St John, Jill (1995) ***Feeding ecology of the coral trout, Plectropomus leopardus (Serranidae), on the Great Barrier Reef, Australia.*** **PhD thesis, James Cook University.**

Feeding ecology of the coral trout, *Plectropomus leopardus* (Serranidae), on the Great Barrier Reef, Australia.

by
Jill St John
(BSc. Hons, Sydney)

A thesis submitted for the degree of Doctor of Philosophy
in the Department of Marine Biology
at James Cook University of North Queensland.
August 1995

Third fisherman :

Master I marvel how the fishes
live in the sea

First fisherman :

Why as men do a-land
the great ones eat up the little ones

Shakespeare Pericles Act ii sc 1 l. 29 1608

STATEMENT OF ACCESS

I, the undersigned, the author of this thesis, understand that James Cook University of North Queensland will make it available for use within the University library and, by microfilm or other means, allow access to users in other approved libraries. All users consulting this thesis will have to sign the following statement:

> In consulting this thesis I agree not to copy or closely paraphrase it in whole or in part without the written consent of the author; and to make proper public written acknowledgement for any assistance which I have obtained from it.

Beyond this, I do not wish to place any restriction on access to this thesis.

8-8-96

(Jill St. John) (Date)

STATEMENT ON SOURCES

DECLARATION

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived form the published or unpublished works of others has been acknowledged in the text and a list of references is given.

8-8-96

(Jill St. John) (Date)

ACKNOWLEDGEMENTS

One of the major conclusions of this study is that PhD's are not accomplished alone. Mine is no exception. I extend my sincere thanks to all of you who helped me along the way.

I'd like to thank the people who made this all possible by providing a stipend. I am gratefully indebted to the members of the Australian Federation of University Women - Queensland, particularly those volunteers who run a business to fund women in academia. This thesis is dedicated to them.

I am very grateful to my supervisor, Garry Russ for his continuous support, guidance and advice throughout this study. Garry read and re-read all of my thesis except this section. I found Garry to be accessible, dependable and humorous, three qualities of a good supervisor. I was fortunate to have two associate supervisors. Hugh Sweatman provided invaluable logistical and statistical assistance. Hugh's answers to endless questions and his provision of important equipment such as access to statistical programs and a coffee machine has greatly improved this thesis. Bruce Mapstone supported me with sensible and logical advice on many matters including statistics and design. Bruce assisted me a lot in the early stages of this study. Thank you.

A special thanks to Lyle Squire who helped me get this thesis up and running. Lyle provided much needed practical assistance and advice as well as connections to the Townsville Spearfishing Club. Lyle gave me his time, his hospitality and a heap of specimens speared privately (by himself and by his sons) or in connection with his work.

Many thanks to the following people (mentioned in no particular order) for their various roles.
In the field, many trout were collected by the spearos from Townsville Skindiving Club, Bill Roberts, Todd Protheroe, Geoff Ramm, John Goebels, Dave Welsh, Angelo Angeli and John Robinson. Chris Robb was particularly helpful as he volunteered his spearing skills on other field trips. Others kept trout guts for me.... a smelly business, Lyle Squire Jnr and Snr, Campbell Davies, Jeff Bibby, Beatrice Ferreira, Phill Laycock, Hugh Sweatman and Melita Samoilys. Phill Light dissected 150 tiny stomachs for me. Data was provided by Peter Doherty (Australian Institute of Marine Science), Ian Brown and Melita Samoilys (Southern and Northern Fisheries Research Institute QDPI), Tony Ayling (Sea Research) and Bruce Mapstone (GBRMPA). At Orpheus Island Research Station helpful staff included Russell Bathard and Snow and Virginia Downton. These people and Jo Goudie fed fish for me. Volunteer assistants included Dave Hocking, Dave Welsh, Debbie Rae and Carole Wallace. Bill Gladstone took some great photographs. Line fishing was done by Michael Osborne, Doug and John Clark and Jim Higgs. Laura Castell-Perez and Hugh Sweatman assisted me in the field. Technical help

was provided by Leigh Winsor, Don Booth, Leigh Owens, Phill Osmond, Colleen, Anita, Ann Sharp, Savita and Jan Woodley, who also sent my mail on. Brett Molony, Hugh Sweatman, Garry Russ sent me references when I was in Japan. Kyoko Tamate and Keiichi Matsuura provided me with access to references in Japan. H. Hirakawa provided me the use of a microscope at the Onahama Fisheries Research Institute. Prey fish were identified by Jeff Leis, Doug Hoese, Dirk Zeller, Alison Green, Garry Russ, Hugh Sweatman, Ann Cabanban and Bill Gladstone. Cephalopods were identified by Natalie Moltschaniwskyj. John Collins and Danielle Johnston identified crustaceans. Chapters were read by my supervisors, as well as Leigh Winsor, Melita Samoilys, Bill Gladstone, Bryce Stewart, Lin Schwarzkopf, Kathy Kavanaugh, Jean Deklerk, Brett Molony, Jo Beukers, Barry Goldman, Julian Caley, Ilona Stobbard and Ivana Noell. Maps and diagrams were drawn by Steve Clarke. References were typed by Lishu Chen with the help of Suzy Dormer. The thesis was greatly improved by discussions with Geoff Jones, Beatrice Ferriera, Melita Samoilys, Campbell Davies, Julian Caley, Bryce Stewart, Jo Beukers and my supervisors.

Warm friendships and fun times were enjoyed with many kind people. People who have been particularly supportive include Jo Beukers, Suzy Dormer, Bea Ferreira, Jane Fromont, Bill Gladstone, Gina Mercer, Libby Moodie, Brett Molony, Debbie Rae, Mary Robertson, Carole Wallace and Jan Woodley. Thanks to Mary Robertson, Cheryl Hercus and Grant Whiteman, Carole Wallace and Chris Hill, Jane Fromont and Dave Sutton and Ivana Noell for providing a place to live. Baby sitters include Mary Robertson, Mary Stafford-Smith, Jane Fromont and Dave Sutton, Julia Shand and Rob MacCauley, Gina Mercer, Suzy Dormer, Hugh Sweatman, Laura Castell and Lishu Chen.

Finally, I thank my family. Both my parents, and , played a vital role in all of this. Little I was born to this thesis and has had to share me with a computer for her first year of life. Her joy of life and thrill of learning has kept my work in perspective. lived this thesis with me from field work to editing. His endless support, encouragement and patience helped me the most.

ABSTRACT

The Great Barrier Reef (GBR) is the largest coral reef system in the world and the coral trout, *Plectropomus leopardus* (Pisces: Serranidae, Lacepede 1802) is one of its most widespread and abundant piscivores (Ayling and Ayling 1986). Despite the importance of the coral trout fishery, very little is known about the feeding ecology of *P. leopardus* on the GBR.

The principal objective of this study was to describe the diet and feeding of *P. leopardus* on this large reef system. Variation in the diet of this piscivore over a range of latitudes along the GBR and on reefs open and closed to fishing was examined. Seasonality of feeding by *P. leopardus* was addressed by comparing rates of digestion, consumption of food and diet in the austral summer and winter. Within populations of *P. leopardus,* the ontogenetic shifts in diet and individual feeding behaviour were examined.

Plectropomus leopardus is one of the major predators of adult coral reef fishes on the GBR. After their first year of life, *P. leopardus* are almost entirely piscivorous on adult fishes (99% of fish diet). The dominance of fish in the diet does not vary temporally or spatially.

Feeding studies have shown that *P. leopardus* are intermittent feeders, consuming an average of one prey item daily. After 24 hours, approximately 90% of prey items were digested. Thus, contents of stomachs represented daily feeding in *P. leopardus.* Seasonal rates of food consumption were not related to rates of digestion in *P. leopardus.*

In *P. leopardus*, the major dietary shift in the type, species composition, length and shape of prey occurred at approximately 20 cm SL and corresponded to the onset of sexual maturity. Juvenile *P. leopardus* consumed a higher proportion of benthic crustaceans, mostly penaeid prawns. Though families of prey fish in the diet varied ontogenetically, the breadth of the diet (in terms

of family richness) did not increase with the size of predator. This shift in diet must be due to a change in feeding behaviour because juvenile *P. leopardus* live in similar habitats to adults.

Overall, Pomacentridae were the dominant family in the diet of *P. leopardus.* The main families in the diet of *P. leopardus* were divided into two groups. Common families (Pomacentridae, Labridae, Caesionidae and Scaridae) constituted a consistent and substantial portion of the diet. Small schooling fishes (e.g. Clupeidae), were a highly variable component of the diet both temporally and spatially. Sporadic appearances of small schooling prey in the diet of *P. leopardus* were the main cause of the reduction in dietary overlap between reefs and times.

The abundance of prey in three common families varied latitudinally in the diet of *P. leopardus*. Pomacentridae and Caesionidae were consumed more in the northern GBR whereas Scaridae were eaten more in the south. There were no detectable effects of fishing on the diet of *P. leopardus.* Dietary overlap among reefs zoned for different levels of fishing were within natural spatial and temporal variations for the GBR. Most of the major changes in the diet of *P. leopardus* occurred before the piscivores entered the fishery (current legal minimum size is 38 cm FL). Adult *P. leopardus* prey on juvenile *Plectropomus* spp. and thus high densities of adults may reduce abundances of juveniles.

The major seasonal difference in feeding was a higher consumption of food in winter that coincided with increased production of mesenteric fat that is stored in preparation for reproduction (Ferreira 1993). Family richness in the diet increased during winter months because rare prey were consumed to meet a higher requirement for food. Otherwise, composition of the diet did not vary seasonally. *Plectropomus leopardus* did not appear to respond to the seasonal influx of recruits to the reef during summer; newly recruited prey individuals were consumed rarely.

Plectropomus leopardus appear to be selective feeders in terms of both families and species of prey. At a family level, 37 families were identified in the stomachs of *P. leopardus*. Many abundant families of fishes on the GBR (e.g. Chaetodontidae, Holocentridae, Pomacanthidae and Siganidae) were rarely eaten while others (e.g. Haemulidae) were not identified in the diet at all. The choice of species among the Pomacentridae was examined. Approximately 25% of the 120 possible species of Pomacentridae were identified in the stomachs of *P. leopardus*. Some of these prey species were eaten in much higher proportions than expected when compared to their general abundance on reefs (e.g. *Acanthochromis polyacanthus*) whereas other species were eaten in much lower proportions (e.g *Pomacentrus amboinensis, Pomacentrus moluccensis* and *Neopomacentrus azysron*).

The abundance of families (measured by digested weight) in the diet of *P. leopardus* was compared to the biomass of prey fishes on another midshelf reef on the Central GBR (Williams and Hatcher 1983). The top five ranked families in the diet of *P. leopardus* (Pomacentridae, Caesionidae, Scaridae, Labridae and Serranidae) were also the top five families in terms of biomass on reefs. Furthermore, these five families represented approximately 80% of both fishes on reefs and the total biomass of the prey in the diet. Prey in families were not eaten in exactly the same ranking as biomass on reefs. There was a large difference between the proportions of the two major prey species, Pomacentridae and Caesionidae, on midshelf reefs. *Plectropomus leopardus* consumed more Pomacentridae than Caesionidae even though the biomass of Caesionidae on the reef was more than double that of Pomacentridae. The modes of life of schooling, mobile Caesionidae and demersal, site attached Pomacentridae differ on coral reefs and this may explain the reversal of ranks of these two families in the diet of *P. leopardus*.

In general, the size of prey and composition of the diet *P. leopardus* was related to the size of the predator. As the gape of *P. leopardus* limits the size of prey ingested, the critical dimension of the prey is depth rather than length.

When feeding on larger prey items, small to medium-sized *P. leopardus* (< 35 cm SL) appear to feed optimally as defined by Werner (1974) with respect to body-depth of prey. This size-related feeding did not occur under all circumstances. Size of prey was decoupled from size of predators for all *P. leopardus* larger than 35 cm (SL) and when the prey were small schooling fishes. It appears that *P. leopardus* switch to feeding on small schooling fishes when they are available.

Predatory behaviour of *P. leopardus* in tanks was highly variable among individuals. Both the success of capture of *Acanthochromis polyacanthus* (F. Pomacentridae) and the consistency of predatory abilities varied among individuals. Individual variation in feeding may help explain the high variability in growth and fecundity of individuals observed within populations of *P. leopardus* (Ferreira 1993; Davies 1995).

The abundance and species richness of the families common in the diet of *P. leopardus* suggests that food for the coral trout fishery is sufficient on the GBR. Furthermore, feeding by *P. leopardus* appears to be unaffected by this human activity at present levels of fishing. Other aspects of this study, however, suggest that fishery managers cannot be complacent. The effects of cannibalism within the fishery need to be understood. Fishing may reduce predation on prey on reefs directly by removing predators and, in the case of line fishing, indirectly by feeding predators. Data from the fishery should be treated with caution for two reasons. Firstly, Catch Per Unit Effort (fish per fisher per hour) was considered a poor method to estimate or compare the population density of *P. leopardus* as more of the catch was taken by line when a high proportion of the population was hungry. Secondly, line fished samples of *P. leopardus* should not be used for dietary studies as the abundance and composition of prey was biased by regurgitation and the presence of bait. Line caught fish had fewer natural prey in their stomachs and the composition of the natural diet differed from the sample caught by spear.

In conclusion, the major sources of variability in the diet and feeding behaviour of *P. leopardus* were the following:

1. ontogenetic shift from juveniles to adults,
2. high individual variation in successful capture of prey, and
3. regional variation in the diet.

In contrast, seasonality and varying levels of fishing had little effect on the diet of *P. leopardus*.

TABLE OF CONTENTS

CHAPTER 1

1.0 GENERAL INTRODUCTION

In ecology predation is one of the most important processes structuring marine and freshwater communities (Connell 1975; Zaret 1980; Sih *et al.* 1985). Predation is considered to maintain high diversity in tropical marine systems (Paine 1966; Connell 1975). As coral reefs are one of the richest environments for fishes on earth (Sale 1991; 30-40% of all fish species inhabit coral reefs, Cohen 1970) it may be surmised that predation would be important in this marine system too. Indeed, nearly twenty years ago predation was proposed to be an important process structuring coral reef fish communities (Smith 1978; Talbot *et al.* 1978). In contrast to other marine systems such as the rocky intertidal (see reviews by Connell 1972; Paine 1977; Fairweather 1990) and soft sediment communities (see reviews by Peterson 1979; Choat 1982; Dayton 1984; Wilson 1991), where predation has been the focus of many ecological studies, predation has received relatively little attention on coral reefs (Hixon 1991).

To date there have been three basic approaches that attempt to define the role of predation in structuring assemblages of coral reef fishes: experiments where the level of predation is manipulated, correlative evidence, and dietary and behavioural studies of piscivores. The most direct tests of the impact of predation on coral reef fishes are manipulative experiments. To date, these have been largely unsuccessful (see review by Hixon 1991). The aim of such experiments was to describe the effect of reduced predation on community structure. Without information about the diet of predators and their feeding behaviour, the outcome of the experiments was difficult to interpret. Other problems included the difficulties of maintaining different densities of piscivores in experiments in the field. Removal of predators from small patch reefs was often ineffective over several months because rates of recolonization by predators were high (Shpigel and Fishelson 1991; Caley 1993). Cages used to exclude predators produced artifacts which obscured the effect of predator removal on the community structure (Lassig 1982; Doherty and Sale 1985). On a larger spatial scale, reef-wide spearing of piscivores did not alter the broad community structure of reef fishes (Bohnsack 1982).

Secondly, correlative evidence provided indirect information about the role of predation on coral reefs. The importance of the impact of predation on communities of coral reef fish has been inferred from:

1. the large proportion (numerical or biomass) of piscivorous coral reef fishes (Goldman and Talbot 1976; Williams and Hatcher 1983; Norris and Parrish 1988) as well as the numerous small, generalist piscine carnivores with very opportunistic feeding habits (Hiatt and Strasburg 1960);
2. high rates of natural mortality of young and small coral reef fishes (Shulman and Ogden 1987; Sale and Ferrell 1988; Meekan 1988; Mapstone 1988); and
3. studies on small experimental patch reefs where a presumed increase in predation caused by an increase in abundance of piscivores correlated with a decrease in the number of recruits (Thresher 1983a, b; Shulman *et al.* 1983; Hixon and Beets 1989; Bohnsack 1990).

