Figure 4.4, Table 4.1). In the bag only controls, juveniles were often closer to their refuge than adults (Figure 4.4). The majority (72%) of juveniles were positioned less than 10 cm away from the *Pocillopora damicornis* coral head with a maximum distance observed of 32 cm (Figure 4.4). The majority (82%) of adult foraging was wide ranging, from 0 to 40 cm with a maximum distance of 51 cm.

4.3.1 Distribution of foraging distances in response to predators and non-predators

P. moluccensis responded differently to the two species presented in this experiment. Both size-classes changed foraging distance in the presence of the non-predator (Figure 4.5). When faced with *C. rainfordi,* juveniles ventured further away from their habitat to a maximum distance of 51 cm and occupancy of the 30-60 cm range rose from 6.3 % to 20.1%, although this apparent shift in distribution was not statistically significant (Figure 4.5, Table 4.1, K-S test, D = 0.3333, p = 0.154). Adults travelled to a maximum distance of 58 cm and occupancy of the 30-60 cm range rose from 21.6% to 56.5%, representing a significant change in distribution of foraging distances (K-S test, D = 0.1905, p = 0.022). By contrast, in the presence of a potential predator, both size-classes reduced their distances from the coral (Figure 4.6,

Table 4.1). Juveniles reduced occupancy in the 10-40 cm range from 36.1% to 18.6% while occupancy in the coral-10 cm range increased from 63.9% to 81.4% (K-S test, D = 0.25, p = 0.038). Adults reduced occupancy of the 20-50 cm range from 47.4% to 12.5% while occupancy in the coral-20 cm range increased from 52.6% to 87.5% (K-S test, D = 0.2024, p = 0.035). The majority of juveniles in all three treatments were sighted closer to their coral refuge as than were adults in the same group (Figures 4.4; 4.5; 4.6)

4.3.2 Foraging changes in response to predators and non-predators

Foraging distance away from the coral varied with the exposure treatment but the treatment effects interacted with both group size and ontogenetic stage, separately (Table 4.2). Despite the interaction, however, both adults and juveniles increased mean foraging distance in the presence of the corallivore non-predator and reduced it in the presence of the wrasse predator (Figure 4.7, Table 4.2, ANOVA, F = 856.90, 2 d.f., $p < 0.05$). Adults exhibited a larger relative increase and decrease in mean foraging distance than juveniles in response to the non-predator and predator treatments, respectively (Figures 4.7a). On average, adults moved 8.1 cm (+32%) toward the non-predator while juveniles only moved 2.56 cm (+19%). In response to presence of a predator, adults reduced their foraging distance by 13.3 cm (-52%) while juveniles retreated 3.9cm (-21%).

The number of bites taken per 10-second interval also changed in response to the non-predator (Figure 4.7b), again in interaction with the other factors (Table 4.2). Both juveniles and adults exhibited similar increases in bite-rate in response to the corallivore, by 1.75 and 1.82 bites per ten seconds respectively. A predator, however, caused adults to reduce absolute bite rates more than juveniles, by 0.8 and 0.4 bites per 10 seconds respectively (Table 4.2, ANOVA, F = 24.83, $p < 0.01$). Adults proportionally increased (+37.9%) and decreased (-18.1%) their bite-rate more than juveniles (+21%, -4%) in response to the corallivore and predator respectively (Figure 4.7b). When juveniles were faced with a predator, changes in proportional bite-rate were not statistically different from the procedure control (the empty balloon) and so it can be concluded that no significant reduction in bites of juveniles occurred because of exposure to the predator.

4.3.3 Effects of group size on responses to predators and non-predators

Responses to a potential predator and a non-predator varied across group sizes in interaction with treatment (Table 4.2). There was a significant interaction in change in foraging distance between the exposure treatment and group size (F = 65.86; 4, 45 d.f., $p < 0.01$). Proportional reduction in foraging distance was similar between low and medium group sizes, 40% and 49% respectively, but decreased at high group size, 25% (Figure 4.8a). In the presence of a non-predator, however, proportional change in distance increased between low, +19%, and medium group sizes, +55%, but was similar between medium and high (+51%) group sizes (Figure 4.8a).

Similarly, bite-rate responses were statistically different within exposure treatments but exposure interacted with group size (Table 4.2, F = 134.97; 2, 45 d.f., $p < 0.05$). Proportional reduction in bite rate due to predation risk decreased with increasing group size (Figure 4.8b: low, -20%; med. -9%; high -2 %). In contrast, proportional increase in bite rate due to non-predator increased with group size (Figure 4.8b: low +10%; med. +15%, high +23%).

4.3.4 Predator density and prey vigilance

The proportion of prey individuals in a group that display vigilant behaviour increased with an increase in piscivore density (Figure 4.9). A regression suggests that this relationship is saturating (Figure 4.9, $y = y_0 + a[\ln(x)]$ $r^2 = 0.754$). Time spent being vigilant decreased with an increase in prey group size (Figure 4.10). This relationship was well described by an exponential decay model (Figure 4.10, $y = ae^{-bx}$, $r^2 = 0.47$).

4.4 Discussion

Although the risk of predation is sufficient to significantly modify the behaviour of many animals and alter individual fitness and population dynamics (Lima and Dill 1990), few studies have investigated the effect of predation risk on juvenile and adult prey in different group sizes. This study shows that individuals of the species *Pomacentrus moluccensis*, respond differently to a piscivore *Epibulus insidiator*, than to a non-piscivore *Chaetodon rainfordi*. These prey fish reduced distance of their foraging excursions significantly while the number of bites they took was maintained or reduced only slightly in the presence of a predator. Reductions in foraging distance were weaker in large compared with small groups. Larger group size was also associated with smaller reductions in bite-rate. Juveniles, in particular, exhibited a proportionally smaller reduction in foraging effort (distance and bites) than adult fish.

4.4.1 Trade-offs in planktivorous pomacentrids

Foragers frequently trade-off feeding and foraging activity against safety (Abrams 1990, 1991; Werner *et al.* 1993). Many species of pomacentrids feed in aggregations over reefs during the day and seek refuge at night, or from predators, in the same reefs (Hobson 1991; Hixon 1991; Sackley and Kaufman 1996). Individuals move away from their refuge to increase food availability and evade competition ("the wall of mouths": Hamner *et al.* 1988; Sackley and Kaufman 1996) that can be found close to reefs (Coates 1980; Forrester 1991). Increased distance from refuge, however, incurs an increased risk of predation. In this study, *P. moluccensis* avoided a potential predator by retreating towards shelter (decreasing total foraging space) while maintaining bite rates close to normal levels, especially in larger groups. Similarly, coho salmon reduce foraging distance for food items in the water column when under risk (Dill and Fraser 1984). The response of *P. moluccensis* to potential predators may mean that these fish suffer reduced mortality whilst continuing to ingest food particles under risk. Such a behavioural response would be advantageous if foraging and resources acquired were time-limited (Holbrook and Schmitt 1988) or patches of plankton might be lost if not consumed immediately, before being carried away with the prevailing current (Hamner *et al.* 1988; Hobson 1991; Noda *et al.* 1991).

P. moluccensis individuals from larger groups reduced their foraging less when exposed to a predator than individuals from smaller groups. Solitary fish or those in smaller schools are likely to be more vulnerable to predators than members of larger groups (Parr 1927; Forrester 1991). Members of larger groups will benefit from increased total vigilance ("many eyes": Pulliam 1973; Trevis 2000), alarm signals from group mates (Pitcher 1986; Peacor 2003), and an increased probability of escape and survival ("dilution effect": Hamilton 1971; Bertram 1978; Pitcher 1986) compared to those in smaller groups. In addition, individuals in larger groups will potentially experience higher competition from conspecifics than those in smaller groups. These factors will cause fish to spend less time being wary of predators and more time feeding. This was evident from the observational surveys which showed that per capita vigilance of *P. moluccensis* decreased with an increase in the size of the group.

4.4.2 Ontogeny-dependent foraging

Size-class segregation may be a consequence of intraspecific competition in social groups of pomacentrids (Coates 1980; Jones 1987) and other coral reef fish (Shulman 1985). Dominant large adults have first choice of food items (Coates 1980) and adult presence may have a negative effect on juvenile growth (Jones 1987). Juvenile *P. moluccensis* foraged closer to coral colonies than adults. Similar behaviour was observed for *Chromis nitida*, another tropical planktivorous pomacentrid, where large individuals had greater foraging distances than small ones (Sackley and Kaufman 1996). Foraging distance might also be correlated with fish size because there will be a greater number of predators that may ingest a small fish over a larger one (because of gape-limitation), meaning that smaller fish are at relatively greater risk than larger fish when far away from their shelter. Larger fish can also swim faster than small ones (Bainbridge 1958) and can reach reef refuges more rapidly (Hobson 1991; Sackley and Kaufman 1996). Juvenile *P. moluccensis* were usually at the centre of the aggregation and may be at an advantage because they are more protected than those on the periphery (Hamilton 1971). Unlike birds, whose dominant members seek the centre of a flock (Pulliam 1973), it has been speculated that dominant and larger damselfish individuals seek the periphery of a group presumably to maximise first exposure and best pick of (larger) planktonic food items carried by the current (Coates 1980). This contrasts with suggestions by McCormick and Kerrigan (1996) that social damselfish with strong size-related hierarchies allow subordinates less favourable access to refuge from predation.

Where mortality risk declines with body size, animals should increase foraging activity as they increase in size (Werner *et al.* 1993). Adult *P. moluccensis* did forage further and had higher bite rates than younger conspecifics in the absence of predators. This may be necessary to meet physiological and reproductive demands associated with larger body size. However, adults reduced their foraging excursions proportionally more than juveniles in the presence of a predator. This may indicate that older individuals are more cautious foragers than their younger counterparts and are less likely to risk foraging excursions away from refuge when predators are present. Such conservative foraging behaviour in the presence of predation risk may reflect learning from past near lethal interactions with predators or observing lethal episodes on group mates or conspecifics (Pitcher 1986; Warner 1997; Peacor 2003). Results of Chapter 3 also suggest that adults are more likely to engage in vigilance (that interrupts feeding) than juveniles when exposed to a predator, which may also explain the larger reductions in number of bites taken by adults as compared to juveniles.

4.4.3 Interspecific aggression

Many damselfishes are highly territorial and display aggressive behaviour towards trespassers (Bay *et. al* 2001). This study shows that *P. moluccensis* could differentiate between predatory and non-predatory fish. In the presence of *C. rainfordii,* there was an increase in foraging distance that may have resulted from interspecific aggression, cooperative defence, or curiosity. Similar recognition behaviour and aggressive response have been documented in freshwater and other coral reef fish (Karplus and Algom 1981; Karplus *et al.* 1982; Webb 1982; Shulman 1985; Magurran and Girling 1986; Bay *et al.* 2001). The aggressive effect was heightened with an increase in group size of *P. moluccensis,* a trend observed in higher vertebrates such as chimpanzees, where aggression on neighbours occurs if numerical advantage of the group reduces the cost of attacking (Wilson *et al.* 2001). It is unlikely that *P. moluccensis* reacted to *C. rainfordii* as a competitor as the chaetodon does not feed on plankton or shelter in coral colonies of *Pocillipora damicornis*. Such aggression may be due to trespassing (Bay *et al.* 2001) and dominance in aggressive encounters between different species of reef fish may be determined by relative size and species identity (Shulman 1985). *C. rainfordii* was comparatively equal in size to adult *P. moluccensis* (~57mm) and therefore the behaviour exhibited by *P. moluccensis* may have been a confrontational or aggressive encounter to discourage trespassing.