None of these studies, however, provide direct evidence for a causal relationship between predation and mortality of young coral reef fishes, since the diet and behaviour of the piscivores involved were not investigated.

The third approach used to examine predation on coral reefs has focused on feeding and behaviour of the predator. On coral reefs, two main methods examine feeding in predatory reef fish: dietary analysis and behavioural studies. The most common method used to describe the diet of one or more piscivores is by stomach content analysis (Hiatt and Strasburg 1960; Randall 1967; Hobson 1974; Harmelin-Vivien and Bouchon 1976; Sano *et al.* 1984; Parrish *et al.* 1985; Norris and Parrish 1988; Kingsford 1992). Behavioural studies which examined the natural feeding rates of reef piscivores are more rare (Goeden 1974; Sweatman 1984; Diamant and Shpigel 1985; Samoilys

1987). Some studies have examined both feeding behaviour and stomach content analysis (Hiatt and Strasburg 1960; Randall 1967). Neither of these methods are without problems on coral reefs. Many of the dietary studies on coral reefs cover a wide range of predatory species and sample sizes of predators were often low (n<50, but see Choat 1968; Kingsford 1992). This contrasts with dietary studies of predatory fishes collected by trawls from other tropical ecosystems. In general, dietary studies on coral reef fish only outlined the diet of a large number of piscivorous fish species. Details of taxonomy and size of prey were not recorded. Prey items were usually classified into major taxonomic categories only (e.g. fish, mollusca) for two reasons. Firstly, a high proportion of piscivores, particularly large species, provide no information on their diet because their stomachs are empty (Randall and Brock 1960; Randall 1967; Choat 1968; Goeden 1974; Hussain and Abdullah 1977; Kingsford 1992). Secondly, only a small proportion of the diet can be identified to family or genus (Connell and Kingsford 1992) due to their advanced stage of digestion. Small samples of predators exacerbate this problem. Furthermore, on coral reefs, dietary studies involving small to moderate sample sizes are often compromised by the low numbers of identified prey. The absence of particular prey in the diet does not mean that they are not consumed. This is especially problematic for predators on coral reefs where prey fish communities are diverse and species are abundant (Sale 1977). The prey of these piscivores are expected to be similarly diverse. Finally, the interpretation of dietary studies is difficult unless information is available on the digestion rate and consumption rate of prey by the piscivore. In behavioural studies, field observations are very time consuming. Successful predatory strikes are rare and difficult to confirm (Goeden 1974; Sweatman 1984; Diamant and Shpigel 1985; Samoilys 1987).

It is particularly difficult to disentangle the complex food chains on coral reefs (Parrish *et al.* 1986). Predation on coral reefs is an inter-woven process because trophic pathways change temporally and trophic roles can be reversed. Trophic interactions have been investigated by poisoning a fish community and relating the diets of piscivores to the abundance of the prey (Chave 1978; Parrish *et al.* 1986). Documenting the diets of piscivores is the first step to understanding the trophic food web within communities of coral reef fishes.

The Great Barrier Reef (GBR), in Australia is the largest coral reef system in the world. The GBR covers nearly 2500 km in a north-south direction (Latitude 24° S to 9° S). Communities inhabiting the GBR are likely to experience a wide range of temporal and regional variations of environmental conditions due to differences in latitude and reef structure as well as seasonal and sporadic weather conditions (e.g. cyclones). Along the GBR temperatures vary more seasonally than those of other coral reefs (e.g. the Caribbean). In addition to these environmental variations on the GBR, much of this ecosystem has been zoned for various levels of protection from fishing. Due to the high natural and man-made variation on the GBR, communities of coral reef fishes are not similar along the reef (Williams 1991). These environmental variations cannot be overlooked when examining the biology of a widespread predatory species of fish on the GBR.

Coral reef fisheries tend to selectively remove large piscivorous fishes from the community (Bohnsack 1982; Russ 1985, 1991; Huntsman and Waters 1987; Koslow *et al.* 1988) because these fishes are often targeted by the fisheries and are highly vulnerable to most fishing gear. One such group of large piscivores, groupers, represent an important fishery resource throughout the tropics (Ralston 1987). The coral trouts (*Plectropomus*) are members of the groupers (Serranidae) and are widely distributed in shallow tropical and sub-tropical seas of the Indo-Pacific region (Randall and Hoese 1986). On the GBR, coral trout are one of the most popular food fishes (Beinssen 1989). Coral trout comprised the largest single component (30% or 1200 metric tons) of the total annual catch of Queensland's commercial line-fishing industry in 1989 (4000 metric tons, Trainor 1991). In addition to the annual catch of the commercial fishery, recreational fishers are estimated to catch two to three times more (Craik 1981). Of the coral trouts, *Plectropomus leopardus* (Lacepede 1802), is the most abundant and widespread species on the GBR (Ayling and Ayling 1986; Randall and Hoese 1986). Not surprisingly *P. leopardus* is the dominant component of catches of coral trout by both commercial and recreational line fishers (Williams and Russ 1994) and spearfishers (Steven 1988; StJohn unpubl. data).

Selective and opportunistic predators are at either end of a continuum. The placement of a predator on this continuum depends on its diet in relation to the number and identity of prey present. Predation occurs within the limits imposed by predator/prey size ratios, and is a function of both the perceptive and handling capabilities of the predator and the period when the predator is active (Jaksic 1989). Jaksic (1989) defined opportunistic and selective predators as follows. In the patches where predators hunt, opportunistic predators take all prey in the same relative abundances as present whereas a selective predator takes all or some prey in proportions which differ from those present (Jaksic 1989).

Serranids are characterised as generalist, opportunistic carnivores and there is considerable variation in their diet (Parrish 1987). *Plectropomus leopardus* are considered to be polyphagous opportunistic predators, consuming a wide range of prey fishes. As a generalist, *P. leopardus* would be expected to eat a wide range of prey species due to the huge diversity of prey fish on coral reefs. Kingsford (1992) suggested that the diet of *P. leopardus* reflected abundances of available prey. Nevertheless, *P. leopardus* cannot be categorised as generalist or specialist until the abundance of prey in the field is related directly to their diet. Because of the huge numbers of potential prey species and the difficulty of assessing abundances of prey throughout the GBR, determining the abundance of potential prey of *P. leopardus* on coral reefs is not feasible until the actual prey are identified and any variation in the diet is described. A detailed dietary study of *P. leopardus* on the GBR is the first step in determining the role of predation by one of the top predators in this coral reef system.

In comparison to commercially important fishes in other ecosystems, relatively little is known about the diet of *P. leopardus* throughout the GBR. The few studies of the diet focused on just two reefs in the southern GBR (Choat 1968; Goeden 1978; Kingsford 1992). These studies were not designed to detect regional variations nor the effects of fishing on the feeding of *P. leopardus*. This lack of information on the diet of *P. leopardus* is surprising given the huge numbers removed from the reefs by fishing.

The major aim of this thesis was to describe the diet and feeding of *P. leopardus* on the GBR. Specifically, the study included investigations of patterns of variation in the diet and feeding caused either by environmental factors on the GBR or by differences within populations of *P. leopardus*. The thesis comprises nine chapters. In chapter two, details of the methods of stomach content analysis are described. In this chapter separate pilot studies were used to determine the best method to collect coral trout and to assess methods used in processing the specimens. In chapter 3, information on rates of digestion, feeding and consumption of food, including seasonal variations in these rates, provide the basis for the interpretation of the subsequent dietary studies. Patterns of feeding throughout the entire reef associated phase of *P. leopardus* were examined in Chapter 4. In Chapter 5, temporal variation in the diet was investigated throughout the year at one reef. Patterns of spatial variation in the diet within and among different geographic regions on the GBR were examined in Chapter 6. Chapters 5 and 6 provided the baseline dietary information for *P. leopardus* that was used to assess differences in the diet on reefs subjected to various levels of fishing in Chapter 7. Finally, in Chapter 8 predatory behaviour and success in capturing prey by *P. leopardus* were examined in tank experiments. Ancillary aims of this study address feeding and diet of *P. leopardus* further. Firstly, selectivity in the diet of this large piscivore is examined in terms of size and taxon of prey. Patterns of predation by *P. leopardus* are related to the size, shape and behaviour of the prey and the morphology of the predator (Chapter 4). The overall diet of *P. leopardus* on a midshelf reef is compared to abundances of families of fishes on a nearby reef (Williams and Hatcher 1983, Chapter 5). Secondly, potential impact of predation by *P. leopardus* on the prey community is discussed in terms of the annual consumption of prey (calculated from dietary composition, Chapter 7) and the proportions of young fish in the diet of *P. leopardus* (Chapter 4). Thirdly, cannibalism in this species is discussed with reference to the effects of fishing (Chapter 7). Fourthly, individual variation in predatory success by *P. leopardus* is related to variability in growth and fecundity.

CHAPTER 2

2.0 GENERAL METHODS

This chapter comprises five sections. In the first section, the collection of coral trout is detailed. Analyses of their stomach contents are explained in the second section. In the third section, I describe four small pilot studies in which I evaluated some of the methods used to analyse stomach contents. A description of these methods of analysis precedes descriptions of the corresponding pilot studies. The fourth section contains the methods for the tank experiments in Chapters 3 and 8. The last section describes the statistical analyses used throughout the thesis.

2.1. THE STUDY SPECIES, CORAL TROUT

Digestion in coral trout

The contents of the alimentary canals of several coral trout, *Plectropomus leopardus*, were examined to determine which organ/s provided most information on the prey ingested. The alimentary canal and its functions are described briefly.

Coral trout, which are mostly piscivorous, swallowed their prey whole. The oesophagus expanded to allow the prey to enter the stomach. The stomach was sack-like with elastic walls that stretched very thin (< 1 mm) to accommodate large prey items. The prey found in the stomach, ranged from undigested fish to a few hard skeletal structures or small particles. Most chemical digestion occurred in the stomach.

The small intestine is connected to the stomach by a small aperture of approximately 2 mm in diameter. The contents of the intestine were in an advanced state of digestion, consisting of liquefied flesh with some small decalcified bones and partially digested scales. These remains could not be used to identify prey and, therefore, were not useful in analyses of gut contents. Further digestion of the prey was not evident in the small intestine, which suggested that its main digestive function was absorption. The condition of digested skeletal structures in the faeces was similar to those in the small intestine.

The conclusion of this examination was that only the stomach provided recognisable prey contents useful for dietary studies. The wide variety of prey eaten by coral trout prohibited the use of otoliths or bones to identify prey.

Field collections

Approximately 2500 stomachs from coral trout were collected for this study (for sample details see Table 4.1, Table 5.1, Section 6.2.2 and Table 7.1). A few coral trout were caught using fence nets, traps and rotenone. Approximately 250 coral trout were caught by hook and line. Most coral trout were speared. Although the methods of capture and storage of coral trout varied among the different collectors, data recorded for each sample were consistent. The essential information was date, reef, method of capture and storage, with the extra information including time of capture, sites and fisher.

Measurement of coral trout

Some coral trout were processed by fishery biologists at the Department of Primary Industries and at the Australian Institute of Marine Science. When the methods of the other biologists differed from mine, they are noted within brackets (i.e. [ ]). Every coral trout was identified to species. I received samples as either whole coral trout or frames (the carcass without its fillets). Whole fish were weighed to the nearest 25 g [1 g]. Fork length is defined as the length from the tip of the snout to the caudal fork and standard length is defined as the length from the front of the upper lip to the posterior end of the vertebral column. The fork length (FL) and standard length (SL) were measured to the nearest 1 cm [5 cm, FL only]. I then removed the stomach, opened it and scraped any contents into a jar containing fixative

(FCA). I examined the mouth and gills of each coral trout for regurgitated prey which may be retained (Parrish 1987). An empty stomach and any observations about the coral trout (e.g. damaged fish or gut) or its prey (position in stomach) were recorded.

When I was not present for the capture of the coral trout, one of three procedures occurred.

1. Whole fish were chilled on ice (for up to 48 hours) or, after filleting, frames were frozen long-term. The stomachs were removed when the whole fish were filleted or the frames were taken out of storage.
2. Data on the coral trout were collected soon after capture and the stomachs and gills were frozen.
3. Some juvenile fish were measured when fresh then the whole fish was preserved in 70% ethanol.

2.2 ANALYSIS OF STOMACH CONTENTS

Methods of analyses

Methods of analysis of stomach contents vary with the aims of the study and the type of data (Hyslop 1980). Many of the standard techniques applied to dietary studies are useful for fish which consume a large number or a wide variety of prey types. These techniques do not apply to the piscivorous coral trout that have, on average, one prey item per stomach (Kingsford 1992). In his revision of the methods of gut content analysis, Hyslop (1980) concluded that there were three requirements to obtain maximum information on diets:

1. measurement of the amount of prey in the gut;
2. measurement of the bulk of the prey, which should be related to fish size or stomach capacity;
3. allowance for differential digestion rates of different taxa.

The amount of prey was counted because the number of prey in the stomachs of coral trout range from 1 to 18. The bulk of prey was measured gravimetrically using wet weights of total stomach contents and individual undigested prey items. Differential digestion of major taxa was not considered because coral trout eat mostly fish (95% of diet.) The digestion stage of the prey, however, affected the measurements of the prey and it was recorded using a digestion scale (see Table. 2.1).

Preserving and weighing of stomach contents

Fixation and preservation of biological tissue alters the size of specimens (Baker 1958). The degree of change depends on the preservative and the period of preservation (Kruse and Dally 1990). Several studies have examined changes in the length of whole fish after fixation in bouins solution or formalin (Parker 1963) and preservation in ethanol. After 12 hours in formalin (3.8% formaldehyde) fingerlings shrank to 97% of their live length and this decreased to 96% after one month (Parker 1963). Fish ranging in SL from 7-46 mm shrank 2% after 75 days (Shand 1994). More shrinkage (14%) occurred when higher concentrations of ethanol (95% anhydrous) were used (Kruse and Dalley 1990). In this study I examined the size of prey eaten by predators of varying size. As accurate size data came from intact, undigested fish (stages 1 & 2, see Section 2.1.1), an overall shrinkage of 2% would not exceed the error of measurements of SL and TL (to the nearest 1 mm). The usefulness of calculating fresh weights from preserved wet weight of stomach contents of all stages of digestion was examined in a Pilot Study (Section 2.3).

With the exception of some specimens of juvenile coral trout (see above), stomach contents were preserved in two steps. Specimens were fixed in 10% formal calcium acetate (FCA), a buffered formalin solution, using approximately 10 mls of FCA for every gram of stomach content. After a minimum of 7 days, the stomach contents were then transferred to 70% ethanol for storage.

Wet weights of the stomach contents were measured after preservation in 70% ethanol. Before weighing, the stomach contents were emptied into a sieve and shaken, sponged or both to remove excess surface liquid.

Because a major source of error in wet weights is variation in the amount of surface moisture removed from the prey (Parker 1963), I compared the amount of liquid removed using sieves of two mesh sizes, 1.2 mm mesh and 110 microns. Smaller fragments of digested prey in the finer sieve retained more liquid than fragments in the coarser sieve. As this increased the weight of the prey items disproportionately I used the coarser sieve (1.2 mm).

Wet weights of stomach contents were excluded from weight analyses when:
1. there was evidence of regurgitation of food from the stomach (see Discussion in Pilot Study 1, this Chapter 2.3); or
2. the volume of thick sticky digestive fluid, that coated the contents of the stomach, was equal to or more than the volume of the stomach contents. This was assessed visually.

Stages of digestion

Individual prey items were classified into a stage of digestion using a digestion scale modified from Goeden (1974, Table 2.1). (Table 2.1). Although the digestion scale was specifically designed for fish prey, I used it to classify other prey taxa, crustaceans and cephalopods, to maintain consistent numbering of digestion stages throughout the data. Other tables of classification of digestion specifically for Crustacea used fewer digestion categories (Mathur and Robins 1971).

Measurements of individual prey

The size of an individual prey item was described by weight and/or two basic dimensions. The degree of digestion of the prey determined which measurements were taken.

1. Weight (measured to the nearest 0.01 grams).

Only undigested prey (Stages 1 and 2) were weighed individually

2. Length (to the nearest 1 millimetre (mm)).

Both total length (TL) and standard length (SL) were measured when possible, and SL was the most common length measurement . The total length (TL) was measured when either the whole or the upper or lower caudal fin lobe was intact. The SL was measured when the backbone of the prey was unbroken. If the backbone and skull were complete, but in pieces (in digestion stages 3, 4, 5 and 6), the SL was measured and recorded as an estimate. The total length of crustaceans was measured from the tip of the rostrum to the end of the tail.

3. Transverse-section (to the nearest mm).

The largest transverse-dimension of the fish was measured. In most fish this measurement was the depth or dorso-ventral measurement, however, the width of the fish was measured in a few dorso-ventrally flattened prey fish.. When the fish was slightly damaged by digestion (as in digestion stages 2 and 3), the transverse-dimension was estimated.

Identification of prey

Every prey item was identified under magnification, using the taxonomy of Randall *et al.* 1990, to the lowest possible taxonomic group or trophic group or both. Undigested prey were keyed out using appropriate keys (Allen 1975, for Pomacentridae; Myers 1991; Masuda *et al.* 1984). When important meristic characteristics were absent, other features were used to identify the prey fish. These characteristics included shape, distinctive colourations, skin texture, types and placement of scales and fins (spines and rays), jaws and pharyngeals, armory and modifications. A key to genera and species based on dorsal and pectoral fin counts by Smith and Heemstra (1986) was used for fish with complete dorsal and pectoral fins.

To aid with identification, a reference collection of fish prey was made of the best (least digested) specimens of every prey species or taxonomic group found in the stomachs of coral trout. A reference collection of hard structures (such as jaws, pharyngeal bones and spines) unique to families or lower taxonomic groups was made to identify highly digested prey items. When these unique hard structures were absent, prey that was extremely digested (Digestion Stages 6 and 7) could be identified to higher taxonomic groups only. The remains of scales and bones were used for identification of fish, whereas carapace or limbs were used for crustaceans, and beaks or pens for cephalopods.

Digestion of prey fishes in the stomachs of coral trout was rarely uniform. Several factors influenced digestion of various parts of the prey fish: the number of other prey items in the stomach, position in the stomach, size and shape of the prey and the direction the prey was swallowed. For example, if the prey species had distinctive dentition and was swallowed tail-first so that the tip of its head protruded from the stomach, then the prey could be identified by its jaws regardless of the time the rest of the body had spent in the stomach. Prey fish protruded from the stomach when they were large relative to the size of the predator or when the stomach was full. Thus, identification of species of prey was not always related to its duration in the stomach.

Prey in some families, such as Scaridae and Labridae, were identified by their distinctive jaws and pharyngeal teeth. Other prey in families without distinctive bones may have been under-represented in the sample. As mouthparts were often absent in even partially digested fish, families with distinctive dentition were not always identified.

2.3 PILOT STUDIES TO DETERMINE SOME GENERAL METHODS

2.3.1. Comparison of fishing methods

2.3.1. Introduction

The majority of coral trout taken from the GBR are caught by professional and amateur fishers using hook and line. The other popular fishing method used to catch coral trout is by spear. The three previous studies of the diet of coral trout by Choat (1968), Goeden (1974) and Kingsford (1992) used speared fish.

Specimens used at the start of my study were caught by line. The stomachs of many of these fish were either empty or contained bait, and few contained natural prey only, which was the focus of my study. I suspected that a large number of stomachs were empty because of regurgitation of prey as the predator was pulled quickly to the surface on a line. I define bait as any item of food which was eaten as a result of fishing. This included bait on hooks (i.e. Western Australian pilchards, *Sardinops neopilchardus*) and food scraps or remains of fish dumped in the sea as 'burley'.

To determine whether the methods used to catch coral trout affected the results of the dietary study, I compared the stomach contents of coral trout caught by:

1. two different fishing methods - spear and line; and
2. two groups of fishers using one catch method (line fishing) - commercial fishers and recreational fishers.

I examined two aspects of these data:

1. the proportion of natural prey in the stomachs of coral trout;
2. the proportion of empty stomachs. Empty stomachs occur naturally in approximately one third of coral trout collected for diet studies (Choat 1968; Goeden 1974; Kingsford 1992)

2.3.1. Methods

Samples of coral trout came from a variety of sources. Collections under my supervision were from A. Synder (commercial fisher), JCU (recreational line fishing trips for G. Russ) and Townsville Underwater Club. Additional speared samples were provided by L. Squire and his son. Samples of coral trout were collected from 15 different coral reefs in the Northern and Central section of the Marine Park (see Chapter 7 for definition). Two of these reefs, Britomart and Hopkinson Reefs in the Central GBR, were visited by both spear and line fishers at different times. Although the majority of coral trout for this study were collected from January to July 1990, some were speared in November 1989 and January-February 1991. Of 196 coral trout caught by line, 95 were hooked by commercial fishers and 101 by recreational fishers.

These were compared to 172 speared coral trout. The procedure used to obtain the stomach content data is described in Section 2.2. All stomachs were recorded either as empty, or the contents were classified broadly into bait or natural prey only. The data were analysed by two-sided Fisher's Exact tests because both categories were nominal.

2.3.1. Results

The proportion of empty stomachs in the catches varied significantly between the two methods of fishing (Table 2.2). In coral trout caught by hook and line, 44.4% had empty stomachs compared to 33.1% in the speared catch. The type of prey eaten by coral trout differed significantly between the methods of capture (Table 2.2). Excluding coral trout with empty stomachs, 66.0% of the line-caught catch contained natural prey compared to 99.1% of the speared catch. This result is not surprising as spear fishers do not use bait to catch coral trout. The one specimen containing bait in the speared sample had eaten a coral trout gill which are often removed by spearfishers to bleed the fish.

The proportion of coral trout with empty stomachs varied significantly between the two groups of line fishers (Table 2.2). When caught by commercial fishers, 35.8% of coral trout had empty stomachs compared to 52.5% of the recreational catch. Bait accounted for this difference. Firstly, more commercially caught coral trout had bait in their stomachs (41.0% of prey) than those caught recreationally (25% of prey). Secondly, the proportion of coral trout that contained natural prey did not differ significantly between commercial and recreational catches (Table 2.2).

2.3.1. Discussion

Spearfishing was the best method to collect coral trout for dietary studies. Not only did a higher proportion of speared coral trout have prey in their stomachs, but almost all of the prey was natural. Natural prey accounted for most of the food eaten by speared coral trout and only one third of the food in coral trout caught by line. The proportion of empty stomachs in speared coral trout was 33.1% which was similar to other studies which used samples of speared coral trout. Choat (1968), Goeden (1974) and Kingsford (1992), found that 29.1%, 36% and 29% of their samples respectively had empty stomachs.

A high proportion of fish caught by hook and line have empty stomachs (Randall and Brock 1960; Randall 1967; Hussain and Abdullah 1977). There are two possible explanations for the high proportion of empty stomachs in line-caught coral trout.

1. Baited lines may attract hungry fish (with empty stomachs) more than coral trout that have already fed on natural prey (see Chapter 8).
2. Coral trout regurgitate their food when they are stressed. A hooked fish is stressed for a longer time than a speared fish because line caught coral trout are pulled up quickly from depths of up to 40 m whilst still alive. Speared coral trout, however, are often killed underwater and brought to the surface dead. Furthermore, some line-caught coral trout had everted stomachs. During the rapid ascent of the hooked coral trout, the change in water pressure expands the coral trout's swim bladder. If the bladder over-expands, it exerts pressure on the stomach and forces it out of the peritoneal cavity through the mouth. All everted stomachs were empty.

There was some evidence that speared coral trout had regurgitated prey also. Any fish with digested prey in the mouth or gills, or with an empty stomach that was stretched was suspected to have regurgitated some prey. Regurgitation, however, was not always detected by external or internal examination (Bowman 1986).

Commercial line fishing techniques are different from those used by amateurs. The lower proportion of empty stomachs and high proportion of bait in the commercial catch indicated that, before capture, these coral trout swallowed and retained more bait than those caught by recreational fishers.

Commercial fishers tend to use larger baits (i.e. whole pilchards rather than pieces, Brown pers. comm.) and may drop bait into the water to lure hungry coral trout to the area being fished. Also, commercial fishers capture fish from shallower waters than recreational fishers so regurgitation is less likely to occur (Russ pers. comm.). Both professional and recreational line fishing were unsuitable methods for this study because of the low incidence of natural prey and evidence of regurgitation.

It is likely that each method of fishing catches a different sample of coral trout. Spearfishers catch fish from shallower waters (Roberts pers. comm.) than hook and line fishers (St.John unpubl. data). The catch of line fishers depends on which fish takes the bait whereas the catch of speared coral trout is determined, to a greater extent, by the fisher. Differences in the size structure of the catches were not compared because the coral trout were collected from many reefs over several months. In Chapter 6, I compare diets of coral trout hooked and speared concurrently from the same reef.

2.3.2. The effect of delays in processing specimens

2.3.2. Introduction

In any study of stomach contents, the least digested prey item is the ideal because digestion reduces the amount of morphological information about the prey and, thus the certainty of identification. Digestion in coral trout is a chemical process and so may continue after the piscivore has died. The rate of digestion of the prey would decrease over time after the death of the piscivore because the chemical reaction of existing digestive juices would slow, and eventually halt, as the acids in the reaction neutralise and are not replaced.

The aim of this pilot study was to determine the effect of post-death digestion on the prey of coral trout. Two questions were addressed:

1. Does digestion continue after death and for how long?
2. Does post-death digestion alter the digestion stage of the prey in the

stomach?

2.3.2. Methods

The study was carried out over two days in August 1990, on a collection trip at Broadhurst Reef off Townsville. The study was part of another project (see Section 5.2). A total of 49 coral trout, that were landed on a boat within five minutes of capture, were used in the study. As each coral trout came on board it was randomly allocated to one of three treatments: treatment one was 'zero hours' and was processed immediately (n=21), treatment two was processed 'two hours' after death (n=16) and treatment three was processed 'eight hours' after death (n=12). Processing involved the removal of the stomach and the fixation of the contents of the stomach. On the boat, coral trout were kept at air temperature (25-30° C) in the shade. The coral trout in the eight hour treatment were filleted a few hours after capture, before the flesh spoiled.

The stomach contents were processed (Section 2.2) and classified into eight digestion stages using the digestion scale (Table 2.1). Kolmogorov-Smirnov (K-S) tests were used to compare two samples because the categories of digestion states were continuous and K-S tests are applicable to small sample sizes (Sokal and Rohlf 1981).

2.3.2. Results

As the digestive stages of treatment two (two hours) and treatment three (eight hours) did not differ significantly (Dmax= 0.271, K-S $p>0.20$) they were pooled to provide a larger sample for the comparison with treatment one (zero hours). The digestive stages of treatment one (zero hours) differed significantly from the pooled treatment (two-eight hours, Dmax= 0.3571, K-S $p<0.01$). When the empty stomachs were ignored, the modal digestive state was one for treatment one (zero hours) and three for the pooled treatment (two-eight hours), a shift of two categories down the digestive scale (Fig. 2.1).

2.3.2. Discussion

The results of this pilot study indicated that:

1. digestion continued after death in coral trout;
2. during the first two hours after the death of the fish, digestion changed the condition of the stomach contents; and
3. after two hours, the post-death digestion rate slowed and caused no further detectable change in the prey six hours later.

In conclusion, post-death digestion should be halted immediately after capture. The two best methods to stop digestion are

1. Inject formalin into the stomach or gut cavity of the fish. This method was inappropriate because the flesh of coral trout was used for food.
2. Process the stomach contents immediately after capture. Usually this was impossible to do. Spearfishers often hunt far from the boat and they could not bring each fish to the boat immediately after capture. If I removed fish from the spearfishers floats while they were hunting, the continuous interruptions would reduce their catch. Also, even when landed, delays in processing large numbers of fish were inevitable because many spearfishers fished simultaneously. The speed of processing stomach samples of coral trout was increased with an assistant on the boat.

Since I was unable to stop post-death digestion in fish, the next best alternative was slowing it down. Chilling the fish reduces post-death digestion because the rate of digestion decreases as the temperature drops (Kapoor *et al.* 1975). When delays in processing occurred, catches were put in bins of seawater covered with thick hessian bags to keep them cool (water temperature was more than 10 °C lower than air temperature) and the water was changed frequently. Where possible, the coral trout were chilled on ice before processing. All fish were processed in their order of capture.

2.3.3. Weight changes in stomach contents due to preservation

2.3.3. Introduction

Fresh weights of stomach contents are important measures for dietary analysis as they can be expressed as a proportion of fish body weight or used to calculate average daily food consumption of fishes (Hyslop 1980). In this study, the effect of preservation on the weight of stomach contents needed to be evaluated because all stomach contents were weighed after preservation.

Most studies of the effects of fixatives and preservatives on fish examine shrinkage of various tissues or shrinkage of larval fish (Shand 1994). Previous studies have examined changes in weight due to preserving fish in formalin (Parker 1963) and the effect of preservatives on gut contents of larvae (Hay 1981). Changes in weight of digested fish after preservation in formal calcium acetate and 70% ethanol, however, have not yet been examined .

When exposed to fixatives and preservatives, prey items with larger surface area to volume ratios are fixed faster and more thoroughly than those with smaller surface area to volume ratios. Highly digested prey fish (digestion stages 6 and 7), that are broken down into many small pieces, have a higher surface area to volume ratio than intact prey fish (digestion stages 1 and 2). Thus, the change in weight caused by fixatives and preservatives could vary depending on the stage of digestion of the prey item.

This study investigated the effect of fixation and preservation on the weight of stomach contents. Firstly, I examined the differences in fresh weights of stomach contents for:

1. coral trout of varying sizes; and
2. prey of differing stages of digestion.

I then calculate the percent change in weight of the fresh prey items after two steps: preservation in FCA (step 1), then preservation in 70% ethanol (step 2).

The results of this study are used to determine whether the preserved weight of stomach contents should be converted to fresh weights for dietary analysis.

2.3.3. Methods

From a large sample of coral trout (see Chapter 6) I selected 94 specimens of *P. leopardus* and *P. laevis* with digested fish in their stomachs. These coral trout ranged in size from 11.5 to 55.0 cm SL, and their prey included every stage of digestion except empty (digestion stages 1-7, see Table 2.1). I weighed the stomach contents after every stage of the process; after removal from the stomach when fresh, after 1-4 weeks in FCA (step 1), and after 1-4 weeks in ethanol (step 2). The sample was divided into three groups of digestion stages (group one- stages 1 & 2, group two- stages 3, 4 & 5 and group three- stages 6 & 7).

The association between fresh weight of prey and the standard length of the coral trout was calculated as a correlation coefficient. Bartlett's X^2 statistic was used to test the correlation. The change in weight was the difference between the preserved and fresh weight expressed as a percentage of the fresh weight. I calculated the two means (and standard error) for the percentage change in weight of prey, after step 1 and after step 1 and 2. I compared the mean percentage change in weight after the two steps of preservation among the three groups of digestion stages with a fixed factor one way analysis of variance (ANOVA). Prior to the analysis, homogeneity of variances was tested using Cochran's C test and appropriate transformations were carried out if required.

2.3.3. Results

The weights of unpreserved stomach contents were positively correlated to standard length of the predator (Fig. 2.2), and were highly variable when the prey was undigested (digestion stages 1 & 2, Fig. 2.2). The most digested prey (digestion stages 6 & 7) weighed the least (Fig. 2.2).

Percentage weight of the stomach contents increased by a mean of 20.54% after step 1 (in FCA), but after both steps (in FCA then 70% ethanol), fresh weight was reduced by a mean of 22.54%.

The reduction in weight after the two steps of preservation varied significantly among the three groups of digested prey (Fig 2.3). The mean percentage weight reduction was significantly higher in the most digested prey (digestion stages 6 & 7), than in the other two groups (digestion stages 1 & 2 and digestion stages 3, 4 & 5, Fig. 2.3).

2.3.3. Discussion

On average, the fresh weight of stomach contents increased by approximately 20% after fixation in 10% FCA. After both steps of preservation (in FCA then 70% ethanol), the weight decreased by an average of approximately 20% of the fresh weight. Fixation in FCA, like formalin, increases the weight of the prey fish (Parker 1963), whereas preservation in ethanol decreases prey weight through dehydration and solution of soluble tissue components. The concentration of ethanol determines the extent of dehydration of the tissue (Kruse and Dalley 1990) and the solubility of two tissue components. Carbohydrates and proteins are soluble in the lower alcohols and lipids are soluble in the higher alcohols (Winsor 1994).