4.4.4 Implications of consistent foraging in juveniles

Investigations of temperate and coral reef fish have documented high growth rates in early life-history with a marked reduction in subsequent stages (Tzioumis and Kingsford 1999; Wanties and Thollot 2000; Meekan *et al.* 2001). This study identifies a behavioural mechanism that may be partially responsible for maintenance of high growth rates in early life history of planktivorous fish. Juvenile *P. moluccensis* displayed lower relative reductions in foraging effort as compared with adults when faced with the risk of predation. Maintaining a near normal feeding rate in the presence of a threat may ensure rapid transition to a larger size class (Olson 1996) and increasing survival probability to the next size class in non-reproductive individuals maximises fitness (Werner and Gilliam 1984). Predation on *Pomacentrus amboinensis,* a common tropical damselfish, was found to be selective for low condition and slow growing recruits (McCormick and Hoey 2004). Juvenile size does influence mortality, where larger sized individuals have been shown to have a higher probability of survival (Booth 1995) and individuals that are small are consumed in preference to larger individuals (Anderson 1988). Juvenile *P. moluccensis* may optimize a) survival by remaining relatively close to their refuge and b) growth by maintaining foraging effort even in the presence of predators. High growth rates in damselfish larvae will lead to high survivorship and the contribution of fast growing individuals and cohorts to the replenishment of demersal fish populations is higher than that of slow-growing conspecifics and cohorts (Vigliola and Meekan 2002; Wilson and Meekan 2002). Size-specific predation will have a major effect on populations of fish where size-structured hierarchies govern growth and reproductive status (McCormick and Kerrigan 1996).

4.5 Conclusion

It is clear from this study that *P. moluccensis* could distinguish between a potential predator and a non-predator and respond accordingly. Juveniles and adults modified their behaviour in different ways. Contrary to the predictions stated earlier in this chapter, juveniles displayed little modification (reduction) of foraging behaviour in the presence of predators. This may contribute to high growth rates at an early and critical stage in their life history. Adults modified their foraging more than juveniles and this may reflect adult emphasis on vigilance and survivorship. This behaviour by juveniles and adults supports the conceptual model presented in Figure 3.1 (Chapter 3) which suggests that adults display more flexibility in foraging and refuge-seeking than juveniles. Furthermore, behavioural modifications displayed by *P. moluccensis* suggest that increase in group size may contribute to risk dilution of predators and cooperative aggression on interspecific trespassers. These results suggest that predator dilution and cooperative defence may be important advantages for members of social groups in coral reef fish.

This chapter has shown that predation risk has significant effects on the foraging of the planktivorous coral reef fish *P. moluccensis*. In order for nonlethal predator effects to exert a fitness cost on individuals or modify size-structure of populations, it must modify individuals' energy investments and morphology. In chapter 5, I explore the potential implications of predator-induced foraging reductions on growth of *P. moluccensis*. I also assess the role of group size in modifying the energetic effects of predation risk.

4.6 Figures and Tables

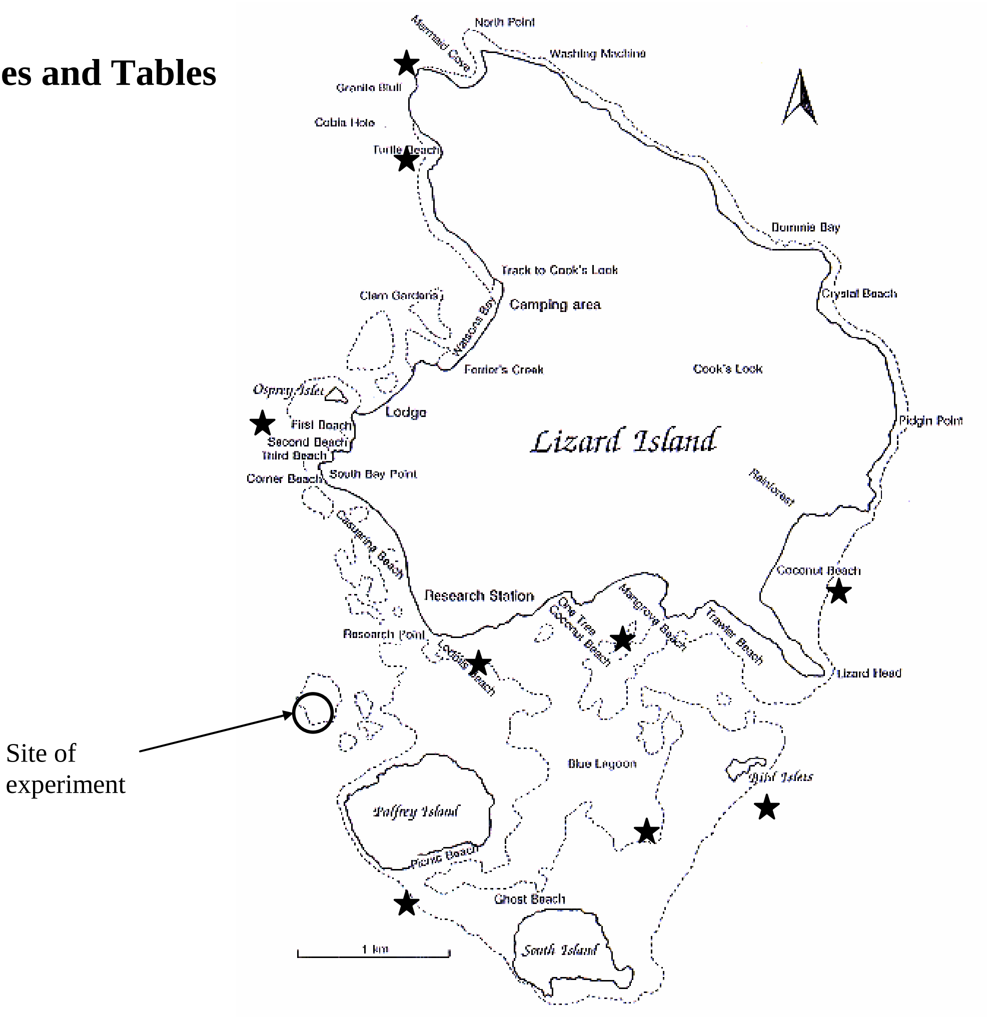

Figure 4.1 Location of naturally occurring coral heads of the species *Pocillopora damicornis* that were used in this experiment. Stars indicate sites where observational surveys of prey vigilance and predator density were done.

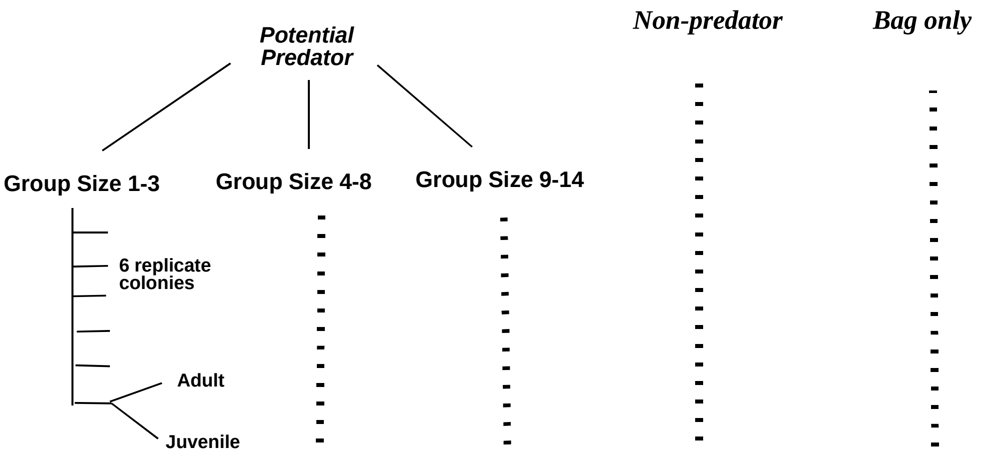

Figure 4.2 The three factor experimental design with Factor A: Exposure Treatment, Factor B: Group Size, and Factor C: Ontogenetic Stage. The Exposure Treatment was made up of *E. insidiator* as the potential predator, *C. rainfordi* as the non-predator, and a bag only as a control. Each treatment had n = 6 groups of fish.

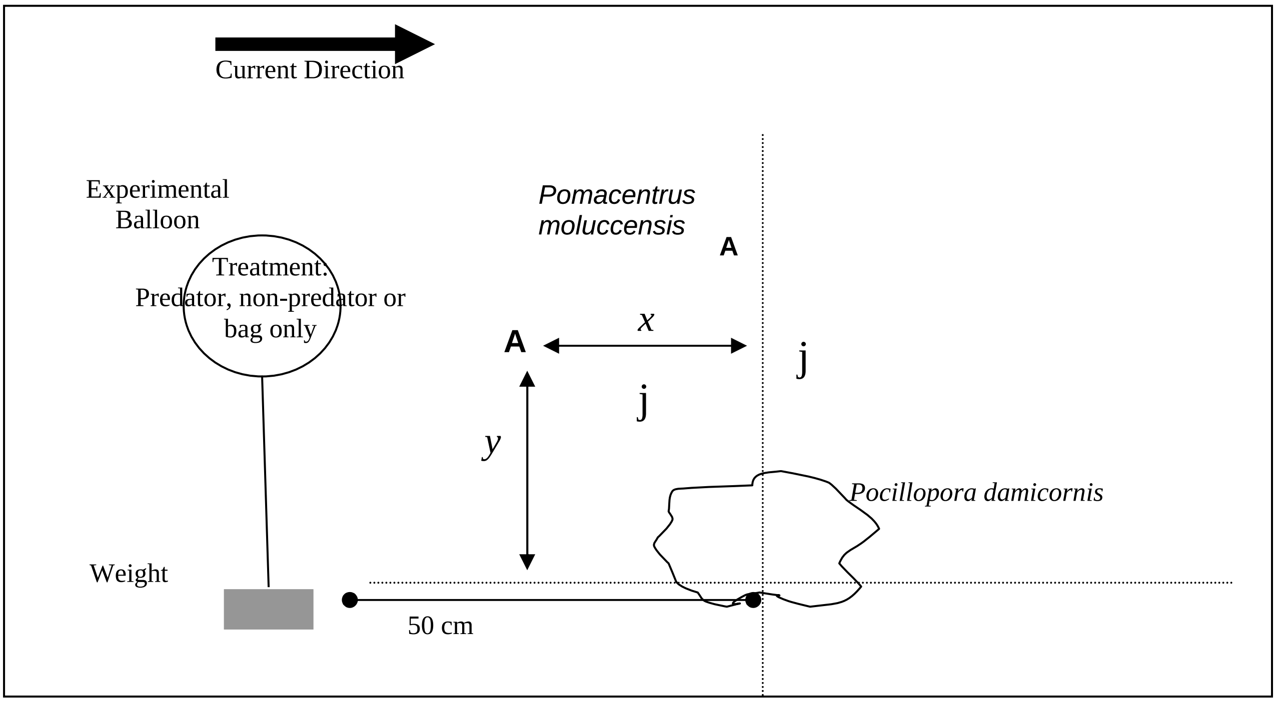

Figure 4.3 Diagrammatic representation of one frame of a video sample showing the position of the balloon with respect to the coral colony and prey species. A = Adult, j = juvenile, *x* and *y* are Cartesian coordinates used to measure distance from the coral refuge.