The percentage change in weight of the prey after the both steps of preservation varied among the stages of digestion of the stomach contents. In the most digested prey (digestion stages 6 & 7), preservation reduced weight by a mean of 50%. This was three times more than the reduction in weight of group two (digestion stages 3, 4 & 5) and six times more than the least digested group (digestion stages 1 & 2) .

Two factors may account for the large weight reduction in the most digested prey. Firstly, individuals in this digestion group would absorb more preservatives than other prey because, highly digested prey are in smaller pieces and have a larger surface area to volume ratio. Secondly, measuring wet weights of highly digested prey may be more imprecise because it was difficult to remove similar proportions of surface liquid from the samples.

Although the weight of unpreserved prey was correlated with the standard length of coral trout, these weights were highly variable. The weights of the least digested (unpreserved) prey (digestion stages 1 & 2) varied more than the most digested prey (digestion stages 6 & 7). Although the mean effect of preservation on weights of prey was highest in the most digested prey (group three), it was put into perspective when the mean percentage reductions were converted into grams (Table 2.3). The mean change in weight of prey due to preservation was less than 3 g for all digestion stages (see 'mean change' in Table 2.3). Due to the high variability among the weights of unpreserved prey, 3 g was considered to be small.

In conclusion, the effect of preservatives on prey weight varied according to digestion stages. Overall, both steps of preservation used in this study reduced the fresh weight of the stomach contents by a mean of 22.9%. The effect of the preservatives on the fresh weight of the stomach contents ranged from a 12.3% increase (in digestion stages 1 & 2) to a 97.0% decrease (in digestion stages 6 & 7). Such a wide range of values implied problems of imprecision when measuring the weights, as the effect of preservatives was considered to be constant among prey at a similar digestion stage. As the wet weights of preserved stomach contents were found to be biased and probably imprecise, I considered whether or not they would be a useful measurement of prey bulk.

Wet weights of preserved prey provided valuable information about the bulk of prey because:

1. The range of fresh weights of prey was very large 0.03 - 151.45 g. Thus large differences in weight were detectable even when errors of measurement occurred, but comparisons among smaller prey items (< 5 g)

were less accurate;

2. Prey weights were compared in relation to weight of predator. Coral trout were weighed wet with a less precise balance than that used for prey, and this lowered the precision of the calculation.

The imprecision of the change in weight due to preservatives, however, precluded conversion of all the preserved weights into fresh weights. Therefore, the weights of preserved contents will be converted back to their fresh weight only when it is required to compare them with other weights of fresh stomach contents. In the majority of cases, preserved weights of stomach contents will be compared to fresh wet weights of whole coral trout which is permissible if the procedure is consistent throughout the study (Hyslop 1980).

2.3.4. Quantifying the digestion scale

2.3.4. Introduction

Digestion scales have several uses depending on the aims of the study. For example, information from the least digested prey only may be useful when examining feeding choices by the predator. Digestion stages could be used to restore undigested prey weights if they are an accurate and precise estimate of digestion in prey. When examining feeding times, the frequency of each digestion stage in the sample indicates whether the species feeds in discrete periods or continuously. If the rates of digestion are known, the digestion scale can be used to estimate the time the prey spent in the stomach, which can be used to calculate times of feeding (Fisher in press) or correlate feeding with environmental factors such as tides (Goeden 1974). Hobson (1965) determined the time required by the prey to reach a certain digestion stage. Digestion scales provide useful information to corroborate experimental data on feeding. When used alone, however, the digestion scale of each species should be evaluated quantitatively for every stage of digestion in the scale.

Digestion can be quantified when the undigested weight of the prey is known.

When digestion in prey cannot be quantified, qualitative digestion scales are used to classify prey into categories based on their degree of digestion. Each category (or stage) in digestion scales describes the physical appearance of the prey. Yet, no single category describes every digested prey item exactly because the physical appearance of prey items varies according to the number and the position of the prey in the stomach. When digested prey are on the border of two categories, the decision of the observer is most important.

This pilot study was carried out during summer and winter because stomach samples were collected throughout the year, and temperature of the water affects the rate of digestion in fishes (Kapoor *et al.* 1975). To quantify a digestion scale that was used throughout the study, I used some data from an experiment on seasonal digestion rates of captive coral trout (Chapter 4). This pilot study addressed two questions.

1. Does the qualitative digestion scale provide reliable estimates of the percentage of individual prey digested?
2. Can the digestion scale be used to estimate the amount of time that the prey has been in the stomach?

2.3.4. Methods

The experiment was done in large tanks (see Sect. 2.4) during February, March, August and September, 1992. The temperature of the seawater in the tanks during the experiments ranged from 21-31 °C. One *P. maculatus* and twenty four *P. leopardus,* ranging in size from 29.2 to 45.7 SL, were each offered a prey fish of known weight. Each coral trout was killed at a fixed period after the prey was eaten. The periods were 3 hours (n=1), 4 hours (n=1), 6 hours (n=7), 12 hours (n=6) and 24 hours (n=10). After death, the coral trout were processed immediately using the same methods as in Section 2.1.1, except that the stomach contents were weighed when fresh.

For this study, the essential information was the length of coral trout (SL in cm), the fresh weight and the digestion stage of each prey.

Percentage digestion was the difference between the undigested weight of the prey and the weight after digestion, expressed as a percentage of the undigested weight. I compared the percentage digestion (% reduction in weight) among five Stages of Digestion (3, 4, 5, 6 and 7) using one way analysis of variance (ANOVA). Prior to the analysis, homogeneity of variances was tested using Cochran's test and log transformations were carried out if required.

2.3.4. Results

The percentage of digested prey varied significantly in five of the seven digestion stages (Fig. 2.4). Digestion stage 5 had the highest variance as the percentage of digestion ranged from 39.19 to 59.17%.

Generally, the stage of digestion did not indicate accurately how long the prey had been in the stomach (Fig. 2.5, Table 2.4). For example, prey that had been in the stomach for 12 hours were classed into digestion stages 3, 5 and 6 (Fig. 2.5, Table 2.4). When a prey item had been in the stomach for 24 hours, it was either at the 7th stage of digestion or completely digested (digestion stage 8).

2.3.4. Discussion

Overall, the qualitative digestion scale provided good estimates of the percentage of prey digested. As n = 1 for digestion stages 1 & 2 combined, they are omitted from this discussion. The variances around the mean of each digestion stage varied: digestion stage 5 had the largest variance. Based on this small sample, Stage 5, appeared to provide the least accurate estimate of the percentage of prey digestion. As the mean percentages of each digestion stage differed significantly, each digestion stage could provide reliable estimates of restored weight. Undigested weights were not restored in this study because of problems with the accuracy of preserved weights (see Pilot Study 3, this Chapter 2.3). Multiplying values with error multiplies the errors.

The percentage digestion of prey in the stomachs of coral trout did not reflect uniformly the amount of time a prey fish had been in the stomach. The poor relationship between time in the stomach and digestion stage suggested that rates of digestion varied among individuals. The uncertainty of the results was compounded by the small size of the sample. Seasonal variation in digestion rates is discussed in Chapter 3.

The digestion scale could not be used to estimate the time of prey ingestion. Parts of the digestion scale, however, were accurate. All the prey items at digestion stage 7 had been in the stomach for 24 hours. Prey items at digestion stage 1 were newly ingested, thus coral trout with prey contents at digestion stages 1 and 7 fed at around the same time of day but on different days. This temporal relationship between the two digestion stages may clarify any correlations of feeding (using digestion stages) and time of day and tide.

One of the major problems with qualitative analyses is their reliance on the judgement of the observer. In this study, which was done over several years, I categorised every prey item. When I re-examined my earlier classification, some of the digestion stages differed by one digestion stage but no bias was obvious.

In conclusion, the qualitative digestion scale provided reliable estimates of the percentage of individual prey digested but it could not be used to estimate the amount of time that the prey had been in the stomach.

2.4 TANK EXPERIMENTS

2.4.1 Study sites

All experiments were carried out at Orpheus Island Research Station (18°40' S, 146°30' E), located on the landward side of Orpheus Island in the Palm Islands, north-west of Townsville. The research station has an extensive aquarium and seawater system which provides a continuous supply of filtered, aerated seawater and air to the tanks.

2.4.2 Collection of live predators and prey

Plectropomus leopardus and *P. maculatus* were collected from waters adjacent to Orpheus Island and Rib and Trunk Reefs (Fig. 2.6). Each fish was hooked by handline, hauled into the boat slowly and put into a 40 litre bin with circulated seawater for transportation to the research station. At Orpheus Is., coral trout were kept in circular tanks that varied in size. The smallest tank was about 3 m in diameter, 1.5 m deep and held around 4000 litres of seawater. Up to three individuals were kept in a tank. Dense 'shade-cloth' was laid over the tanks to maintain the temperature of incoming water, prevent coral trout from leaping out of the tank and to reduce the potential effect of external disturbances. The fish were offered either pilchards or squid every day.

Individuals of the planktivorous pomacentrid, *Acanthochromis polyacanthus* (Gill 1863), were caught in a cubic trap (about 45 cm each side) which was operated by a snorkeller. The trap was made of light gauge wire mesh (mesh size = 20 mm) and the inside of the trap was lined with a smaller mesh, either coarse plastic webbing (mesh size = 15 mm) or fine nylon mesh (mesh size = 2 mm), to protect the fish during capture. The trap was baited with pilchards in a fine nylon mesh bag, and positioned on coral substrata so that the lid laid open, downstream to the current. When squeezed, the bait bag released a plume of fine pilchard particles which enticed the planktivores inside. A long string, that was threaded through and attached to the lid of the trap, closed the trap quickly when pulled. If a capture occurred, the trap was hoisted to the surface in the same movement. The lid was opened above the surface, and the trapped fish were collected with a dip net and put into holding jars suspended under the boat. These traps were successful intermittently, with the largest catch rate being around 30 fish per hour per trap. The captured prey were kept in two small holding tanks (1.75 m x 0.7 m x 0.5 m) and fed mashed pilchards daily. After the first week in captivity, survivorship of *A. polyacanthus* was high despite repeated handling.

2.4.3 Problems associated with life in captivity

Coral trout

The rapid change in pressure during capture inflated the swim bladder of many, particularly the larger, coral trout. When this occurred the fish lost control of its buoyancy and, at rest, floated belly up at the surface. Over-buoyant coral trout could die from the exhaustion of trying to remain upright and beneath the surface when released into the tanks. Two actions overcame this buoyancy problem:

1. The swim bladder was punctured with a low gauge hypodermic needle to release the excess gas;
2. A roofed structure was made on the bottom of the tank. The coral trout was placed in the tank upright under the structure where it could rest until its body naturally adjusted to the change in water pressure. After 12 hours, the gaseous exchange through the circulatory system had corrected the size of the swim bladder.

I used the second method because it was least intrusive.

I considered a fish to have adjusted to captivity when it fed. While some coral trout never recovered from capture, most began feeding 3 to 21 days after capture.

In winter, some fish became infected with a fungus immediately after capture. These fish appeared stressed and did not feed. I treated the infected tanks with dissolved Copper Sulphate (0.012 g $CuSO_4$/L of seawater) and stopped the inflow of seawater for 24 hours. I repeated the treatment after 3 days. Although coral trout with minor cases of fungus were cured, some severely infected fish died, and I could not determine whether the Copper Sulphate treatment cured the fish.

Prey

During the first two days of captivity, a high proportion of *A. polyacanthus* developed 'fin rot', a very contagious disease. Although some fish were cured with a commercial fungicide preparation for marine fish, most sick fish died. Once a tank was contaminated, the disease spread to healthy fish. The occurrence of the disease appeared to be linked to their capture. Some fish damaged their skin and lost scales trying to escape from the trap, and all fish were stressed during capture and transportation. To reduce the initial incidence of fin rot, I tried different methods of holding the fish after capture and during transportation. The most successful method reduced the incidence of fin rot in prey from approximately 75% to 5-10% of the catch. Perforated jars (1 litre) which allowed water flow were kept in mesh catch bags. Captured fish were put directly into these jars and remained there throughout transportation until they were released into their holding tanks.

2.5. GENERAL ANALYSES

2.5.1 Analysis of frequency data

Chi Squared (X^2) Goodness of Fit and G-tests were used to compare frequency data in categories (Sokal and Rohlf 1981). Categories were pooled so that the expected values were >5 (Sokal and Rohlf 1981). When sample sizes were small or the data unbalanced, exact non-parametric tests for r * c tables were used (Mehta and Patel 1992). Fisher's Exact tests were used to compare frequency data when both data categories were nominal. Kruskal-Wallace tests (K-W) were used when one category was nominal and the other one was ordinal. Jonckheere-Terpstra (J-T) tests were used when categories on both were ordinal (Mehta and Patel 1992). Probability-values were calculated using exact methods for small data sets and Monte Carlo methods when the data sets were large and sparse. When Monte Carlo methods were used, 6000 tables were generated to estimate the probability value exceeding Manly's (1991) recommendations.

Kolmogorov-Smirnov (K-S) tests were used to compare two samples when the frequency data were continuous (Sokal and Rohlf 1981). Correlations were tested using the Pearson correlation coefficient.

2.5.2 Analysis of parametric data

Paired and independent t-tests or Satterthwaite t-test (when variances were unequal) were used to compare the sample means. For multiple samples, one way analysis of variance (ANOVA) or two way ANOVAs (block design (Winer 1971), or orthogonal and unbalanced) were used to compare the sample means. In all of the ANOVAs the factors were fixed. Post-hoc comparisons of means were done using Tukey's tests (Day and Quinn 1989). Linear regression was used when the data were continuous.

Two way analyses of covariance (ANCOVA), were used to compare means that had a covariate. When the data did not fulfil the assumption of "homogeneity of slopes" ((i.e. observed p {interaction between the covariate and the treatment} <0.25), Day and Quinn 1989) coefficients of the regression lines for each treatment group were compared using a t-test (Sokal and Rohlf 1981).

Prior to analysis of parametric tests, variances were tested for homogeneity using Cochran's test. When the data were heteroscedastic (Cochran's test was significant at $p<0.05$), appropriate transformations were carried out (see Underwood 1981). The data were then retested for homoscedasticity. For linear regressions, data were log transformed when not normally distributed (Wainwright 1988). If the null hypothesis was not rejected, the power of the test to detect specified differences was calculated following Cohen (1988). In the calculations of power, the sample means were assumed to be representative of the parametric means for each treatment group. The null hypothesis was considered to be true only if the power of the test (1-ß) >0.80. Otherwise a non-significant test was considered to be inconclusive.

2.5.3 Probability data

Probabilities and 95% confidence intervals were calculated for dietary data using the binomial distribution (trials = number of *P. leopardus*, successes = number of a certain prey class in the diet).

2.5.4 Indices of relative importance and dietary-overlap

Several measurements of stomach contents were used to describe the importance of prey species in the diet. Commonly used measures were developed for different purposes (see review by Hyslop 1980) and not all measures are appropriate for every study of diet. The best measure to describe the importance of prey categories in the diet depends on the particular diet as well as on the focus of the study. To avoid loss of information, different methods have been used to combine two or more measures into indices (see Macdonald and Green 1983). These indices of relative importance (IRI) are used commonly in studies of fish diets. They may not be necessary if one measure describes most of the relevant information (Macdonald and Green 1983). The measure used to describe the importance of prey in the diet needs to be justified for the particular study (Wallace 1981).

On their own, neither numerical nor proportional weight is the best measure of dietary importance for *P. leopardus*. Although *P. leopardus* have the capacity to eat up to 20 small prey daily, their stomachs usually contain single or few prey items. Furthermore, the size of prey of *P. leopardus* varies widely in size (total weights of undigested prey varied by three orders of magnitude, 0.33 - 560.3 g, Chapter 5). In *P. leopardus,* numerical analysis over-emphasises the small prey eaten in large numbers by a few predators, and analysis using proportional weights of taxa in stomachs only is unreliable because weights vary with digestion.

To determine the best measure to describe the importance of families in the diet of *P. leopardus*, I examined the association among three measures (numerical abundance, (digested) weight and percentage occurrence) using Pearson's Correlation coefficient. Zero values were omitted to avoid spurious correlations. If two measures accounted for less than 25% of the variation (i.e. $r^2 \leq 0.25$), they were included in the index. In Chapter 5, all three measures of each family in each season, % number (N), % weight (W) and % occurrence (O) were correlated (Pearson correlation coefficient N*W - r =0.488, N*O - r=0.939 and W*O - r=0.650). One pair of measures, N and W, was not highly correlated ($r^2 < 0.25$) and thus was used in the IRI. As IRIs are essentially a mean of the constituent dietary measures (Wallace 1981) the IRI used for the diet of *P. leopardus* was

IRI = 0.5 * (% prey number + % prey weight)

This IRI was used in Chapters 5, 6 and 7. In Chapter 6, the number and the total weight of prey in each family in each region were not correlated (zeros omitted, Pearson correlation coefficient = 0.170, Bartletts $X^2 = 0.944$, $X^2_{[1]}$ $p > 0.05$). In Chapter 7, total weight and number of prey in each family in each reef were highly correlated (i.e. $r^2 > 0.25$), but I used the same index because I wanted to compare diets of *P. leopardus* among the three different fishing zones. An absence of large numbers of 'Sporadic' prey probably contributed to the correlation of the two measures in these samples.

Schoener's (1970) index of dietary overlap (Schoener's *a*) was used to compare seasonal differences in the diet of *P. leopardus*, as recommended by Wallace (1981). This is appropriate when the relative abundance of prey is unknown. The IRI above was used in this index of dietary overlap. The value of any index of diet-overlap is strongly dependent on the measure used

(Wallace 1981). Dietary overlaps were classified using Langton's (1982) scale: low overlap 0-0.29, medium overlap 0.30-0.59 and high overlap ≥0.60.

2.5.5 Habitats of prey fishes

To classify prey of *P. leopardus* by their use of habitat, the reef environment was divided into four broad habitats: demersal and benthic reef substrata, midwater and soft sediments. Families of prey fishes were categorised by the habitat in which they were most commonly found. Fishes in the 'demersal reef substrata' habitat swim around and above coral but used the coral for shelter (e.g. Pomacentridae and Scaridae). Fishes categorised as using the 'benthic reef substrata' habitat are benthic dwellers, which remain very close to the substrata (i.e. Blenniidae and Tripterygiidae). Fishes categorised in the 'soft sediment' habitat dwell over, on or within the sandy areas among reefs. Fishes in the 'pelagic' or 'midwater' habitat live around coral reefs near the surface or in the midwaters (e.g. Clupeidae and Caesionidae).

Table 2.1 Stages of digestion in the digestion scale (modified from Goeden 1974).

1.	**FRESH**	Little or no digestion occurred, apparently recently ingested.
2.	**MINOR DIGESTION**	Digestion of surfaces (skin and fins) only. Accurate measurement of length possible.
3.	**MODERATE DIGESTION**	Head and tail mostly digested and prey item an oval lump of flesh showing myomeres. Measurement of length of prey is an estimate.
4.	**CONSIDERABLE DIGESTION**	Prey item broken down into pieces of bone and flesh larger than 1/4 of the size of the SL of the fish.
5.	**MAJOR DIGESTION**	Prey item broken down into pieces of bone and flesh smaller than 1/4 of the size of the SL of the fish.
6.	**ADVANCED DIGESTION**	Hard structures present among small fragments.
7.	**FINAL DIGESTION**	Small fragments only
8.	**STOMACH EMPTY**	Folds of stomach lining are clean.

Table 2.2 The number of coral trout classified into three categories based on the contents of their stomachs; empty, natural food only and bait. Coral trout were captured by three methods: commercial and recreational line fishing and by spear. Speared and line-caught catches of coral trout differed significantly in the type of food in their stomachs (two-sided Fisher's Exact test$_{[1]}$ = 50.67, $p \leq 0.01$) and in the proportion of empty stomachs (two-sided Fisher's Exact test$_{[1]}$ = 15.67, $p \leq 0.01$). In hook and line fishing, the catches by commercial and recreational fishers varied significantly in the proportion of coral trout with empty stomachs (two-sided Fisher's Exact test$_{[1]}$ = 5.50, $p \leq 0.007$), but not in the proportion of trout that contained natural prey (two-sided Fisher's Exact test$_{[1]}$ = 3.02, $p \leq 0.103$).

METHOD OF CAPTURE	**STOMACH CATEGORY**			**subtotal**	**TOTAL**
	empty	**natural**	**bait**		
SPEAR	57	114	1		172
LINE-commercial	34	36	25	95	
LINE-recreational	53	36	12	101	196

Table 2.3 An examination of the effect of the two preservatives on the fresh weight of prey contents. The mean fresh weight of each group of digestion stages was used to convert the percentage reduction in weight into grams.

GROUP	DIGESTION STAGES	MEAN FRESH WEIGHT in g	MEAN REDUCTION (%)	MEAN CHANGE in g
1	1 &2	26.51	8.97	2.38
2	3,4 &5	15.77	16.27	2.56
3	6 &7	2.40	50.36	1.21

Table 2.4 The mean percentage weight of prey digested for each digestion stage in the scale. The duration of digestion (hours in stomach) and the size of the sample is recorded.

DIGESTION STAGE	MEAN DIGESTION (% reduction in weight)	DURATION OF DIGESTION (in hours)	SAMPLE SIZE
1	14.03	3	1
2			
3	18.12	4, 6, 12	4
4	29.80	6	4
5	48.64	6, 12	4
6	65.35	12, 24	4
7	91.23	24	7
8	100.00	24	1

Figure 2.1 The percentage of the sample in each digestion stage for two groups: those processed immediately and those processed two to eight hours after capture. See Table 2.1 for definitions of digestion stages.

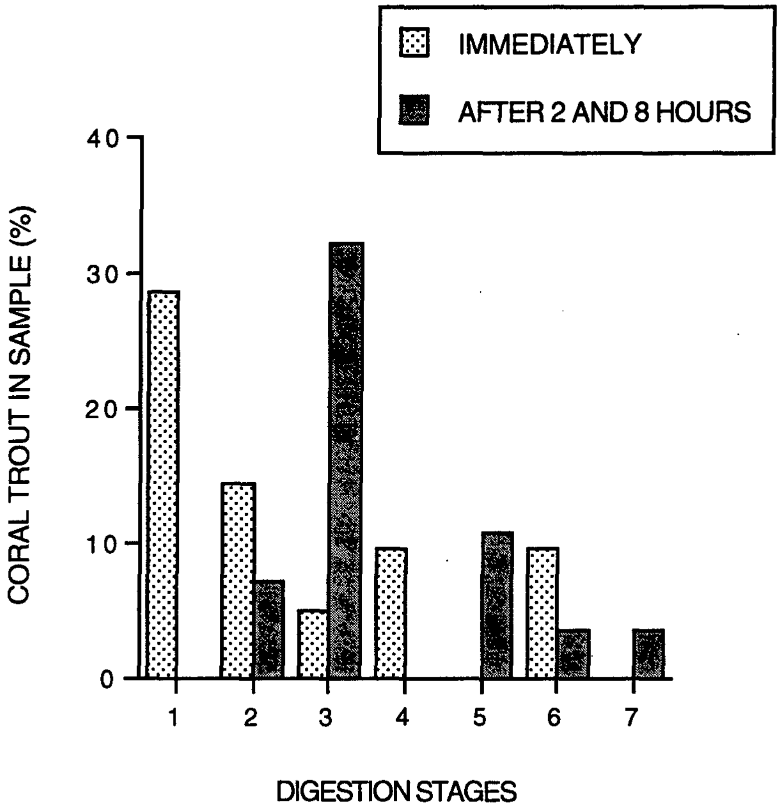


Figure 2.2 Scatter plot of the weights of unpreserved prey in the three groups of digestion: digestion stages 1 & 2; digestion stages 3, 4 & 5; and digestion stages 6 & 7. The weights of unpreserved prey were positively correlated to standard length of the predator (Bartlett's $X_{[1]}^2$ statistic = 21.916 p<0.01).

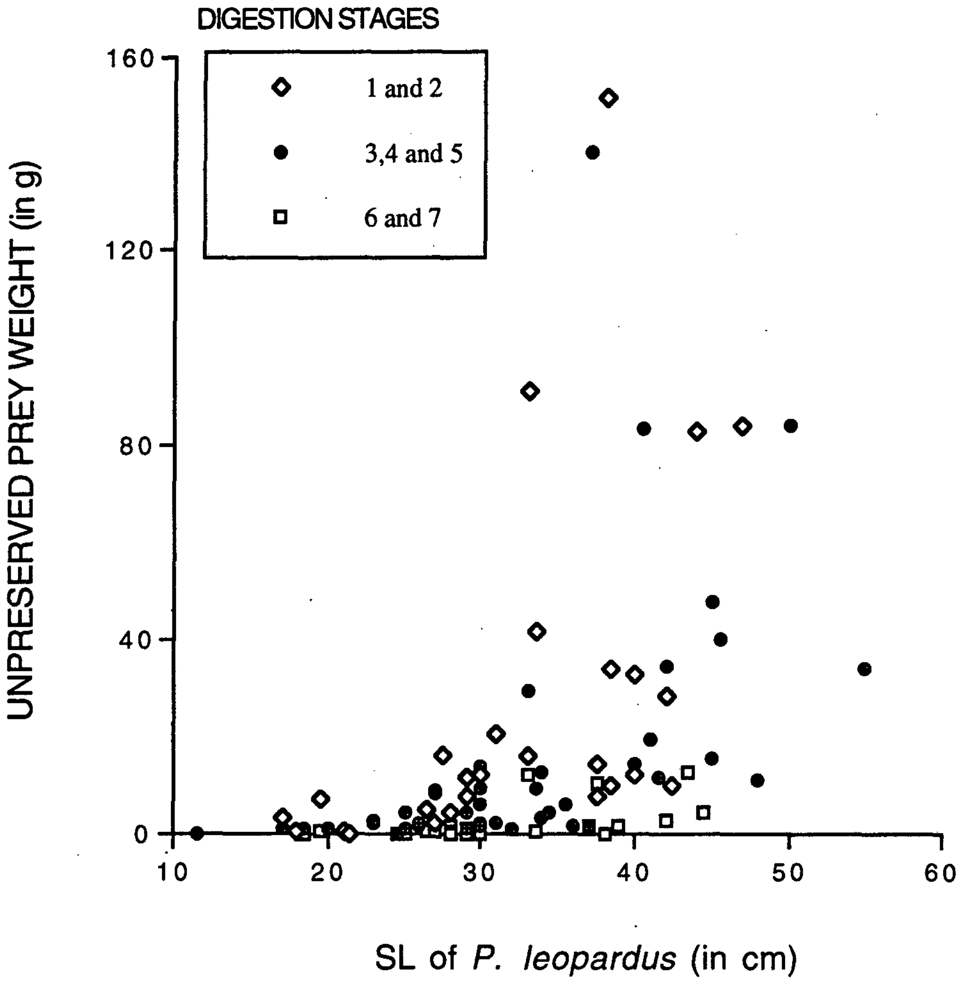


Figure 2.3 The raw mean (and pooled SEs) percentage reduction in weight after preservation of the three groups of digestion: digestion stages 1 & 2 (group 1), digestion stages 3, 4 & 5 (group 2) and digestion stages 6 & 7 (group 3). Percentage reduction in weight varied significantly among the three groups (one way ANOVA $F_{[2,91]}=25.75$, $p<0.01$, data $\log_{10}$ transformed). Group 1 did not differ significantly from group 2 (Tukey's $p = 0.536$) and group 3 differed significantly from the other two groups (Tukey's $p < 0.001$ for comparisons between groups 1 and 2, and groups 1 and 3).

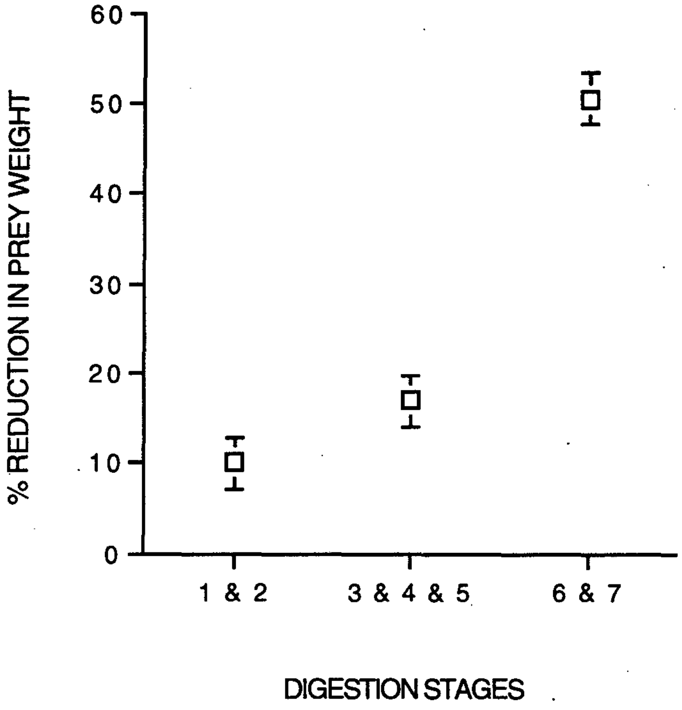


Figure 2.4 The mean percentage (and pooled SEs) of prey digested in digestion stages 3, 4, 5, 6 and 7. Both digestion stages 1 and 8 have a single value, and were not included in the analysis. The percentage of prey digested varied significantly among the five digestion stages (one way ANOVA $F_{[4,17]}=134.3$, $p<0.01$, data $\log_{10}$ transformed).

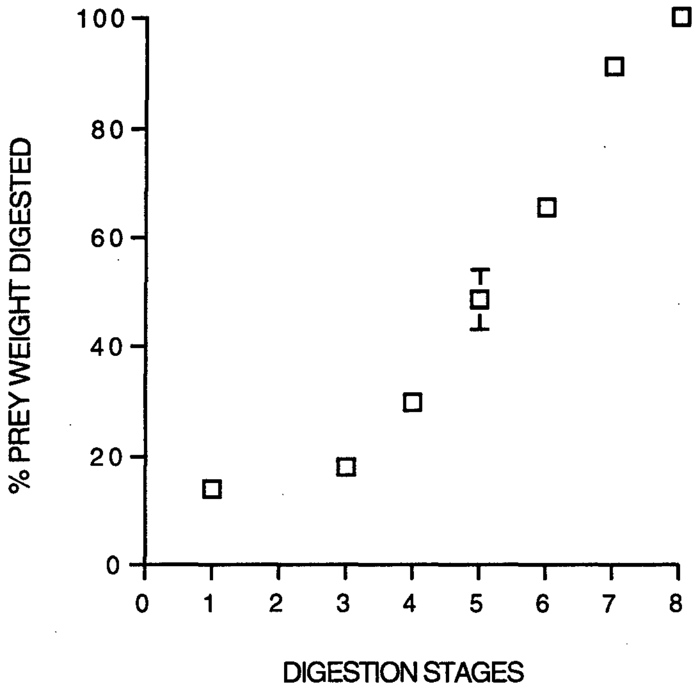


Figure 2.5 The digestion stage of prey after digestion for 3, 4, 6, 12 and 24 hours.