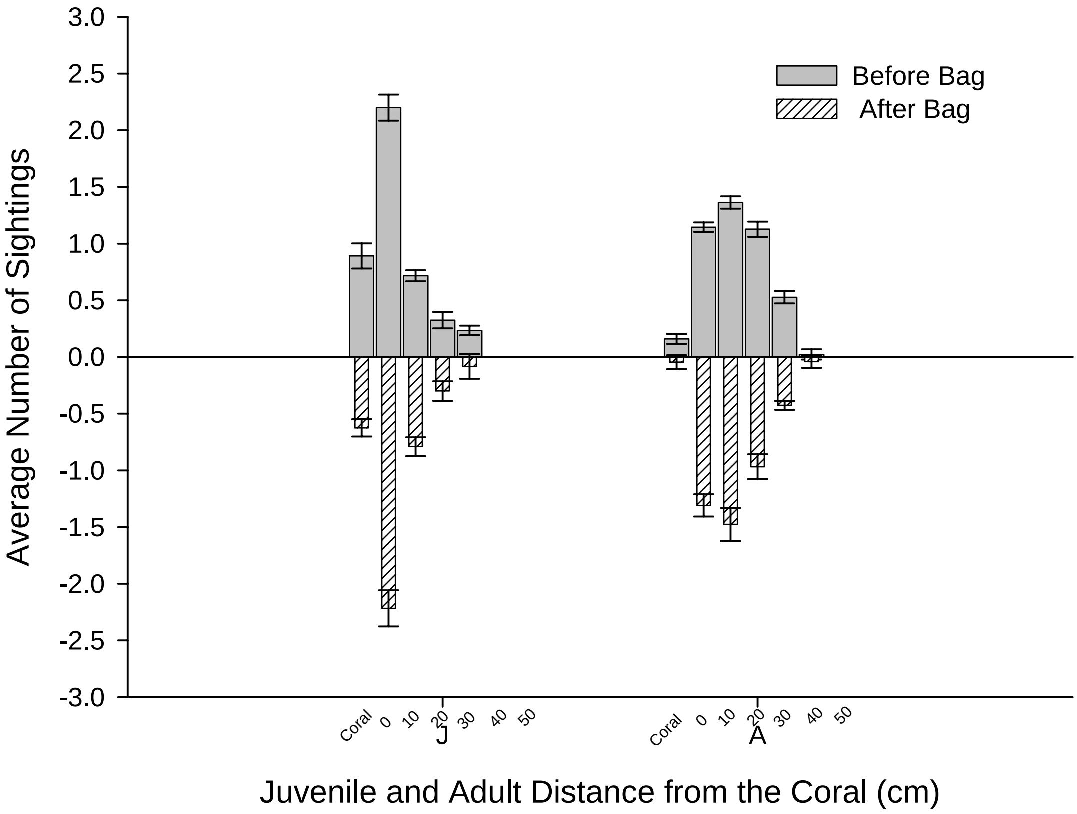

Figure 4.4 Mean number of instances where individuals where sighted at different distances from their refuge. Bars indicate one SE.

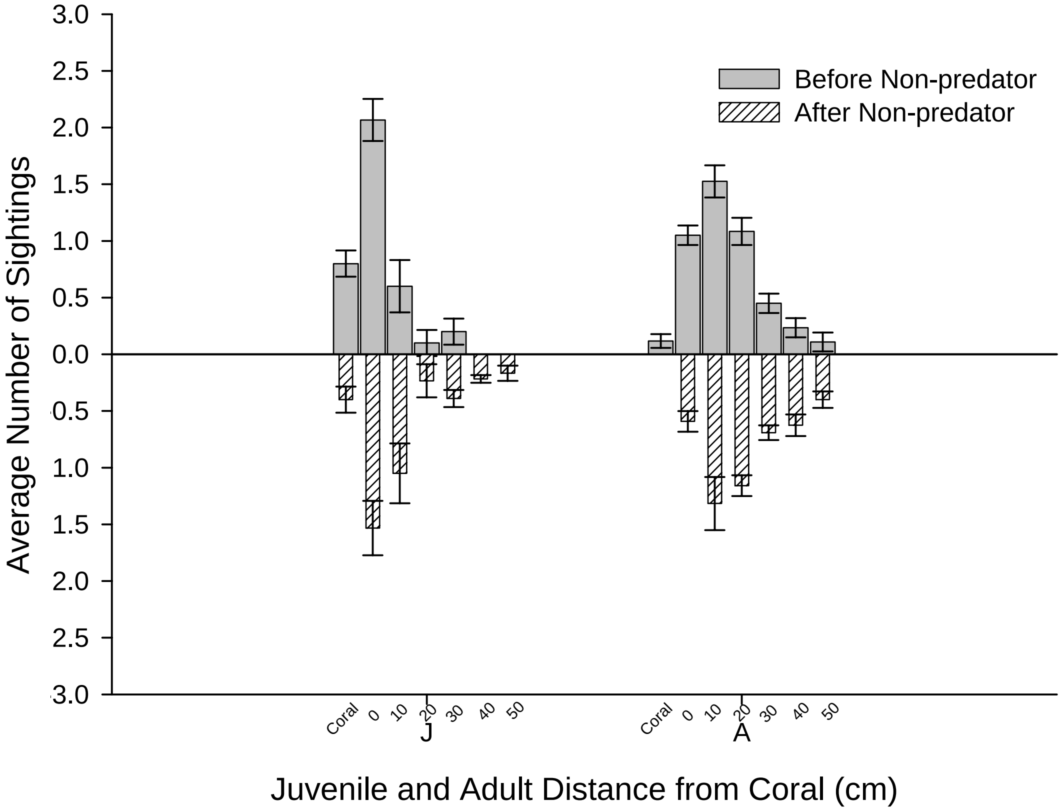

Figure 4.5 Mean number of instances where individuals where sighted at different distances from their refuge in the presence of *Chaetodon rainfordi*. Bars indicate one SE.

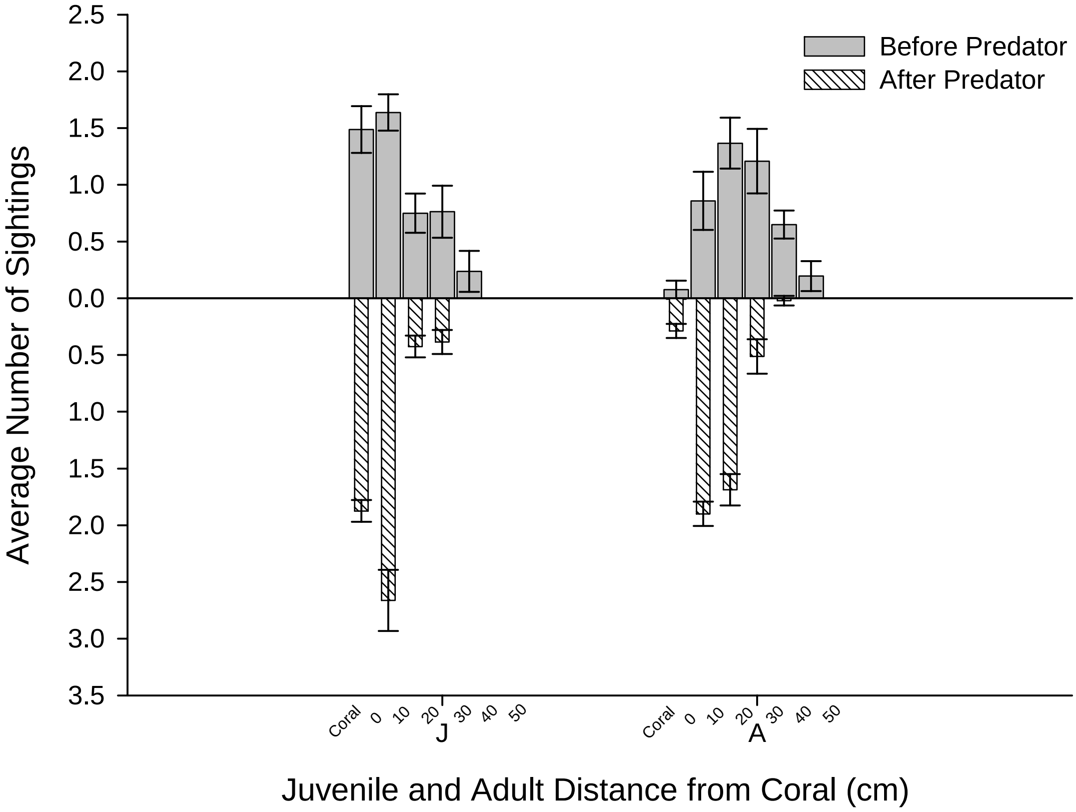

Figure 4. 6 Mean number of instances where individuals where sighted at different distances from their refuge in the presence of *Epibulus insidiator*. Bars indicate one SE.

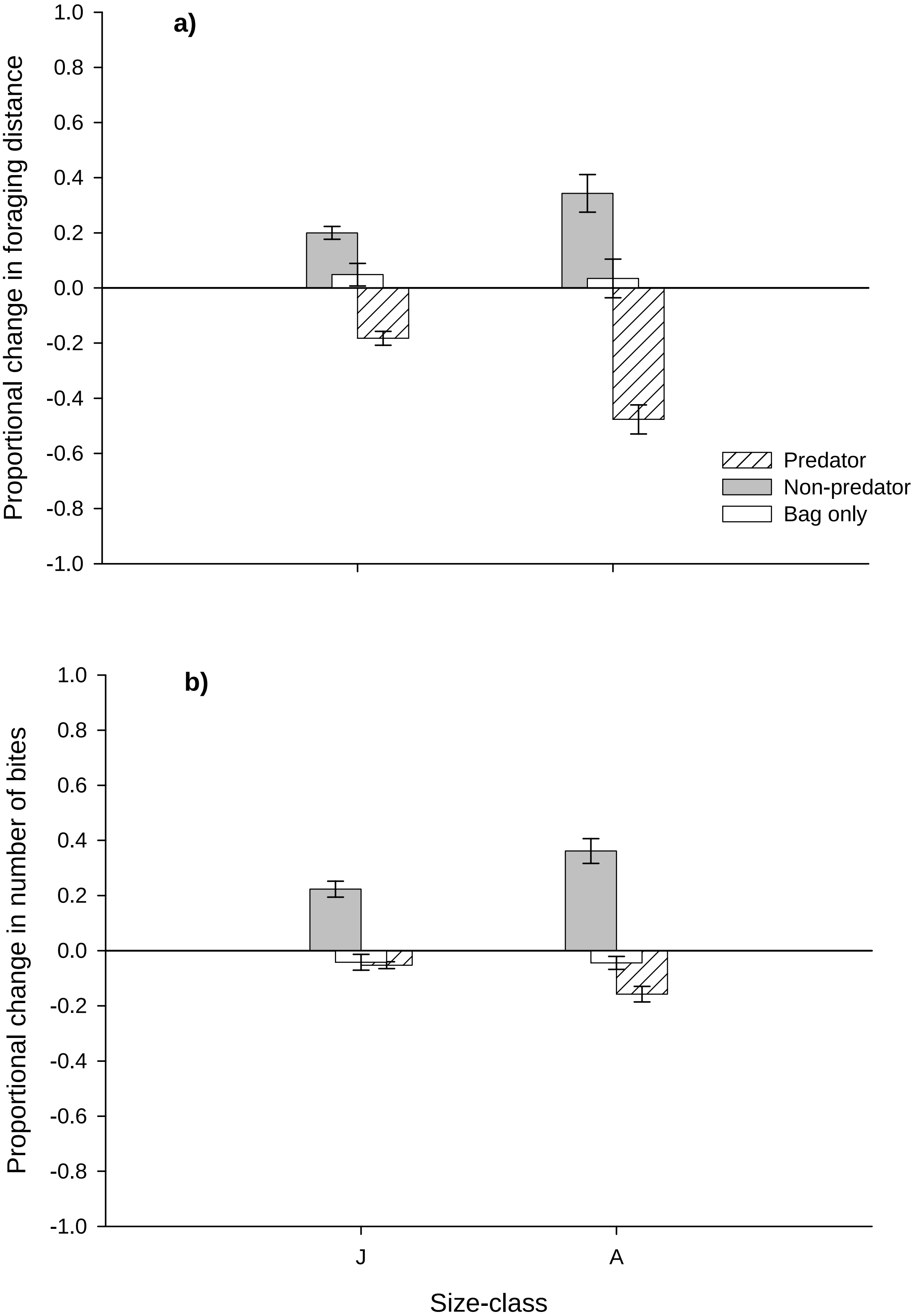

Figure 4.7 Proportional changes in a) foraging distance of, and b) number of bites taken in 10 seconds by juveniles and adults in response to the treatment and treatment controls. Change was calculated as the difference between the distance or bite-rate after and the distance or bite-rate before exposure to the treatment divided by the "before". Bars indicate one SE.