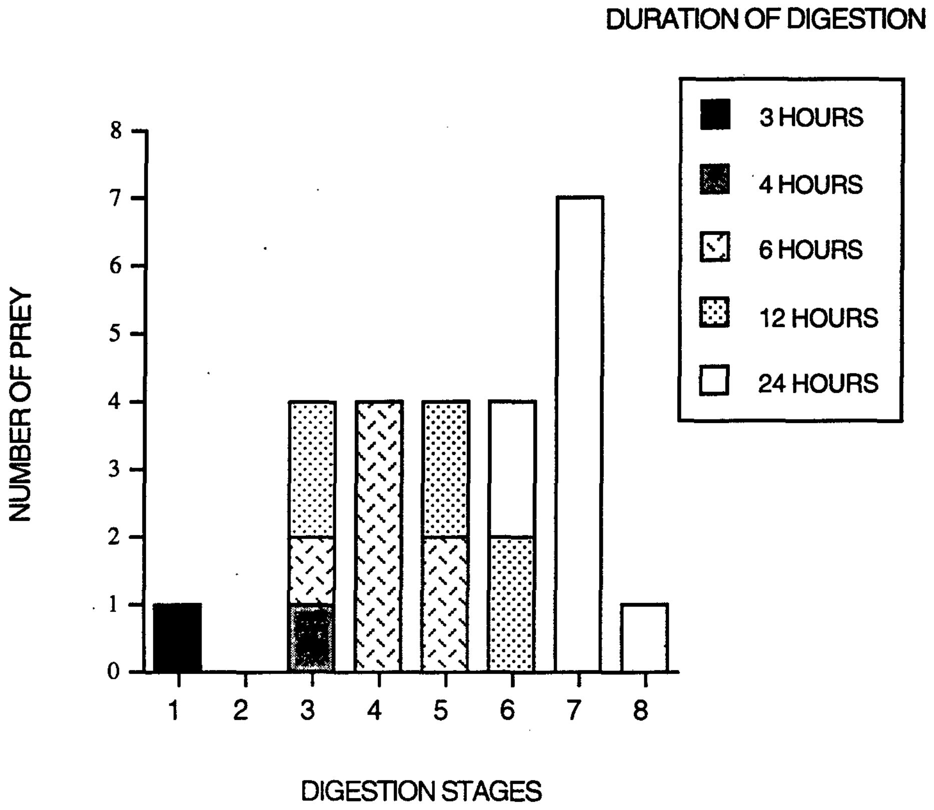
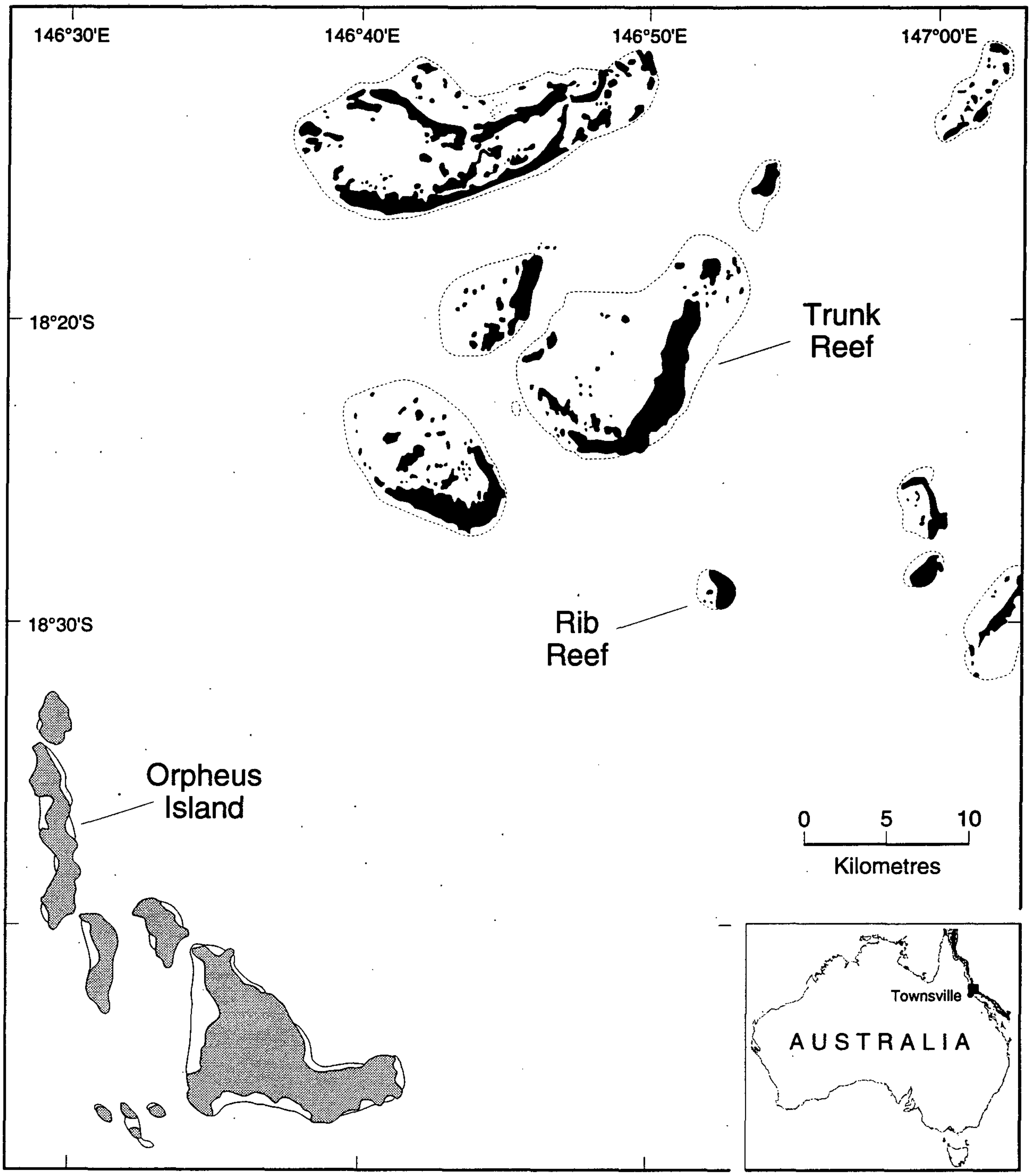


Figure 2.6 A map showing the proximity of Rib and Trunk Reefs to Orpheus Island, where tank experiments were done.



CHAPTER 3

3.0 SEASONAL RATES OF DIGESTION, DAILY CONSUMPTION OF FOOD AND GROWTH IN CAPTIVE *P. leopardus*

3.1 INTRODUCTION

Daily food ration is an important component of feeding and energetic studies as it influences the amount of energy available for growth, reproduction and maintenance of the individual fish (Sainsbury 1986). Daily ration is used in individual and multispecies fishery models to determine the effect of a population of predators on populations of both prey and competitors (Sainsbury 1986). Thus seasonal variations in daily food consumption have a potential impact on fishery models. Even though water temperature fluctuates seasonally and consumption rates of food in some tropical fishes are related to water temperature (Menzel 1960), seasonal differences in consumption rates of food by fish have rarely been considered (but see Gladstone 1988).

Temperature is a basic factor determining rates of gastric digestion in fishes (Kapoor *et al.* 1975). Rates of digestion have been compared among fishes from cold, temperate and tropical waters (Tseitlin 1980). Predatory, tropical fishes have higher rates of digestion than do fishes of middle and high latitudes (Reshetnikov *et al.* 1972) but seasonal differences have not been examined. Also, the rate of digestion in freshwater piscivorous fish varies according to water temperature (Elliot 1991). Seasonal differences in digestion are related to seasonal differences in water temperatures. In winter, the rate of digestion in several cold water, predatory species of fish is decreased due to lower water temperatures (Popova 1967; Fortunatova and Popova 1972). When seasonal temperatures were similar, however, there were no seasonal effects on rates of gastric evacuation in the cod, *Gadus morhua* (Santos and Jobling 1991).

Water temperature does not only affect rates of digestion in fishes. Consumption of food and growth also have been related to water temperatures. In a tropical serranid, *Epinephelus guttatus*, the amount of food eaten and the relative weight gain increased markedly when water temperatures increased from 23 °C to 28 °C (Menzel 1960). Furthermore, consumption of food is related to growth rate (see Elliot and Persson 1978). On coral reefs, growth in small fishes increased when food availability increased (Jones 1986; Eckert 1987; Forrester 1990). The few studies that have examined seasonal growth in small coral reef fishes found that growth rate was higher in summer than in winter (Jones 1986; Gladstone and Westoby 1988; Mapstone 1988; Booth 1991 cited in Booth 1995) which corresponds to the period of highest temperatures.

Seasonal variations in water temperature influenced the amount of prey consumed by a predator in a bog-lake community (Reimchen 1990). A large proportion of the annual consumption of prey (65%) occurred in summer where sticklebacks, *Gasterosteus aculeatus*, were the major diet of the trout *Oncorhynchus clarki* (99.5%, Reimchen 1990). As sea water temperatures vary seasonally on the GBR, piscivorous fishes may have seasonal rates of predation. There are no studies on seasonal rates of piscivory on coral reefs fishes since the few studies on predation have focused on new recruits and thus were restricted to summer (Doherty and Sale 1985; Martin 1994). One study which examined seasonal feeding found that the feeding rates of *Canthigaster valentini* varied seasonally (Gladstone 1988).

In this study seasonal variations in the rates of digestion, consumption of food and growth of *P. leopardus* were examined in tank experiments. The specific questions addressed are -

Does consumption of food in coral trout vary seasonally?

Are meals digested faster in summer than in winter in coral trout?

Does growth in coral trout vary seasonally?

3.2 METHODS

The study is divided into three sections: daily consumption of food; rate of digestion of food; and growth rates of *P. leopardus* in tanks. The methods of statistical analysis for all three of these sections are described in Section 2.5.

3.2.1 Daily consumption of food

Experiment

In the summer of 1991-92 and the winter of 1992, a five-day feeding trial on captive coral trout determined the quantity of food eaten by 11 *P. leopardus* ranging in size from 32.2-45.7 cm SL. Coral trout were kept in tanks (see Section 2.4) for more than one week prior to the feeding experiments to habituate them to captivity. As feeding in captivity indicated that the coral trout were healthy and not stressed, the experiment began if the coral trout had been feeding in the previous week. Individual fish varied in their eating habits. Some coral trout fed daily on small quantities while others ate large quantities every second or third day. Thus feeding was measured over 5 days to obtain an average daily ration. Feeding experiments on individuals began the day after an individual had fed. The coral trout were offered several pieces of prey (WA pilchard) of known weights twice daily (morning and evening). The uneaten food was removed from the tank after one hour and the food consumed was recorded. Where tanks had more than one coral trout, feeding by individuals was watched and if there was any uncertainty about the food consumed by each coral trout, the experiment was rerun. All feeding experiments ran for five consecutive days.

Data used in analyses

The total weight of prey consumed was converted to an average daily feeding rate of grams.day^{-1}. The meal weight was standardised into grammes per 100 g body weight per day (Menzel 1960).

Comparison with field data

Consumption of food was estimated by direct measurement of the food consumed by fish held in laboratory conditions. As tanks do not necessarily represent natural conditions, feeding in captivity may vary from natural feeding in at least two fundamental ways: in the frequency of feeding and in the weight of ration (or meal-size). As natural feeding by *P. leopardus* is very difficult to measure (see Goeden 1974; Samoilys 1986), the frequency of feeding could not be compared to rates of feeding in the field. The size of meals in captivity were compared to the natural meal-sizes of *P. leopardus*, which came from the stomach contents of all *P. leopardus* (see Chapter 4) that fitted three criteria:

1. the size of *P. leopardus* fell within the size range of the captive coral trout;
2. the stomach of the *P. leopardus* contained a single prey item (or prey items which weighed more than 70% of the total weight of the stomach contents);
3. the prey item was undigested (digestion stages 1 or 2, see Chapter 2).

All meal-sizes were standardised by the size of the coral trout and expressed as the percentage body weight of predator. When the weight of coral trout was unknown, it was estimated using the length-weight relationship for *P. leopardus* in Chapter 4. For the experiment, the percentage body weight was calculated from the maximum meal-size consumed at any one feeding period during the five days. Maximum meal-size was used because the meal-size of wild coral trout was limited to larger prey items only (large (weighing >70% total weight of the stomach contents), single, undigested prey items). The samples from the field and the experiment were pooled over seasons.

3.2.2 Rates of Digestion

Preliminary Trials

To examine digestion in coral trout, I needed to obtain the contents of the stomach after digestion had occurred. Two methods to remove digested food from the stomachs of live *P. leopardus* were attempted so that the predator could be reused in experiments. As most *P. leopardus* vomit their stomach contents after they are captured, I tried to stress fishes to induce them to regurgitate. Captive *P. leopardus* were placed separately in a 20 L plastic bin with and without the anaesthetic Quinaldine for up to 30 minutes. During this time the fish could see the experimenter and although every *P. leopardus* showed the mottled colouration of stress, none regurgitated their food. The second method was to flush out the stomach contents of anaesthetised fishes by inserting a rubber tube into the stomach, but this method injured the fish. As both methods were unsuccessful, I killed each fish at the end of each digestion period and thus, the sample size of the experiment was reduced drastically to n=24.

Experiment

The rate of tissue breakdown of prey during digestion by *P. leopardus* was determined by experiments in tanks during late summer (February and March 1992) and late winter (August and September 1992). The aquarium system was described in Section 2.4. The water temperature in the tanks was measured during experiments with max-min thermometers and the temperature range was recorded at the end of each experiment. *Plectropomus leopardus* were starved for at least 24 hours prior to the experiment to ensure there was no other food in their stomachs. Intermittent feeding, where the predator digests all or most of its prey before consuming another prey item, is a natural feeding pattern in *P. leopardus* as approximately 30% of fish in any sample have empty stomachs (Chapter 2).

A total of twenty four captive *P. leopardus,* ranging in size from 29.2 to 45.7 cm SL, were offered a single prey fish of known weight and were killed a fixed period (6, 12 or 24 hrs) after the prey was eaten. Some predators had a limited choice of prey size because they were offered different fish on several occasions. One of the larger *P. leopardus* ate two pomacentrids during the experiment. Predators were processed immediately after death using the same methods given in Section 2.2, except that the stomach contents were weighed when fresh. One *P. leopardus* vomited during recapture and was used twice (with more than one week between experiments). The experiments began at haphazard times throughout daylight hours as *P.*

leopardus do not feed at night (Goeden 1978).

Plectropomus leopardus were allowed to digest their prey for one of three different time periods: 6 hours (n=2 for summer and n=5 for winter), 12 hours (n=3 for summer and n=3 for winter) and 24 hours (n=4 for summer and n=5 for winter). Two additional times, three hours (n=1) and four hours (n=1), which were used in an initial trial in the summer were included in the analysis. Each individual *P. leopardus* was assigned randomly to its time period.

Two types of prey were used in the experiment because some *P. leopardus* would not eat the pomacentrid prey offered during the experiment. During their period of captivity, these fish appeared to have become accustomed to feeding only on their staple diet, Western Australian pilchards. Although the main prey used in the experiment were two species of Pomacentridae, *Amblyglyphidon curacao* and *Acanthochromis polyacanthus*, four *P. leopardus* in summer and seven *P. leopardus* in winter consumed pilchards for this experiment. All prey were dead when they were fed to the *P. leopardus*.

Data used in analyses

The amount of digestion of the prey was calculated by determining the difference between the weight of the undigested prey and the weight after digestion, and was expressed as a percentage of the undigested weight.

As several factors, which were known to affect the rate of digestion in fish, were not constant in the experiment, the size range of *P. leopardus*, the weight of the two prey types and the temperature of the water in the tanks between the two seasons were compared. The range of the water temperature in the tanks was measured during each experiment and the median temperature was used to calculate seasonal means.

3.2.3 Growth rates of captive *P. leopardus*

Experiment

Plectropomus leopardus were measured (FL and SL in cm) when captured and placed in tanks. All coral trout were offered food twice daily and the uneaten portions were removed approximately one hour after feeding. Individual coral trout were remeasured after a period of captivity and these measurements were used to calculate monthly (31 day) growth of individuals.

Growth was measured after 32 to 79 days of captivity in summer and 24 to 42 days in winter. To reduce errors in growth estimates from unquantified errors in measuring, the fish was removed from the analysis if its two measurements of growth (using FL and SL) differed greatly (more than 100%).

To determine whether growth in tanks was artificially high, rates of growth in captive *P. leopardus* were compared to natural rates of growth from two sources, tagging (Davies 1995) and length frequency data (Ferreira and Russ 1995). Growth was calculated from the length frequency data of populations of *P. leopardus* collected from reefs off Townsville using Von Bertalanffy growth parameters (for fish > age 2 , $L_\infty = 68.274$, $K=0.106$, $t_0 =$ -4.131, Ferreira and Russ 1995). FL was converted to SL using the formula $SL = 0.308 + 0.852\ FL$ (Brown *et al.* 1994).

3.3 RESULTS

3.3.1 Daily consumption of food

The meal-size expressed as a percentage of predator weight did not differ between captive and wild coral trout (Fig 3.1). The experimental mean was slightly higher than the field mean because maximum meal-size (rather than average meal-size) was used in the analysis.