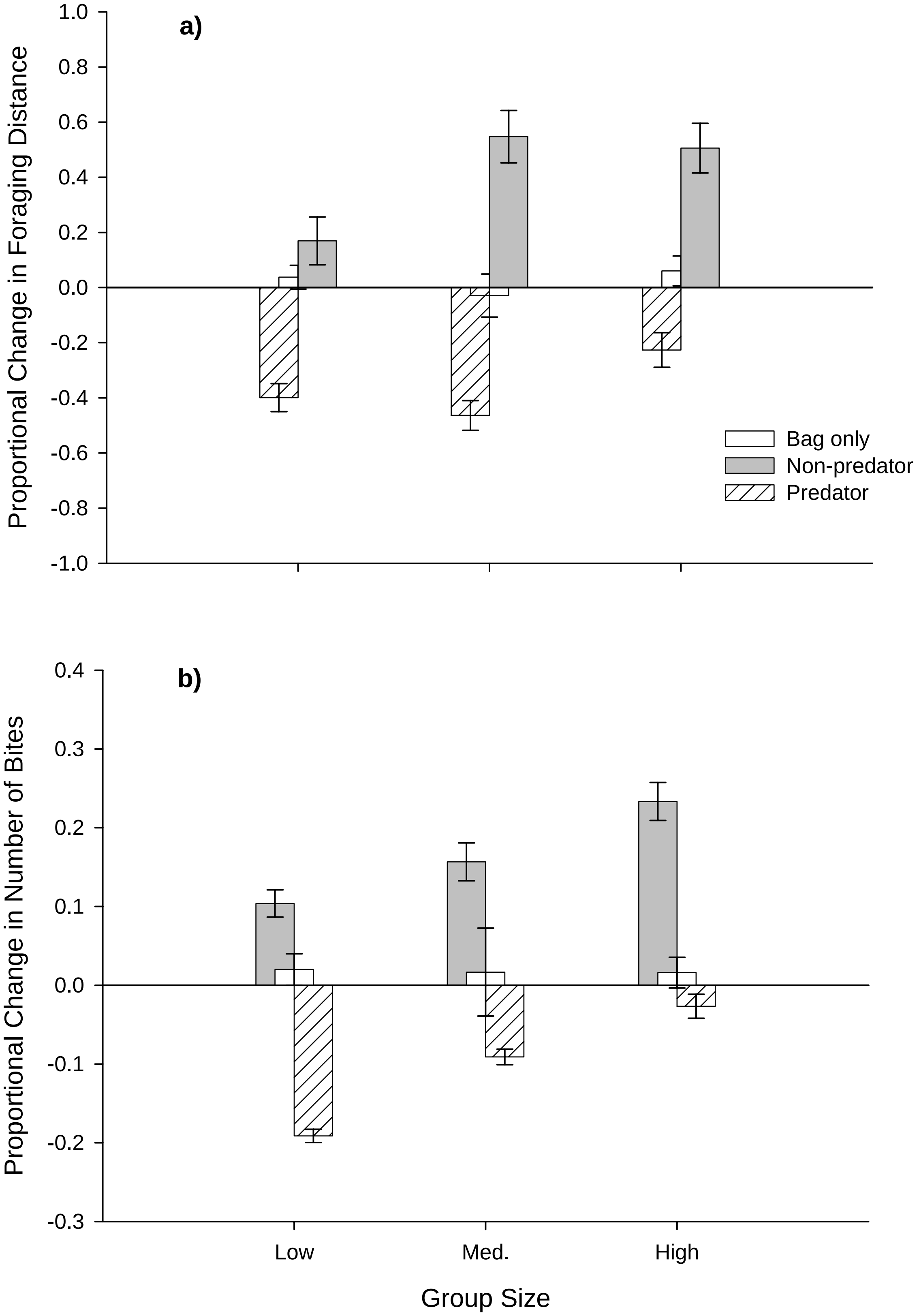

Figure 4.8 Proportional changes in a) foraging distance, and b) number of bites taken in 10 seconds across group size, in response to the treatment and treatment controls. Change was calculated as the difference between the distance or bite-rate after and the distance or bite-rate before exposure to the treatment or treatment controls divided by the "before". Bars indicate one SE.

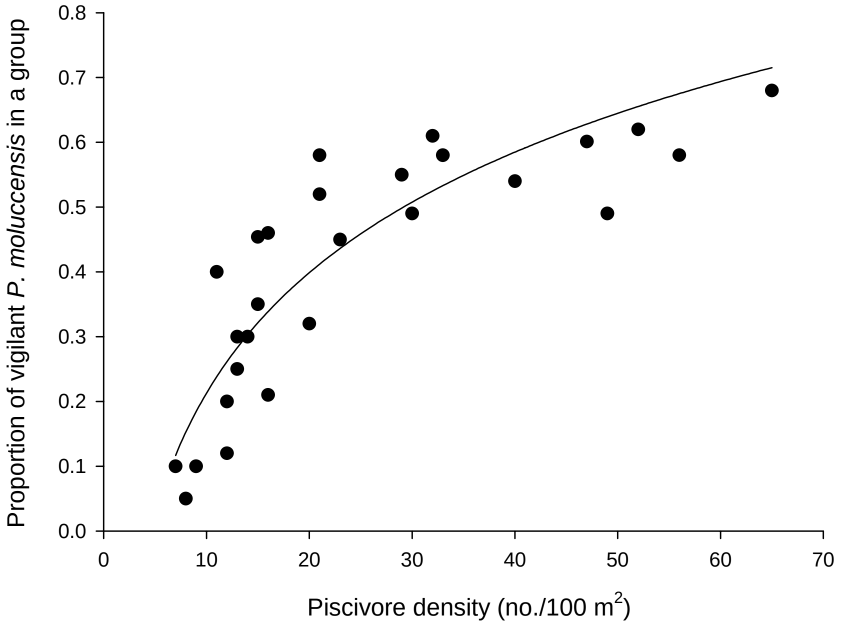

Figure 4.9 Regression plot of group vigilance (the proportion of individuals displaying vigilant behaviour) versus piscivore density measured as the number of piscivores per 100 m^2. The data were fit to a logarithmic model, $y = y_0 + a[\ln(x)]$, ($r^2 = 0.754$, $y_0 = -0.376$, $a = 0.257$, d.f. 25, $p = <0.01$).

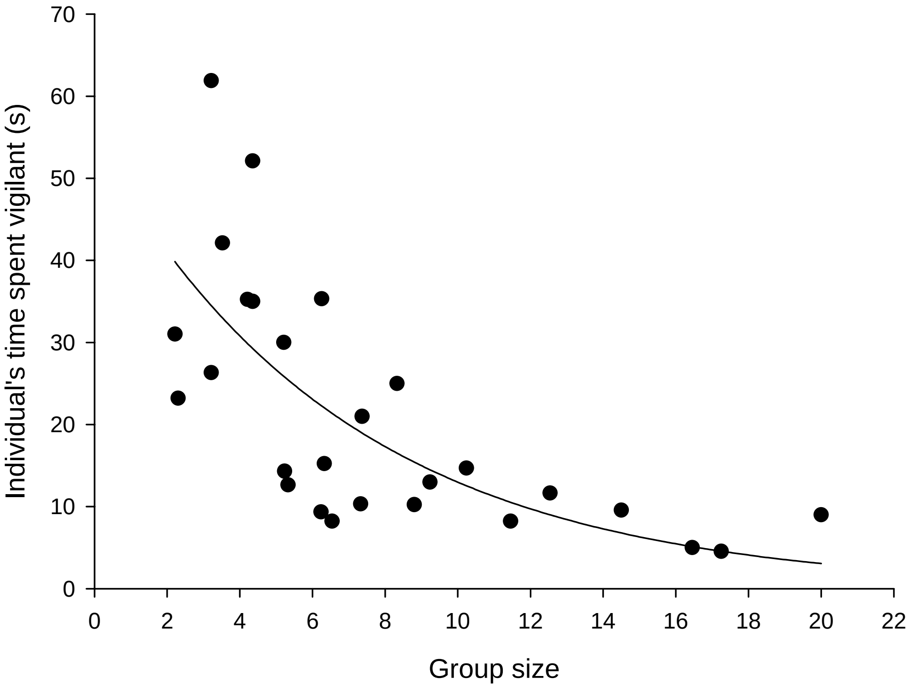

Figure 4.10 Regression plot of per capita vigilance (the time spent by one individual on vigilant behaviour in a three minute observational sample) versus group size measure as the number of conspecifics that associate with a discrete coral head. The data were fit to an exponential decay model, $y = ae^{-bx}$ ($r^2 = 0.47$, $a = 54.80$, $b = 0.144$, d.f. = 25, $p < 0.01$).

Table 4.1 Kolmogorov-Smirnov tests comparing foraging distances of prey individuals before and after treatments.

Test Comparison Before versus After	Bag only		Predator		Non-predator	
	D	p	D	p	D	p
All individuals	0.1008	0.56	0.1964	0.02*	0.1905	0.181
Adults	0.1039	0.778	0.2024	0.035*	0.1905	0.022*
Juveniles	0.0952	0.987	0.2500	0.038*	0.3333	0.154

*D value significant at p<0.05

Table 4.2 Repeated Measures ANOVA of the foraging responses

	Δ Distance			**Δ Bites**		
Source of variation	**df**	**MS**	**F**	**df**	**MS**	**F**
Between Subjects						
Exposure Treatment	2	1772.41	856.90*	2	62.94	1863.05*
Group Size	2	90.31	60.35*	2	16.54	335.64*
Exp. Treatment x G. Size	4	65.86	44.02*	4	6.650	134.97*
Residual	45	2.068		45	0.034	
Within Subjects						
Ontogeny	1	63.87	27.02*	1	0.812	25.44*
Exp. Treatment x Ontogeny	2	551.02	233.14*	2	0.792	24.83*
G. Size x Ontogeny	2	0.068	0.29	2	0.043	1.359
Exp. Treatment x G. Size x Ontogeny	4	1.108	0.55	4	0.030	0.943
Residual	45	2.364		45	0.0319	

*F value significant at p<0.05

Chapter 5

The potential effects of predation risk and group size on fitness of a common prey fish on coral reefs

5.0 Abstract

In this chapter I investigate some potential non-fatal interactions and explore how intraspecifc density may influence them. Using experimental manipulations of group sizes of *Pomacentrus moluccensis*, a tropical reef damselfish, and a system of artificial coral reefs and cages at Lizard Island on the Great Barrier Reef (GBR), I tested the prediction that predation risk will reduce foraging and growth in this species while grouping will dilute this risk and ameliorate some of these negative effects. Results indicate that the risk of predation affects the behaviour and reduces the growth rate of the prey and that these effects were most pronounced in small prey group sizes. Observational data collected from natural reefs in the immediate vicinity (Chapter 4) suggest that a reduction in per capita vigilance with increase in group size may explain the diminished individual costs of predation risk recorded in large groups. I present a conceptual foraging model that predicts predators will significantly reduce the growth of a prey individual at low prey group size, but will have a smaller effect at higher prey group sizes due to a reduction in per capita vigilance and corresponding increase in time available for foraging. This suggests that social groups in coral reef fish systems may have evolved, in part, to optimise the trade-offs between survival and growth. Suppression of growth due to predation risk may affect population dynamics of adult coral reef fish by regulating the rate of individuals reaching reproductive maturity and/or by increasing the probability of size-selective mortality on juveniles.