The average food consumed daily varied between summer and winter (Fig 3.2). *Plectropomus leopardus* consumed 50% more in winter than in summer (winter mean=32.1 g, summer mean=20.7 g). The range of daily food consumption was wider in summer (8.58 - 37.1 g) than in winter (25.95 - 37.19 g, Table 3.1). Individual variation in food consumption was high in summer and the maximum prey ingested in one day ranged from 20.3 g to 73.6 g. The number of prey *P. leopardus* fed on daily ranged from none to three prey items.

Plectropomus leopardus were intermittent feeders as no coral trout fed every day during the five day experiment. Coral trout that fed most frequently in the experiment ate on three of the five days. The pattern of daily feeding varied among individuals, with some coral trout feeding on consecutive days while others fed on alternate days. Consumption of food was not related to size of coral trout (Fig 3.3), and the largest mean ration was eaten by one of the smallest fish (Fig 3.3)

3.3.2 Rates of Digestion

The size structure of the *P. leopardus* used in the digestion experiment did not differ between seasons (Dmax = 0.250, K-S $p>0.05$) nor among the three treatments of the experiment: six, 12 and 24 hours of digestion (three comparisons of K-S were $p>0.05$, 6-12 hr Dmax = 0.095, 12-24 hr Dmax = 0.222, 6-24 hr Dmax = 0.222).

The weight of the two types of prey fish fed to *P. leopardus* differed significantly between seasons (Table 3.2). The lowest and highest mean prey weight occurred in summer, where the average weight of pilchards consumed was approximately twice the weight of the pomacentrids (Table 3.3). In winter, weights of the two types of prey were similar. The length of each *P. leopardus* (SL) and the weight of prey it consumed was positively correlated because larger fish ate larger prey (Fig. 3.4).

The temperature of the seawater in the tanks during the experiments ranged from 22-31 ^{o}C in summer and 20-27.5^{o} C in winter. Overall, the mean temperature of the tanks was four degrees lower in winter (mean = 24.73, SE

=0.384) than in summer (mean=28.47, SE=0.424, $t_{[18]}=6.586$, $p<0.01$).

The rates of digestion of the two types of prey fish appeared to differ in winter but not in summer, but these results are tentative because sample sizes are very small (Fig. 3.5). Digestion of pomacentrids appeared to be slower in winter than in summer, with the largest difference after 12 hours of digestion. Digestion rates of pilchards were similar between seasons. Weight and type of prey could explain these results because there were significant seasonal differences in the relative weights of the two types of prey (Table 3.2). After 24 hours of digestion there were no detectable differences between seasons or between prey type, when the weight of the prey was considered (Table 3.4). In summer, a mean of 92.21% of the prey was digested after 24 hours of digestion compared to 84.19% in winter.

3.3.3 Growth rates of captive *P. leopardus*

Although growth rates (cm SL.month^{-1}) of individuals appeared to be mostly lower in winter, there was no detectable difference in monthly growth between seasons (Fig 3.6). Growth rates varied greatly among individuals, and rate of growth was not related to length when seasons were combined (Fig 3.7). Growth estimated from natural populations of *P. leopardus* on reefs off Townsville (Ferreira and Russ 1995) were generally lower than growth rates of captive *P. leopardus* (Fig 3.7). For a similar size range of *P. leopardus*, mean growth was estimated to be 0.217 cm per month for natural populations from reefs off Townsville compared to 0.421 cm per month in captive fish.

3.4 DISCUSSION

An increase in water temperature did not lead to an increase in daily food consumption in *P. leopardus.* In fact, the reverse occurred. Relationships between temperature and consumption of food differ among studies (Menzel 1960; Caddy and Sharp 1980; Palomares and Pauly 1989; Reimchen 1990). Some studies have found seasonal differences in the consumption rates of prey (Reimchen 1990) related to temperature (Menzel 1960). Other studies did not link food consumption to temperature (Palomares and Pauly 1989; Caddy and Sharp 1980). Maintenance rations in the tropical piscivore, *Lutjanus russelli*, decreased at higher temperatures (Smith *et al.* 1991)

The annual spawning cycle may account for the seasonal difference in food consumption by *P. leopardus*. From April to August male and female *P. leopardus* lay down mesenteric fat, which is converted into gonads by October (Ferreira 1993). *Plectropomus leopardus* reproduce throughout spring (September- November, Ferreira 1993). Variations in seasonal growth support this interpretation because despite a 50% increase in daily food consumption in winter, rates of growth (in length) appeared to be lower. Growth rates of captive *P. leopardus* were highly variable and probably not very precise due to errors in measuring and the short duration of the growth period.

The apparent seasonal patterns of growth in *P. leopardus* were similar to other coral reef fishes. Growth in wild populations of two small pomacentrids, *Pomacentrus moluccensis* and *Pomacentrus amboinensis,* and another small reef fish *Canthigaster valentini* was lower in winter than in summer (Jones 1986; Mapstone 1988; Gladstone and Westoby 1988). The present study is the first to suggest seasonal differences in growth rates of a large tropical piscivore on the GBR. Evidence from other studies on wild populations suggest that *P. leopardus*, like all fish, follow the decaying exponential model of growth and smaller *P. leopardus* grow faster than larger fish (Ferreira and Russ 1994; Davies 1995). In this study there were no size-related differences in growth but it was not designed to test such differences.

The expected effect of rates of digestion on consumption of food was not apparent. Rate of digestion appears to be independent of feeding because *P. leopardus* has an intermittent feeding pattern. This was observed in the tank feeding experiment where *P. leopardus* were offered food twice a day but did not feed daily. Also, wild coral trout have periods of starvation as over 30% of *P. leopardus* have empty stomachs (Chapter 2). Sainsbury and Jones (unpubl. ms) also concluded that higher digestion rates in tropical fishes do not result in higher food rations.

After 24 hours, *P. leopardus* had digested 92.2% of the prey in summer compared to 84.2% in winter. Kingsford (1992) estimated from stomach content analysis that *P. leopardus* digested a prey item in 1 to 1.5 days, based on one observation, but he did not specify the season. Rates of gastric digestion increase with temperature in both tropical piscivores and freshwater trout (Reshetnikov *et al.* 1972; Elliot 1991). The digestion rates of *P. leopardus* were similar to those of tropical lutjanids, which digested 85-95% of the food within 24-33 hours at a temperature of 28-29.5 ^{o}C (Reshetnikov *et al.* 1972). Seasonal differences in energetic gain from food would be unlikely because temperature does not affect the absorption rate of food (Menzel 1960).

The seasonal difference in digestion rate of *P. leopardus* was small (10%) and statistically inconclusive due to the low power of the test. Furthermore, seasonal patterns of digestion of the two types of prey appeared to vary, but may represent variations in prey weight rather than differences in rates of digestion. The results were difficult to interpret because of high variations in the digestion rates, small sample sizes and seasonal variability in the weight of the pomacentrid prey. For example, in the 24 hour sample of pomacentrid prey, the smallest (weighing 18.5 grams) was completely digested, whereas 65.1% of the largest (weighing 56.7 g) was digested. These two replicates increased the variance around the mean and thus, small changes in the seasonal rates of digestion were difficult to detect.

Digestion studies on tropical and freshwater fishes, that examine factors affecting rates of digestion, have produced conflicting results. Although digestion rates of tropical piscivorous lutjanids were affected by type of prey, meal-size and predator size (Reshetnikov *et al.* 1972), none of these factors influenced digestion in freshwater trout (Elliot 1991). Elliot (1991) attributed the different conclusions of various studies on freshwater fishes to the use of wet or dry weights of prey in the analyses of digestion studies. Despite the inconclusive results, this experiment suggested that the rate of digestion by *P. leopardus* may be affected by the type and weight of prey as well as water temperature. Digestion rates were not affected by predator size but this may have resulted because larger fish were fed larger prey. The two prey types varied morphologically. Pomacentrids have large, thick scales that would hinder digestion initially whereas pilchards have small, fine scales. Delicate clupeids, *Jenkinsia lamprotaenia*, were digested almost twice as fast as the sardine *Harengula sp.* by tropical lutjanids (Reshetnikov *et al.* 1972).

Plectropomus leopardus were intermittent feeders and did not feed every day. This type of feeding has not been documented in large tropical piscivores. Growth rates of *L. russelli* fed daily or twice daily in captivity were similar to growth rates in the wild which might suggest that this carnivore feeds daily in the wild (Smith *et al.* 1991). In another large tropical piscivore, the skipjack tuna (*Katsuwonus pelamis*), fish did not fill their stomach at the first, second or third feeding but filled their stomachs slowly over a two hour period (Magnuson 1969).

The mean meal-size of wild and captive *P. leopardus* was between three and four percent of their body weight.day^{-1} which was similar to that of other large tropical predators. When fed on pilchards, maintenance rations of the lutjanid, *L. russelli,* were an average of 3.8% of their body weight.day^{-1} at 26.4 ^{o}C (Smith *et al.* 1991). The serranid, *Epinephelus striatus,* ingested on average 3.6% of their body weight.day^{-1} (Reshetnikov *et al.* 1972).

The tank environment may have influenced the results of these experiments. Daily water temperatures in the large outdoor tanks used in the study fluctuated more than the daily temperature of the sea. The mean difference between seasonal water temperatures in the tanks was only 4 °C as seasonal temperatures overlapped considerably. At Orpheus Is. the mean natural surface water temperature ranged 8 °C annually (Lee pers. comm.). Seasonal rates of digestion may vary more in natural populations of *P. leopardus* where water temperatures have smaller seasonal ranges yet differ more between seasons. Seasonal rates of digestion in populations of *P. leopardus* at different latitudes on the GBR may vary because of differences in the temperature of seawater. *Plectropomus leopardus* in the southern waters of the GBR would experience colder temperatures during winter and summer than those in central or northern waters.

Seasonal variation in consumption and growth in captive coral trout may be higher than in natural populations because the availability of food was higher in the tanks. The frequency of feeding by captive *P. leopardus* is difficult to compare to natural feeding rates, which are rarely seen or measured (see Goeden 1974; Samoilys 1986). Feeding rates by captive *P. leopardus* were considered to be fairly similar to natural feeding rates on reefs because captive *P. leopardus* did not feed regularly and their meal-size fell well within the range of meal-sizes acquired naturally. Captive *P. leopardus* grew approximately twice as fast as tagged individuals in the field (Davies 1995) and natural populations of *P. leopardus* on reefs off Townsville (estimated from Ferreira and Russ 1995) . This result is not surprising. Growth of *P. leopardus* in tanks is expected to be higher because the coral trout were offered excess food and restricted in their movement. Furthermore, growth in tagged fish is expected to be lower because of the stress of capture and tagging (Davies pers. comm.). The two studies that measured growth in individuals, the feeding experiment and the tagging study, both found high variations in growth within populations of *P. leopardus* .

Offering *P. leopardus* food twice daily in the experiment was considered adequate because *P. leopardus* eat the majority of their daily ration in a single gulp (more than 50% of *P. leopardus* that had fed had one prey item in their stomach see Chapters 4, 5, 6 and 7) and digest most of their prey within one day. Thus the opportunity to feed twice daily allowed individual fish to feed on either a partially full stomach (if they had fed in the previous time of feeding) or on an empty stomach

The seasonal difference in food consumption in this study suggests that *P. leopardus* may eat up to 50% more individuals in winter than in summer. If this is the case, then *P. leopardus* have the potential to have a greater impact on prey in families that are eaten mostly in winter, particularly if their abundance is low and doesn't fluctuate annually (e.g. *Canthigaster valentini* Gladstone pers. comm.). Adult individuals in these families may have a higher risk of predation in winter than in summer. Effects of seasonal variation in predation rates are discussed in Chapter 5.

There are few studies on digestion rates of large tropical fishes because large predators require large tanks with temperature control. The few studies on digestion in tropical fishes have had differing results. Clearly, more studies are needed before generalisations, if any, can be made about seasonal feeding and digestion in tropical piscivores, and seasonality in predation.

As *P. leopardus* feed rarely, detailed information on the diet and some aspects of feeding of this large predator can only be collected by stomach content analysis. The conclusions about feeding of *P. leopardus* in this chapter provide a better understanding and interpretation of the stomach contents collected in the field. In addition, these results point to potential variations in the diet of this predator and potential problems in the sampling. Information on rate and duration of digestion provides an accurate feeding period for the dietary information. Every stomach of *P. leopardus* represents a 24-hour history of feeding prior to capture and an empty stomach indicates that this piscivore has not fed for at least 24 hours. Seasonal variation in the consumption of food suggests that the diet of *P. leopardus* may vary seasonally, and thus, the seasonal composition of the diet of *P. leopardus* on

Broadhurst Reef will be examined in Chapter 5. There would be no expected seasonal differences in field collections of stomach contents because digestion rates between seasons are similar. Finally, the switching of several captive *P. leopardus* to feeding on pilchards only, and the potential different rates of digestion of the two types of prey fishes, indicate that feeding by *P. leopardus* may change on re efs where line fishing occurs.

Table 3.1 Seasonal daily consumption of prey in weight measured over five days in individual *P. leopardus* (SL in cm).

SUMMER		WINTER	
SL	**gram/day**	**SL**	**gram/day**
42.5	31.14	33.4	37.19
32.2	30.16	34.5	31.95
36.2	29.62	38.6	32.18
39.2	16.41	45.7	25.95
33.9	14.20		
32.9	14.42		
32.2	8.58		

Table 3.2 Mean weights in grams (and standard errors) of the two types of prey, pomacentrids and pilchards, fed to experimental *P. leopardus* during summer and winter.

PREY TYPE	SUMMER	WINTER
Pomacentridae	21.44 (3.77)	34.57 (4.46)
pilchards	43.10 (4.99)	27.90 (3.77)

Table 3.3 Two factor ANOVA of the weight of prey (in grams) consumed in the experiment. The treatments are season (summer and winter), prey-type (pomacentrids and pilchards). 'ns' is non significant at $p>0.05$.

Source	df	SS	MS	F	*P*
Season	1	5.848	5.848	0.059	ns
Prey Type	1	305.24	305.24	3.066	ns
S*PT	1	1090.8	1090.8	10.957	p<0.05
Error	19	1891.4	99.55		

Table 3.4 Two factor ANCOVA of the digestion in prey $((W_1-W_2)/W_1)$ after 24 hours (data is log$_{[10]}$ transformed). The treatments are 'season' (summer And winter), 'prey-type' (pomacentrids and pilchards) and 'undigested weight of prey' is the covariate, 'ns' is non significant at $p>0.05$. After 24 hours, there was no detectable differences in the weight of the digested prey between seasons or prey type, when the undigested weight of prey was considered ($1-\beta = 0.39$).

Source	df	SS	MS	F	*P*
Season	1	0.024	0.024	1.336	ns
Prey Type	1	0.020	0.020	1.116	ns
S*PT	1	0.011	0.011	0.597	ns
Weight	1	0.047	0.047	2.654	ns
Error	3	0.053	0.017		

Figure 3.1 Mean (and SE) of maximum meal-size expressed as a percentage of body-weight of *P. leopardus* in the field and in the experiment. There were no detectable differences in the meal-size of captive and wild *P. leopardus* ($t_{[129]}$=-0.767, p>0.05, 1-β = 0.04).

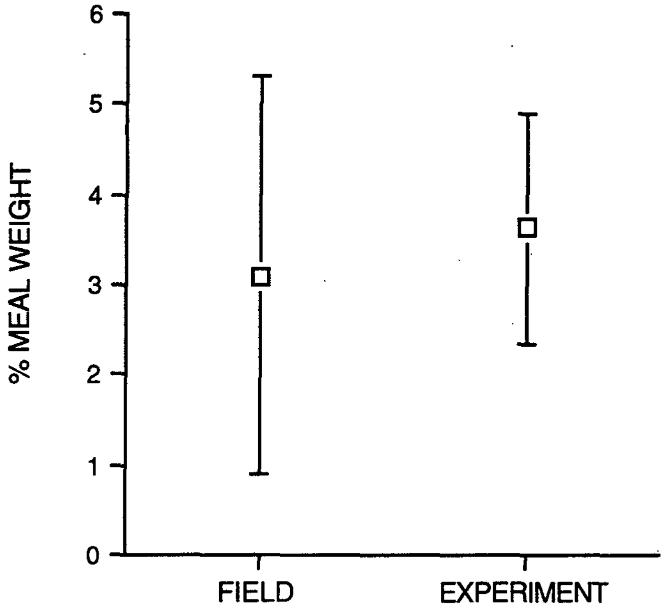


Figure 3.2 Seasonal means (and SE) of food consumed on a daily basis (in grams.day^{-1}) by captive *P. leopardus*. The average food consumed daily varied between summer and winter ($t_{[9]}$=-2.692, p<0.05).