5.1 Introduction

Most marine species have a bipartite life history in which larvae are planktonic and juveniles settle to the benthos. Patterns established at settlement are modified by post-settlement, benthic processes such as competition and predation, particularly when settlement rates are high (Gaines and Roughgarden 1985; Jones 1991; Caley *et al.* 1996; Menge 2000; Webster 2002; Almany In press). Recently, lethal effects of predation have received considerable attention in marine systems, with coral reef fish frequently used as a model system (Norris and Parrish 1988; Hixon 1991; Caley 1993; Hixon and Carr 1997; Webster 2002). These studies show that the effects of predators on post-recruitment mortality of coral reef fish are often large enough to modify the size and structure of prey populations (Hixon and Carr 1997; Hixon and Webster 2002; Webster 2002; Webster and Almany 2002).

In contrast to studies of lethal effects of predation on coral reef fish, nonlethal effects of predator-prey interactions have received little attention in coral reef fish, although recognition of its potential importance is growing (see Steele 1998; Steele and Forrester 2002; Jones and McCormick 2002). Evidence from other systems suggests that such effects are widespread and important. The risk of predation may cause individuals in prey populations to reduce their foraging and growth (Werner *et al.* 1983; Taylor 1984). Such modifications in foraging behaviour may be significant and can affect prey fecundity and population size and structure in terrestrial systems (reviewed by Lima and Dill 1990). These behavioural modifications may, in turn, indirectly affect a third individual or species such as a competitor to the prey (Polis and Winemiller 1996; Schmitz 1998). Direct and indirect behaviour-mediated effects (trait-mediated indirect effects) play a significant role in food webs in many communities (Roughgarden and Diamond 1986; Schoener 1993; Peacor and Werner 2000; Jones and McCormick 2002; Peacor 2002) and have recently been observed in coral reefs (Webster and Almany 2002).

In social animals, behavioural modifications that improve fitness under predation risk can be achieved by altering locomotory activity, group size, level of vigilance, or social hierarchy (Godin and Smith 1988; Lima 1988). In planktivorous, site-attached coral reef fish, individuals under threat may reduce their total foraging space by limiting excursions and reducing feeding distance away from shelter, and they may also reduce their bite rates (Chapter 4). Therefore, the foraging effort (rate and distance from refuge) displayed is likely to be determined by an evolutionary trade-off between increased access to resources and the increased risk of mortality through predation. This trade-off can be modified further by the interaction of other processes. For example, as school size increases, individuals can spend less time being vigilant for predators and more time feeding (Pulliam 1973) because grouping enhances the probability of detecting and avoiding predators where initial detection is broadcasted to the rest of the group (Hamilton 1971; Neil and Cullen 1974; Taylor 1984). Groups can also dilute an individual's chance of being captured by a predator (Bertram 1978) providing predators don't aggregate in response to higher prey density (Connell 2000).

However, intraspecific density (Dill and Fraser 1997; Sih 1992, 1997) and access to shared food (Kerrigan 1994) will modify growth rates of individuals. Intraspecific competition is well-recognised as a growth inhibitor in reef fish (Jones 1987; Jones and McCormick 2002). Due to its patchiness and scarcity on coral reefs (Noda *et al.* 1992), food has been suggested as a limiting resource in planktivorous fish populations and one that is central to behavioural / competitive interactions at densities well below carrying capacity (Jones 1986). Individuals will compete for food over a range of food levels and group sizes, although the intensity of the interactions is contingent on seasonal recruitment (Jones 1986). Therefore, the persistence of social groups suggests that the advantages of shoaling may outweigh the disadvantages. Group size may be a function of available habitat and level of predation risk.

Fish communities and populations on coral reefs are likely to be significantly influenced by non-lethal species interactions (Jones and McCormick 2002). These interactions and resulting behavioural modifications are likely to be intense, as abundances and species diversity on reefs are characteristically high. As many reef fish prey display strong and consistent habitat preferences and occupation (Light and Jones 1997; Ohman *et al.* 1998; Munday 2001) within reef habitat units, this leads to localised aggregations of predators and a consistent but variable source of risk (Hixon 1998; Stewart 1998; Marnane 2000). Furthermore, highly variable biophysical environments characterise coral reefs and require equally high behavioural and phenotypic plasticity of member species and individuals (Stearns 1989; Warner 1997). Generally, fecundity in reef fish is a function of body condition and size, both of which may be influenced by behavioural interactions with conspecifics and predators (Jones 1987). Consequently, predation risk, intraspecific competition, and food limitation are likely to have strong impacts on adult numbers and population structure if their effects on growth and reproduction of individuals is large (Jones 1991; Gerking 1994).

Although coral reefs are ideal models for the study of marine and demersal fishes (Sale 1991; Hixon 1998; Hixon and Webster 2002), there is a paucity of studies examining processes affecting the energetics of coral reef fish populations (Jones and McCormick 2002). Few examples exist of direct behaviour-mediated responses and the associated fitness costs due to predators on coral reefs (Connell 1998; Steele and Forrester 2002). Social groups are a common feature in these systems (Coates 1980; Forrester 1990) but the extent to which these increase competition and dilute predation risk remains unclear. The aim of this study is to test for the operation of direct, non-lethal interactions on demographic rates (survival and growth) that have the potential to affect the fitness and population dynamics of coral reef fish, using a pomacentrid that is a planktivorous and relatively ubiquitous prey item on the Great Barrier Reef. I examine the importance of predation risk relative to the effect of group size of conspecifics. Specifically I ask the questions, does predation risk significantly affect growth of coral reef fish prey; and does grouping behaviour influence the effects of risk? I expect that predation risk will cause a reduction in prey fish growth as they forage less and become more vigilant (Chapter 3 and 4) and although growth will be reduced with an increase in group size (presumably due to intraspecific competition), survivorship will increase due to predator dilution.

5.2 Methods

5.2.1 Study species

The prey fish studied here was the Lemon Damselfish, *Pomacentrus moluccensis*, one of the most abundant species of the family Pomacentridae (Mapstone 1988). *P. moluccensis* range from the Andaman Sea to Fiji and from Papua New Guinea to the Southern Great Barrier Reef. The species occurs across a depth range of 1- 20+m and are mainly planktivores. Spawning is seasonal in GBR populations, beginning in October and continuing until January (Mapstone 1988). Individuals have a planktonic larval phase averaging 24 days duration and first appear on the reef at approximately 8-10 mm total length (Bray 2001). Individuals associate closely with live coral (Eckert 1984) especially *Pocilipora damicornis* (Jones 1991). For the purpose of this study, damselfish <25mm SL were considered juveniles (sensu Mapstone 1988; Jones 1991) and those ≥ 25mm SL adults.

5.2.2 Field Experiment: The effect of predation risk and competition on growth

If predation risk significantly affects foraging behaviour of prey (see Chapter 3 and 4), then it might be expected that this reduction of foraging would reduce the somatic growth rate of prey. The risk of predation may be less at high prey densities than at low prey densities, due to dilution and schooling effects. Therefore the indirect effects of predation on prey growth may be less at high prey densities than at low prey densities. I used a transplant experiment (sensu Jones 1986) to test this prediction. Experimental units consisted of small, caged and exposed artificial patch reefs (0.75

m^2) built in a sandy area in the lagoon of Lizard Island that was bordered by continuous reef (Figure 5.1). Approximately 0.75 m^3 of dead coral branches and fragments was collected to form each rubble reef. Artificial reefs were constructed by placing a 0.125 m^3 living colony of *Pocillipora damicornis* at the apex of each rubble reef. Building standard-size reefs from live and dead coral helped control for factors such as habitat size and prior residence (Webster 2002). Reefs were built 20 m apart from the surrounding reef and from each other as studies using similar distances between reefs have shown that this effectively eliminated immigration to and emigration from patch reefs (Jones 1987; Webster 2002). Three rows of 12 reefs were constructed parallel to the natural reef where average depth was 6-8 m. The reefs within each row were arranged in 4 clusters of three reefs each representing the two predation risk treatments (high risk, low risk) and control treatment (Figure 5.1).

A 3 x 3 factorial design was used for the experiment to examine the effects of group size and predation risk on prey foraging behaviour and growth, with two predator treatments (predator-exposed and unexposed) and a cage control treatment being crossed with three prey fish densities. Treatments were assigned randomly to patch reefs but with no identical treatments being in the same cluster or adjacent to the same treatment in the next block. Twelve reefs were protected from predators using 1 m^3 cages. Cages consisted of anchored frames made of 16-mm diameter PVC piping and 15mm-mesh plastic netting on the sides and the top. This mesh size excluded predators larger than ~60mm TL, but observations suggested that it did not restrict the foraging of the damselfish. Twelve cage control reefs were the same as caged reefs except that the tops of the cages were removed (fenced reefs). A further twelve reefs were free of any cage or fence structures. Any differences between the treatments could be attributed to the effects of predators and not cage artifacts if survival and growth of fish in partial cages and those in exposed colonies without cages were statistically similar. The cages were initially monitored for two weeks to assess their susceptibility to wind / wave action and algal bio-fouling. The physical protection of the surrounding reef and the heavy weight of the cement anchors stabilised the cages while feeding of herbivorous surgeonfish kept algal growth to a minimum.

Newly recruited *P. moluccensis* (age 0+) were collected using clove oil (see Munday and Wilson 1997) and transparent plastic bags, and their total and standard lengths were measured. As young and small individuals face the highest risk of predation (Doherty and Sale 1985; Sogard 1997) and rate of growth is highest in early life history, I chose to use newly settled recruits/juveniles in this experiment, ranging in size from 12 to 15mm, to maximise responses to treatments. Size of these individuals was standardised (differences between individuals within and between groups were not significant). Individuals were subcutaneously tagged with visible implant fluorescent elastomer (VIE) in order to identify experimental animals. Microtag retention is 100% for juvenile reef fish and tagging does not affect survivorship or growth of *Pomacentrus moluccensis* (Beukers *et al.* 1995; Frederick 1997). Different coloured elastomer was used to represent the different prey densities and to enable any movement between the treatment reefs to be identified. In order to maximise the growth response further, I chose the warmest month of the year, January, where metabolic rates of fish are at their highest.

Using these fish, the artificial reefs were then stocked with a range of densities: 2, 5, and 8 individuals. This range of group sizes was chosen to represent natural densities observed on similar sized *Pocillopora* colonies (mean = 5.84 individuals per reef, S.E. = 3.45) and avoid extreme agonistic behaviour and emigration caused by highly dense groups (Huntingford and Turner 1987). This species is amenable to this type of transplant experiment because juveniles readily resumed normal foraging activities and were not observed to leave the experimental reefs to which they were transplanted. The three damselfish-density treatments were crossed with three predator treatments: caged, cage-control, and exposed. After 32 days from the start of the experiment, fish present on reefs were collected using clove oil, handnets, and plastic bags and taken back to the laboratory where total and standard lengths were measured. Experimental fish were readily identified and distinguished from recruits by their subcutaneous tag. Species abundance and diversity of other fish resident on the reefs were recorded and sizes of individuals estimated.

Visual surveys (forty 50 x 5-meter belt transect) were done on the surrounding reefs to estimate abundance and diversity of potential predators of *P. moluccensis*. The most common predators of *P. moluccensis* at Lizard Island are rockcods, including *Cephalopholis cyanostigma, C. boenak, Epinephelus coiodes*, the coral trout, *Plectropomus leopardus*, lizardfish such as *Synodus dermatogenys*, and the sling jaw wrasse, *Epibulus insidiator*.

5.3 Results

5.3.1 Local predators

Survey of predators in the area surrounding the artificial reefs and cages indicated that the majority of piscivores belonged to four families: Seranidae, Labridae, Lethrinidae, and Synodontidae (Table 5.1). The majority of predators were sit-and- wait, ambush hunters with *Plectropomus leopardus* and *Epibulus insidiator* as clear exceptions.

5.3.2 Survivorship of P. moluccensis

Total mortality for all tagged *P. moluccensis* was approximately 28%. Total emigration from these experimental reefs was assumed to be less than 1% as only two tagged individuals were recovered after an exhaustive search of nearby reefs and no tagged individuals were observed on the reefs of the wrong treatment. Survivorship was lowest in the exposed treatment and cage- control at 0.61 and 0.71 respectively, in contrast to the higher survivorship of 0.83 in caged treatments (Figure 5.2). Survivorship was lowest in groups made up of 2 individuals and increased with increasing group size (Figure 5.2).

As power transformations do not work well when data are percentages or proportions (Emerson 1991), the arcsin transformation was attempted to adjust for heteroscedasticity in the survivorship data (Quinn and Keough 2002). Nonetheless, heterogeneity of variances in survivorship prevented the use of a two way ANOVA. However, graphical inspection of the data suggests that survivorship decreased with exposure to predators. It also suggests an interaction between predator exposure and group size: survivorship appears to increase strongly with group size in predator exposure treatments (no cage and cage-control), while there is little apparent change in survivorship with group size in predator exclusion (caged reefs) treatments. These conclusions are supported by multiple nonparametric tests (Mann-Whitney). Survivorship on caged reefs differed significantly from survivorship on exposed and cage-control reefs (U=16.5, Z = -3.275, p=0.001 and U=18.5, Z=-3.163, p=0.001). Moreover, survivorship increased with group size (between group size 5 and 8) for the no-cage and cage-control treatments (U=0.2, Z=-2.428, p=0.029 and U=12.3, Z=-2.912, p=0.015) but not the caged treatments (U=6, Z=-0.624, p=0.686).

5.3.3 Growth of P. moluccensis

It is possible for survivorship to confound the growth response (Peacor and Werner 2000). Results of a regression showed that there was a weak interaction ($r^2 = 0.144$) between the two variables. To account for this potential confounding, two alternative statistical approaches were used. Firstly, an ANCOVA was used to examine differences in mean growth among treatments, with survivorship as a covariate (Table 5.2). Survivorship did not appear to have a large effect on growth (MS=1.519, $F_{1,34}$=1.267, p=0.272) but predation risk (MS=17.074, $F_{2,34}$=14.239, p<0.01) and group size (MS=31.136, $F_{2,34}$=25.966, p<0.01) did. Secondly, I removed any effect of survivorship on growth by analysing the residuals from a regression of growth on survivorship, rather than the raw growth data. This is tantamount to removing any effect of survivorship on growth, then testing for an effect of predation risk or group size on the remaining variation in growth. These growth residuals were then examined using a two-way ANOVA (see Table 5.3). Results were concordant with the first analysis: growth was significantly different between the levels of the predation risk treatment ($F_{2,34}$=29.585 , p= 0.01) and between the levels of group size ($F_{2,34}$= 25.243, p<0.001). Tukey's HSD detected a significant difference between low and high predation risk treatments (HSD=3.119, p=0.004) and low predation risk and the cage control (HSD=3.1828, p=0.022). No difference (p=0.763) was detected between the exposed and fenced reefs indicating that fenced reefs controlled for caging artefacts. The effect of group size on growth was significant ($F_{2,34}$= 25.243, p < 0.001). Differences in growth between group size-2 and group size-5 were significant (HSD=2.596, p<0.001) but differences between group size-5 and group size-8 were not (HSD=1.0296, p = 0.074). Overall, growth of individuals decreased with increasing group size (Figure 5.3). Predation risk had a stronger effect (SS = 71.1) on growth than group size (SS = 60.67).

Individuals that were protected from predators grew 21-31% more than those that were exposed to predators. The results suggested a weak, though not statistically significant, interaction between predation risk and group size at the $\alpha = 0.05$ level (ANCOVA, $F_{4,34}$ = 2.657 p = 0.058; ANOVA of residuals, $F_{4,34}$ = 2.567, p= 0.063). Graphical inspection of results suggests that growth decreases with group size more strongly in the absence of predators (Figure 5.3). Although not significant at the 5% level, the near significance of the result, coupled with the close concordance between the exposed and cage-control trends (Figure 5.3) suggest that the interaction is real.

5.4 Discussion

The threat of predation can modify prey behaviour and may affect growth and fecundity (Lima and Dill 1990; Jones 1991; Jones and McCormick 2002). Its impact relative to other trophic interactions, such as competition, has not been examined in phenotypically plastic marine organisms. Both competitive and predator-prey interactions are regulated by behavioural modifications which may have flow-on consequences on the energetics of marine organisms (Jones and McCormick 2002). These sublethal effects of predators on prey growth have recently been documented in marine fishes (Connell 1998; Steele 1998; Nakaoka 2000; Steele and Forrester 2002). In addition to providing further evidence for these non-lethal effects, this study clearly demonstrates a trade-off between survival and decreased growth associated with group membership that may be motivated by “safety in numbers”. It also suggests that the growth costs associated with group membership are mediated by non-lethal responses to predation risk that vary with group size. These responses are more pronounced in low group sizes than higher group sizes.

5.4.1 Predation risk on Lizard Island reefs

Predators of coral reef fish are mainly benthic or hovering/transient piscivores and it has been argued that the combined effect between these two functional forms is necessary to induce significant and detectable population regulation of their prey (Hixon and Carr 1997). This predatory synergy can be expected on Lizard Island reefs as the observed piscivores include both functional forms and the most abundant of these piscivores are main predators of *P. moluccensis* (Stewart 1998; St. John

1999; St. John 2001). Predator abundance, rank, and diversity were comparable to similar studies that extensively investigated biodiversity of Lizard Island piscivores (Stewart 1998; Stewart and Beukers 2000; Webster 2002). Some of the most abundant benthic predators surveyed around the artificial reefs and on surrounding reefs included *Cephalopholis cyanostigma*, *Cephalopholis boenak*, and *Synodus dermatogenys* (Table 5.1). These predators were frequently sighted between and amongst the artificial reefs and cages, and may have used the physical structure of these reefs as shelter and foraging space. Some of the main hovering / transient predators in the study area include *Plectropomus leopardus*, *Epibulus insidiator*, and *Lethrinus ornatus*. These species were observed swimming over and from continuous, natural reefs to the experimental patch reefs to examine them for potential prey.

5.4.2 Mortality on artificial reefs

Predators did affect survivorship of individuals on these experimental reefs. As in many social animals (Clutton-brock *et al.* 1999), large group size in *P. moluccensis* was associated with reduced mortality. In all treatments survivorship increased with an increase in experimental group size. The design of the cages provided protection from both the benthic and transient, water-column piscivores and fish in low-risk treatments exhibited highest survivorship. Agonistic behaviour may be more pronounced in low-risk situations (Wright and Huntingford 1993) and fatal competitive behaviour may, in principle, explain some of the mortality observed in this study. However, the available evidence on reef fish suggests that agonistic behaviour of reef fish increases with group size and population density but that competition-induced mortality does not (Steele 1995). In addition, naturally occurring groups of *P. moluccensis* exceed experimental group sizes and can reach up to 12-20 members. Therefore it seems unlikely that my experimental groups reached a lethal level of competition. Mortality of individuals on these exposed reefs was comparable to similar studies on post-settlement mortality of damselfish (Doherty and Sale 1985; Beukers and Jones 1997; Hoey 1999). However, it is important to note that there was a sharper increase in survivorship with group size in exposed as compared to caged reefs. These results suggest that fish in higher-risk circumstances (poor refuge or high abundance of ambient predators) would benefit more from increased aggregation than those under low predation risk. The disappearance of fish from caged reefs was eiter due to a) undetected migration, b) non-predator mortality due to disease or parasites, or c) mortality from predators not excluded by the cages.

5.4.3 Predation risk and growth

Excluding predators from artificial reefs in the Lizard Island lagoon led to an increase in growth of tagged *P. moluccensis* juveniles. As growth of individuals on fenced reefs mimicked that of predator-exposed treatments, the cages did not increase food availability and the increase in growth was probably due to individuals spending more time foraging in predator-exclusion than in predator-exposed treatments. Many aquatic vertebrates spend more time foraging in safe, as compared to risky, habitats (Sih 1997) and prey fish conspicuously reduce their foraging in the presence of piscivores (Wootton 1990). In groups of yellow damselfish, individuals reduce foraging effort in the presence of a threat by reducing their search distance away from the coral and the number of bites taken (chapter 4). Near lethal damage, i.e. injury sustained through predatory attacks, can also reduce growth and in sexually mature individuals interrupt reproductive processes (Peterson and Quammen 1982).

Individuals used in this study were recently-recruited juveniles (12-15mm length). Animals are at most risk when they are young and small (Sogard 1997). In reef fishes early juvenile mortality is high (Doherty and Sale 1985) and slower growing individuals are more susceptible to higher size-specific mortality (Doherty and Williams 1988; Mapstone and Fowler 1988). If sublethal responses to predators are proportional to predation risk, it is likely that reduced growth resulting from predation risk will become less pronounced as individuals grow larger and are more likely to increase their foraging (Steele and Forrester 2002). How the risk of predation with its associated foraging and growth costs change with ontogeny of coral reef fish remains uncertain.

5.4.4 Group size and growth

Similar to juveniles of *Pomacentrus amboinensis* (Jones 1986) but contrary to Connell's (1998) results with *Acanthochromis polyacanthus* juveniles, growth of *P. moluccensis* individuals on artificial reefs was density-dependent, possibly reflecting an effect of competitive interactions. Growth in many animals has been linked to intra- and interspecific density (Dill and Fraser 1997; Sih 1992, 1997) and shared food availability (Kerrigan 1994). Intraspecific competition is well-recognised as a growth inhibitor in reef fish (Jones 1987; Jones and McCormick 2002). Competition within groups could be exploitative or interference-based (Jones 1991). In damselfish, competition is mainly exploitative where individuals race to capture planktivorous food items (pers observation; Coates 1980; Kerrigan 1994*).* Due to its patchiness and scarcity, food has been suggested as a limiting resource in planktivorous fish populations and one that is central to behavioural / competitive interactions at densities well below carrying capacity (Jones 1986). Individuals will compete for food over a range of food levels and group sizes, although the intensity of the interactions is contingent on seasonal recruitment (Jones 1986). Furthermore, social hierarchy is a key element in intraspecific competition in damselfish (Coates 1980; Forrester 1990, 1991) where negative effects of competition may be greater on smaller compared to larger fish (Steele and Forrester 2002). As size of recently recruited individuals used in this experiment was standardised across groups, social dominance would have been unlikely to be responsible for the differences in observed growth among treatments.

5.4.5 Optimising the trade-offs between survival and reduced growth

Optimal foraging theory predicts that animals will maximise net energy gain and so maximise lifetime reproductive success (MacArthur and Pianka 1966; Emlen 1966). The optimal foraging strategy of an individual will change with changes in intrinsic (physiological) and extrinsic (environmental) factors (Gerking 1994). It follows then that throughout their lives, reef fish will modify their behaviour in response to changes in their marine environment. Both vigilance and group size are important considerations in an individual's foraging strategy as they may determine the quantity and quality of food that a member receives, as well as its risk of being consumed by a predator.

Figure 5.6 presents a conceptual model of growth and survivorship in social, coral-associated planktivores that is based on experimental data from this study and observational data from previous chapters. Prey usually trade-off the benefit of increased survival (Figure 5.2) with decreased growth (Figure 5.3) presumably due to increased competition, with an increase in group size. Nonlethal effects of predation (the difference between “P+” and “P-” growth curves) may modify this trade-off. When exposed to predation risk (P+) extra vigilance is necessary, as the probability of individual mortality is higher. As vigilance interrupts feeding (Chapter 3) and individuals are more likely to be vigilant in high compared with low risk situations (Chapter 4), these prey (P+) will experience more reduced growth than those free of risk (P-). Per capita vigilance will decrease with an increase in group size (Chapter 4), and this may partially compensate the reduction in growth caused by intraspecific competition. The result is that individuals relatively free of predators (P-) will experience a sharper reduction in growth with group size as compared with those in high-risk situations (P+). Thus, the group size at which the optimal balance between growth and survival occurs is likely to be at a larger group size with the behavioural modifications than without them.

Different prey fish group sizes and vigilance behaviour (Chapter 4) will be optimal under different densities of coral reef piscivores. The most likely strategy for site-attached prey such as reef damselfish is that larvae preferentially settle to favourite microhabitats and group aggregation and size is a function of local predation risk and post-settlement movement. Many animals have been observed to shift to safer habitat that may be nutritionally sub-optimal (Werner *et al.* 1983; Munday and Jones 1998; Dahlgren and Eggleston 2000; Munday 2001) and reef fish have been observed to move post-settlement (McCormick and Makey 1997). However, conspicuous and less mobile prey such as *P. moluccensis* may prefer to increase shoaling by joining / recruiting to social groups rather than risk individual travel in search of safer coral habitat or reefs that may very well be occupied. Increased shoaling will also reduce vigilance behaviour (Chapter 4) and may diminish potential costs such as interrupted foraging that may be associated with high predation risk.

5.4.6 Predation risk and prey population dynamics

Predation risk may have far reaching implications for the demography of coral reef fish prey. Maturation rates and fecundity in phenotypically plastic organisms are dependent on foraging effort and food intake (Schoener 1971; Wootton 1979; Real and Caraco 1986) and are more likely to depend on size rather than age in fish (Kuwamura *et. al* 1993; Jones 1991; Munday 2001). Size at maturity of *P. moluccensis* populations is variable between latitudes on the Great Barrier Reef (Bray 2001) and estimates range from 25mm (sensu Mapstone 1988) to 31 mm (Bray 2001). However, growth rates of juvenile *P. moluccensis* reared in identical conditions in aquaria but originating from populations at different latitudes on the Great Barrier Reef are similar (Bray 2001). This laboratory study suggests that growth in this species is not genetically, but environmentally controlled and observational studies by Beukers (1996) attributed such latitudinal growth differences to different levels of predation risk. Therefore, predator cues can impact fitness in fish by delaying ontogenetic development and associated territory acquisition or niche shifts (Jones *et. al* 2003). Furthermore, by regulating the number of individuals reaching reproductive maturity (Jones 1984, 1991), coral reef predators may modify size and fecundity of adult prey populations. By constraining individuals to a small size class, size-selective mortality on juveniles will increase (Sogard 1987). This will weaken the strength of a recruiting cohort, which may alter size structure of a population of less mobile, site-attached species especially if they are largely self-recruiting.

5.5 Conclusion

This study demonstrates a trade-off between survival and reduced growth in *P. moluccensis*. The results from the experiment show a direct and realised growth suppression of predation risk that may be as high as 31%. This cost is reduced with increases in group size as individuals spend more time actively feeding and less time being vigilant. The ultimate cost of a reduction in growth with increases in group size may be offset by the increase in survivorship with an increase in aggregation.

The optimal strategy for settling recruits may depend firstly on the availability of appropriate / preferred habitat or refuge and secondly on the level of ambient risk or resident competition faced by a recruit which may induce post-settlement movement or, more likely, risk-specific vigilance. The long-term consequences of risk-induced reduction in growth on fecundity and reproductive fitness require further research on successive cohorts to assess the impacts on population size and structure in small reef fishes.

5.6 Figures and Tables

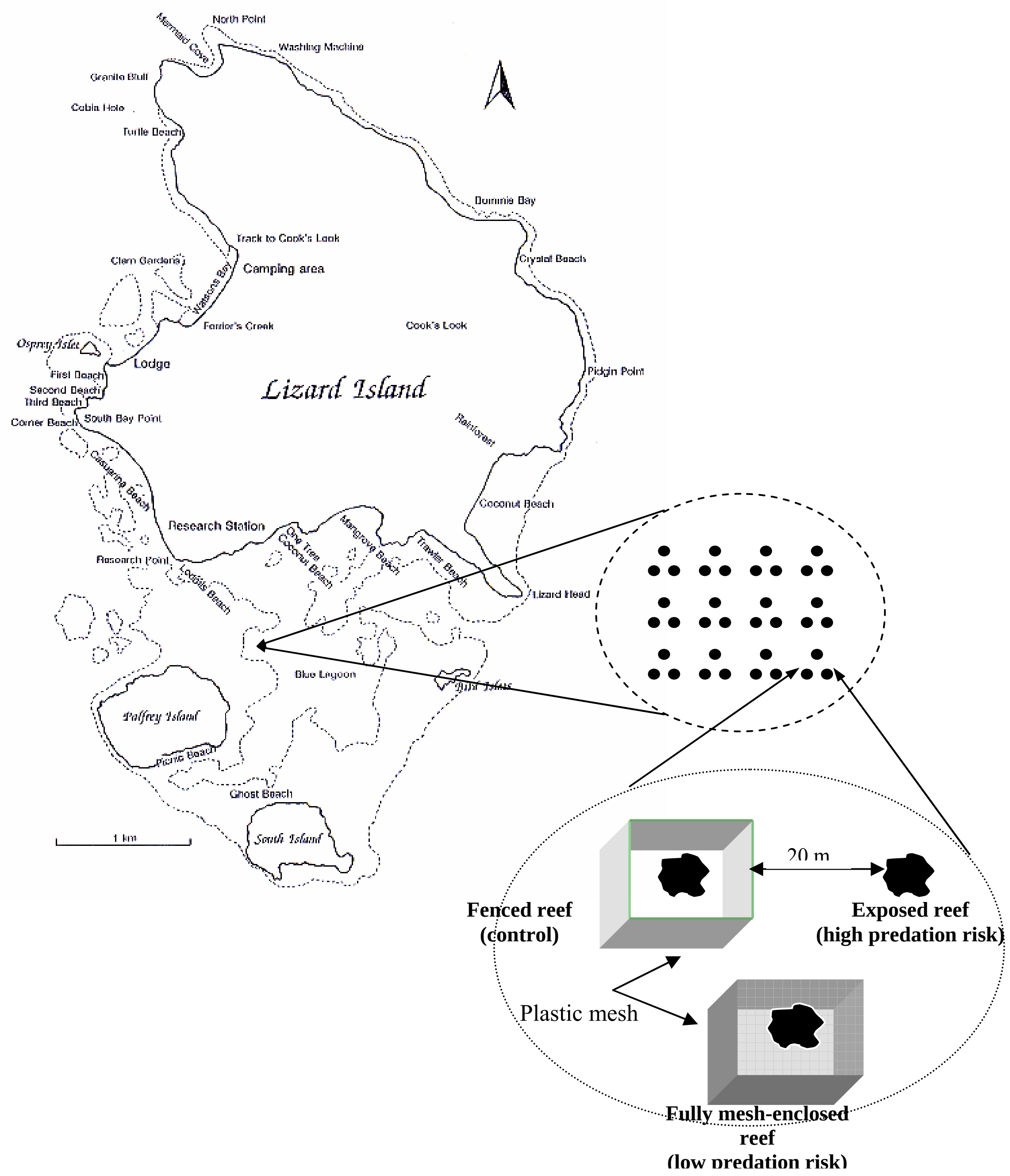

Figure 5.1 Location and structure of artificial reefs and cages used in this experiment. Reefs were built 20 m apart and predation risk treatments were allocated randomly within each cluster of 3 reefs with the condition of including both high and low risk treatments and a control. Similarly each cluster contained all three levels of the group size treatment but they were randomly assigned to reefs. Clusters were placed 20 m apart.

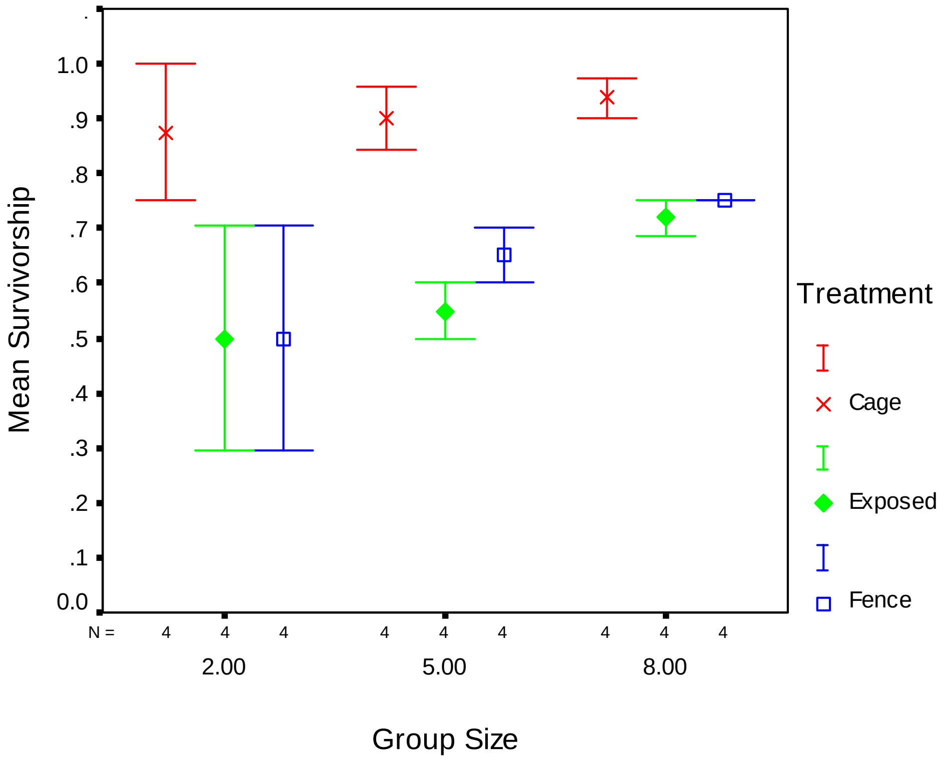

Figure 5.2 Probability of survivorship of *P. moluccensis* averaged within reefs, among group sizes. Caged, low-risk reefs **x**; exposed, high-risk reefs ♦; and fenced, control reefs □. *Error bars* indicate SE

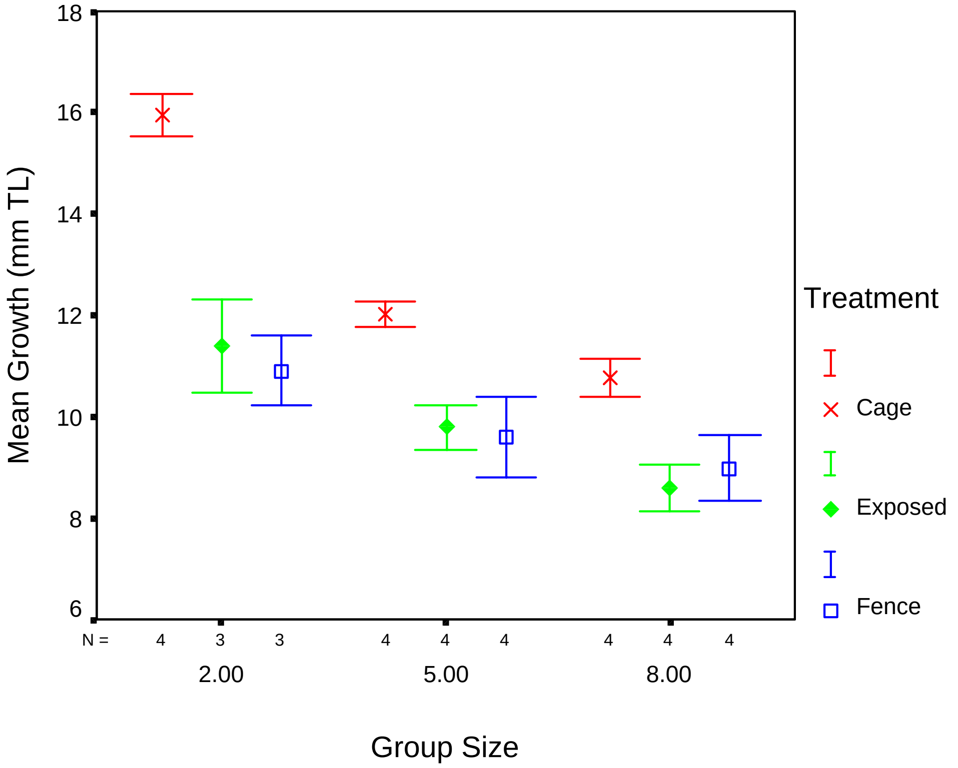

Figure 5.3 Growth of individuals of the species *P. moluccensis* averaged within reefs, among group sizes on caged, low-risk reefs **x**; exposed, high-risk reefs ♦; and fenced, control reefs □. *Error bars* indicate SE.

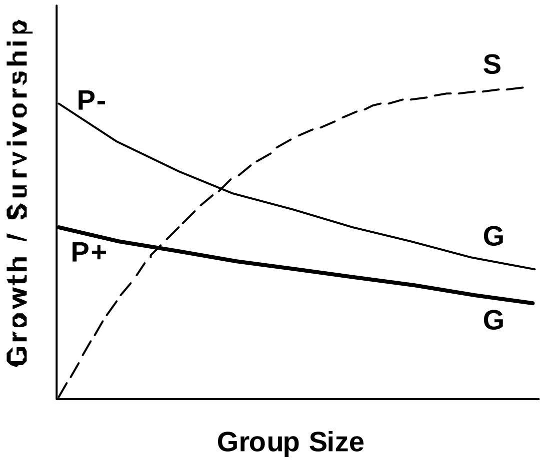

Figure 5.6 A conceptual model of growth, **G**, and survivorship, **S**, in social, coral-associated planktivores. These prey trade-off the benefit of increased survival with decreased growth, with an increase in group size. In low risk circumstances, **P-**, the model predicts that prey individuals will experience decreased growth with group size, presumably due to increase competition. Nonlethal effects of predation (the difference between "**P+**" and "**P-**" growth curves) may modify this trade-off. When exposed to predation risk, **P+**, extra vigilance is necessary, as the probability of mortality is higher. As vigilance interrupts feeding and individuals are more likely to be vigilant in high compared with low risk situations, these prey (**P+**) will experience more reduced growth than those free of risk (**P-**). Per capita vigilance will decrease with an increase in group size, and this may partially compensate the reduction in growth caused by intraspecific competition. The result is that individuals relatively free of predators (**P-**) will experience a sharper reduction in growth with group size as compared with those in high-risk situations (**P+**).

Table 5.1 Abundance of ten most abundant predators surveyed in the immediate vicinity of the artificial reefs.

Species	Behaviour	Observed size range (cm)	Abundance Rank
Seranidae (Groupers)			
Cephalopholis cyanostigma	Benthic, sedentary	20-25	1
C. boenak	Benthic, sedentary	15-20	2
C. argus	Benthic, sedentary	10-15	4
Epinephelus coiodes	Benthic, sedentary	10-15	5
E. spilotoceps	Benthic, sedentary	10-15	7
E. tauvina	Benthic, sedentary	25	9
Plectropomus leopardus	Water column, mobile	15-30	6
Labridae (Wrasses)			
Epibulus insidiator	Water column, mobile	25-30	10
Lethrinidae (Emperors)	Water column, mobile	10-20	8
Lethrinus ornatus			
Synodontidae (Lizardfishes)		5-15cm	3
Synodus dermatogenys	Benthic, mobile		

Table 5.2 Results of ANCOVA examining variation in growth, expressed as total length (TL) of *P. moluccensis* with respect to the different factors and treating survivorship as the covariate.

Source	SS	df	MS	F	Sig of F
Survivorship	1.519	1	1.519	1.267	0.27
Predation risk	34.148	2	17.074	14.239	< 0.001*
Group size	62.273	2	31.136	25.966	<0.001*
P. Risk x Group Size	12.742	4	3.185	2.657	0.058
Error	28.779	24	1.199		

Table 5.3 Results of ANOVA examining variation in growth, expressed as total length (TL) of *P. moluccensis* with respect to the different factors. I removed any effect of survivorship on growth by analysing the residuals from the regression of growth on survivorship, rather than the raw growth data. These growth residuals were then examined using this two-way ANOVA

Source	SS	df	MS	F	Sig of F
Predation risk	71.10	2	35.551	29.585	0.01*
Group size	60.67	2	30.334	25.243	<0.01*
P. Risk x Group Size	12.34	4	3.084	2.567	0.063
Error	30.04	25	1.202		

Chapter 6

General Conclusions

6.1 Nonlethal interactions between marine predators and prey

Many marine organisms are highly phenotypically plastic (given their bipartite lifecycles and heterogenous environment) and therefore predation risk may have an important effect on fecundity of these individuals if the threat of predation modifies their behaviour. This may be especially significant in marine systems with a high diversity of predators and clear trade-offs in prey behaviour stemming from strong refuge / site fidelity and limited food resources. Such traits are typical of planktivorous fish communities on coral reefs. Few studies have investigated interactions between predators and prey on coral reefs (Stewart 1998). Of those, fewer still have examined the nonlethal interactions between these predators and their prey. Nevertheless, individual behaviour and population dynamics of fish on coral reefs are likely to be significantly influenced by non-lethal predator-prey interactions (Jones and McCormick 2002) and both should be examined for a more complete understanding of the system (Sutherland 1996). In this thesis, I use coral reef fish as a case study to examine the effects of predation risk on marine organisms. I also propose that predator-induced behavioural responses may alter phenotypic characteristics such as morphology. Such responses may modify prey energetics and in turn this may affect the reproductive potential and life-time reproductive output of an organism.

6.2 Effects of predation risk on coral reef prey fish

In this study I have shown that some species of coral reef fish modify their behaviour in the presence of a predator. Behavioural modifications included reduced foraging, refuge seeking, and increased vigilance. In the presence of predators, juvenile prey associated more with refuge than did adults. Foraging reduction in planktivorous prey fish resulted from decreases in foraging distance and / or the number of bites individuals took. Individuals in larger groups reduced their foraging less than those in small groups. Juveniles reduced their foraging less than did adults. These reductions in foraging were associated with a reduced growth of prey fish of as much as 31%. Per capita prey vigilance decreased with group size along with growth costs of predation (31% in small groups as compared to 14% in large groups).

6.3 The role of predation risk on prey demography

Fecundity in coral reef fish is a function of body size and condition. Therefore reduced growth arising from predation risk may affect age / size at maturity and thereby modify the size and fecundity of adult prey. Furthermore by constraining individuals to a small size class, size-selective mortality on juveniles will increase. This may decrease the abundance of recruits and alter the size structure of a population. Because vulnerability to predation varies with body size and species, predators influence diet and habitat use within and between species and can therefore affect resource competition (Peacor and Werner 2000). Such predator-mediated resource competition can play a major role in regulating population size structure

(Mittelbach and Chesson 1987). Fitness of certain prey species (growth, reproductive potential) may be enhanced by an increase in food resources caused by predator-induced reductions in a competitor's numbers or foraging efficiency (Vanni 1987).

6.4 Potential implications to fisheries management

The effects of nonlethal predator-prey interactions on coral reefs may be an important consideration in marine conservation and fisheries management. A high abundance of fish prey species has recently been documented on coral reefs that were open to fishing as compared with spatially and structurally similar areas where fishing is not permitted (Graham *et al.* 2003). A higher abundance of predators in areas designated as marine reserves led the authors to conclude that removal of predators by fishing can result in numerical release of their prey species. The results of this thesis suggest that predator-free prey also experience energetic release which may yield larger prey in better condition on fished reefs. Such a second order trophic effect may occur in heavily fished areas.

Therefore, overfishing predators may cause an increase in prey abundance (numerical effects) and growth (energetic effects). Energetic effects can potentially be species-specific and may lead to species-specific competitive dominance in predator-fished zones of the GBR. Highly mobile species that are not closely associated with reefal structure and specific coral colonies, such as many Labrids and Acanthurids, may exhibit density dependant movements (space and habitat-limitation and territorial interactions). However, individuals that are closely associated with coral colonies, such as Pomacentrids, may not move and will experience a reduction in growth with an increase in numbers.

6.5 Future research

The effect of predation risk on modifying reproductive behaviour and strategies, mainly the implications of reduced growth and poor condition on fecundity and reproductive potential of individuals, and the condition of offspring born under such conditions, all need to be explored. Studies using multiple marine predators as potentially complementary sources of risk are also lacking. Although a few studies have examined the effect of multiple predators on density-dependent mortality of prey (eg. Hixon 1997), there are no studies on the synergistic threat of multiple species of predators. The nonlethal effects of different types of predator (diversity) as well as the number of predators (abundance) should be examined in studies of predation risk. The risk effects of different ontogenetic stages of a predator have also not been examined in coral reef or other marine communities. Finally, predator-induced redistribution of prey may be an important determinant of local population levels for vagile marine organisms. Few studies have explored these potential effects (but see Connell 2000) that may modify large-scale behaviour (emigration) in response to localised or spatially extant pockets of high predation risk.

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