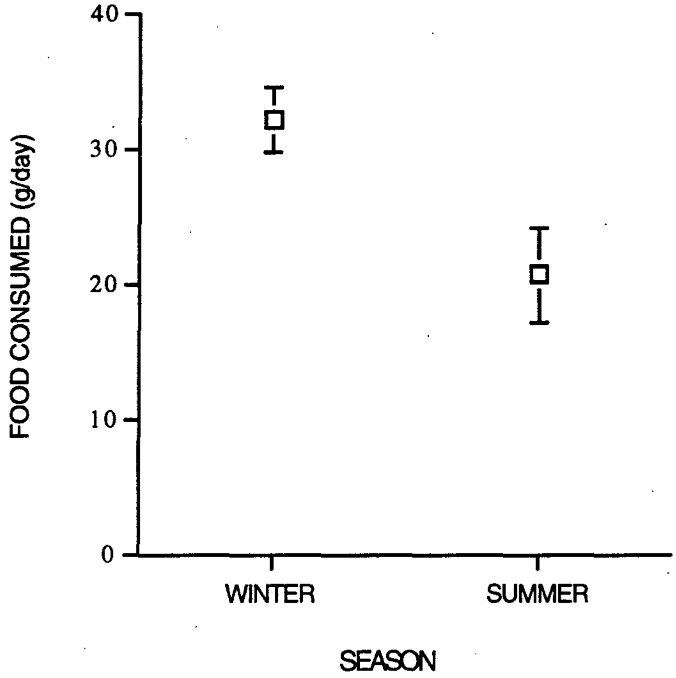


Figure 3.3 The daily food consumed (in grams.day^{-1}) by individual *P. leopardus* of varying sizes in both seasons. Consumption of food was not related to size of coral trout (Regression $F_{[1,9]}=0.386$, $p>0.05$, $r^2=0.41$).

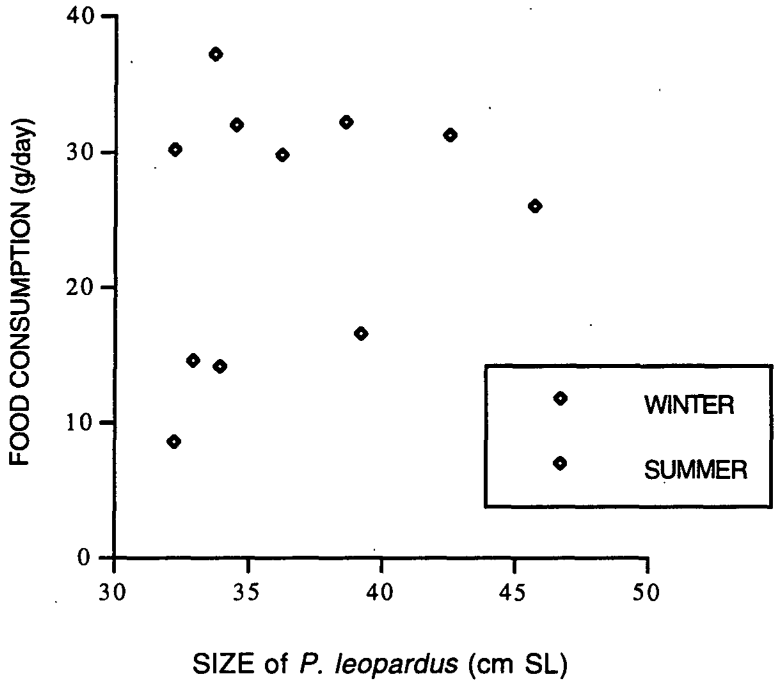


Figure 3.4 The weight of two types of prey eaten by *P. leopardus* of varying lengths (SL in cm) during the digestion experiment. The length of each *P. leopardus* (SL) and the weight of prey it consumed was positively correlated as larger fish ate larger prey (Pearson correlation coefficient =0.583, Bartletts $X^2 = 9.742$, $X^2_{[1]}$ $p<0.01$).

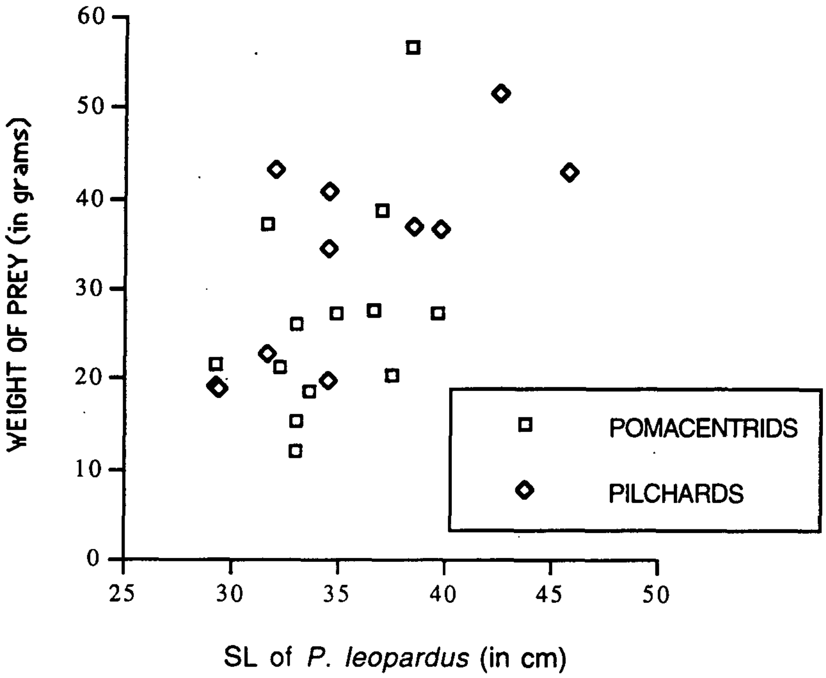


Figure 3.5 Digestion (percentage reduction in weights) of pilchard and pomacentrid prey in *P. leopardus* during summer and winter. The sample sizes are summer-pomacentrids: 3 hr (n=1), 4 hr (n=1), 6 hr (n=1), 12 hr (n=2), 24 hr (n=2), summer-pilchards: 6 hr (n=1), 12 hr (n=1), 24 hr (n=2), winter-pomacentrids: 6 hr (n=1), 12 hr (n=2), 24 hr (n=2), winter-pilchards: 6 hr-(n=4), 12 hr-(n=1), 24 hr-(n=2),. Mean (and SE) are calculated when n≥2. See Chapter 2 for the relationship between reduction of prey weight and digestion stage.

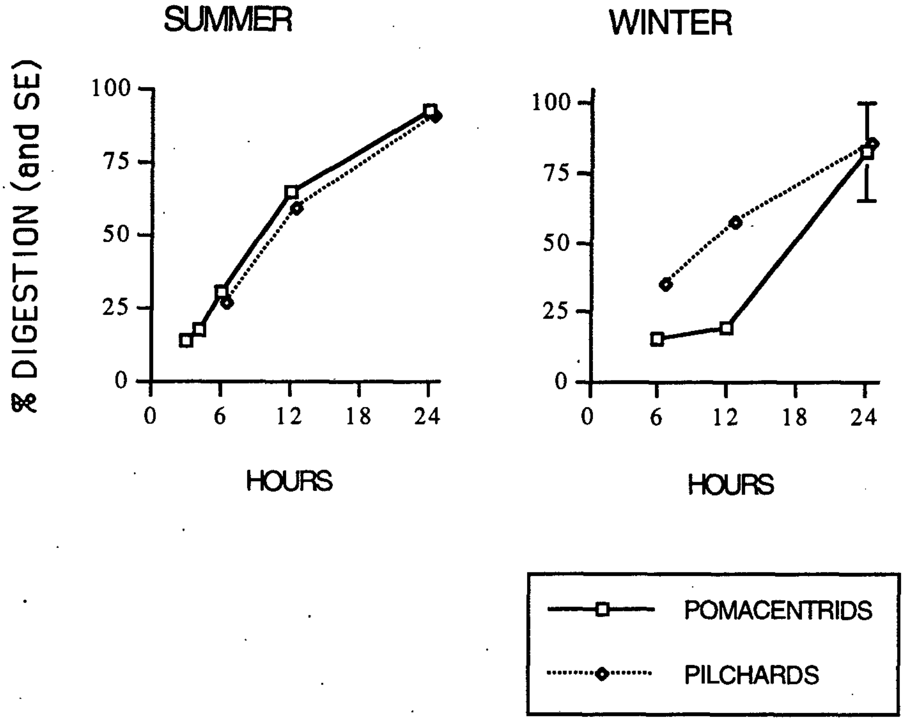


Figure 3.6 Seasonal mean (and SE) monthly rate of growth (SL cm.31 days^{-1}) in captive *P. leopardus*. There was no detectable difference between growth in summer and winter (t-test for unequal variances $t_{[14]}$=-0.62, p>0.05, 1-β = 0.32).

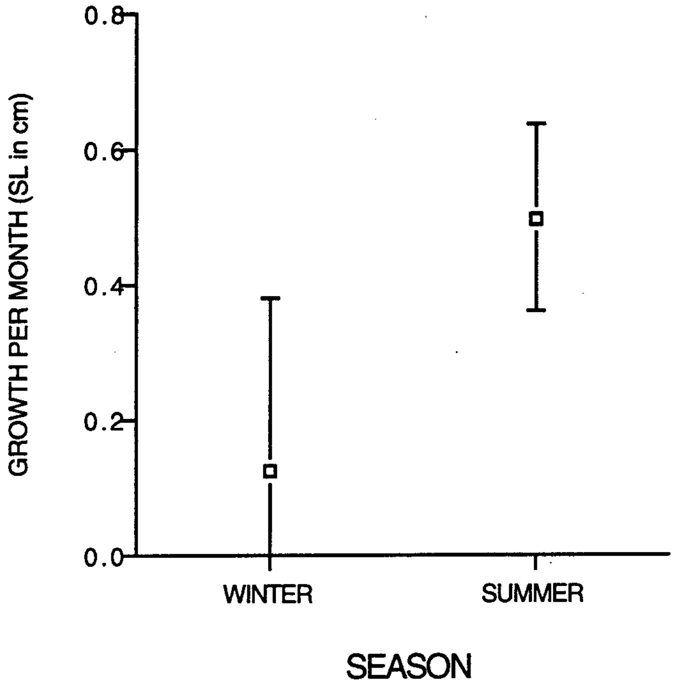
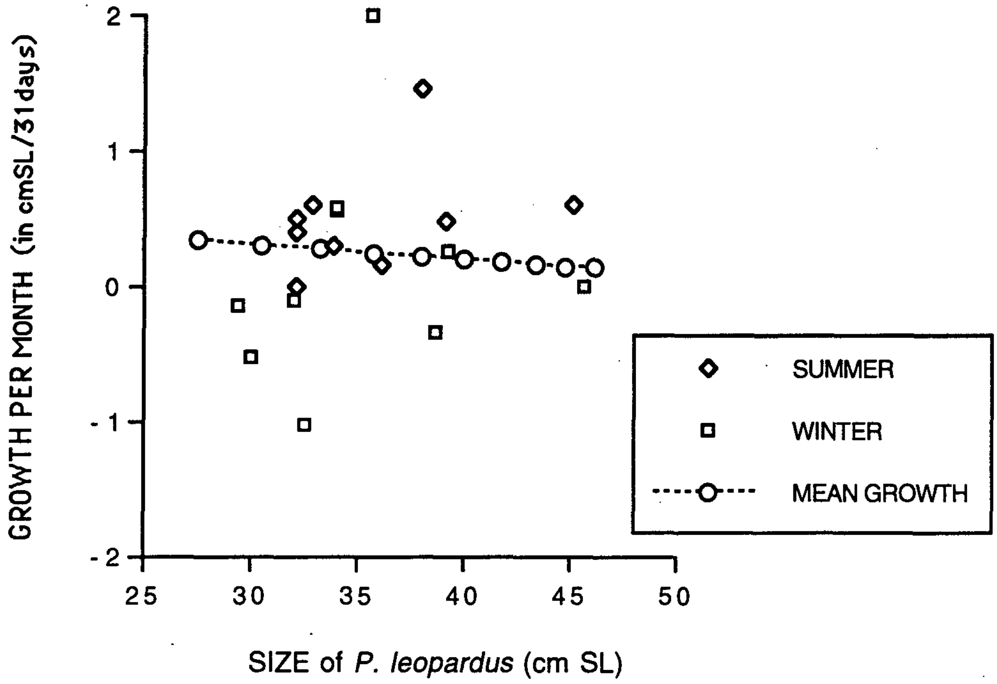


Figure 3.7 Monthly rates of growth (SL cm.31 days^{-1}) by individual *P. leopardus* of varying sizes in summer and winter (Regression $F_{[1,17]}$=1.074, p>0.05, r^2=0.06). The dotted line represents monthly growth estimated from Von Bertalanffy growth parameters of natural populations of *P. leopardus* on reefs off Townsville using Ferreira and Russ (1995).



CHAPTER 4

4.0 ONTOGENETIC PATTERNS IN THE DIET OF *P. leopardus*

4.1 INTRODUCTION

In species of fish of commercial and recreational significance to fisheries it is important to understand the trophic stages juveniles must pass through prior to entering the fishery. Fishing may affect the density of juveniles of large exploited species because these juveniles may be competing with fish that they will eventually prey on (Smale 1987; Werner and Gilliam 1984). Juveniles may be less successful competitors with small specialist feeders if these juveniles are adapted to feeding on slightly different prey types to specialists (e.g. juveniles may have adult dentition that is not completely appropriate for the diet of juveniles, Werner and Gilliam 1984). Although food habit studies should include studies of juvenile and smaller stages, ontogenetic changes in the diet of commercial fishes are rarely examined because smaller individuals are not caught in the fishery.

Morphological feeding limitations have been invoked to explain ontogenetic differences in fish diets (Mummert and Drenner 1986). Morphologies of feeding structures can have considerable predictive power in determining the size of prey selected (Werner 1977). Size of predator constrains the range of prey an animal can utilise (Wainwright 1988). Predators invariably consume only a subset of the prey present in their environment. Traditionally, length of prey has been used to assess size selection of prey in predator-prey relationships. For example, in the serranid, *Epinephelus* spp., the ratio of size of prey to predator ranged from 9-74% in length with a mean of 23% (Reshetnikov *et al.* 1972). More recently, however, body depth of prey has been considered to be a more useful measure for examining prey size selection by gape-limited predators (Hambright 1991). Many piscivores are gape-limited predators since they only consume prey that they can swallow whole (Zaret 1980; Hambright 1991). Gape size limits the maximum size of prey that many fish taxa can eat (Werner 1974, 1977) and the degree to which fishes can ingest prey close to their gape limit varies among species (Schael *et al.* 1991). Some piscivores are not considered gape-limited predators because they do not consume the maximum prey size available within their gape range (Ponton and Muller 1990).

As gape is a function of the length of the predatory fish, the degree of gape limitation in fishes may vary with increases in body size or when diets change. Thus, the breadth of the diet may increase ontogenetically because larger fishes can ingest a wider range of species.

In a review of feeding in serranids, Parrish (1987) concluded that ontogenetic changes in diet were surprisingly small. The spectrum of major food items remained essentially the same. Although many studies reported a trend of more fish and less crustaceans with increasing size and age, other studies that had adequate sample sizes did not (Parrish 1987).

Dietary studies on adult *P. leopardus* have found no change in feeding habits with size (Choat 1968), nor any ontogenetic trend in diet (Kingsford 1992). In a behavioural study Goeden (1974) observed that juvenile *P. leopardus* are carnivorous up to one year old, feeding mainly on benthic invertebrates (Crustacea) and small demersal fishes. As they grow *P. leopardus*, however, feed more on fishes and less on crustaceans until they are almost entirely piscivorous (Goeden 1974). To date, no study has examined the diet of juvenile *P. leopardus* nor of any large, commercially important predatory coral reef fish.

Ontogenetic patterns in the diet of *P. leopardus* in this study are examined in an attempt to answer three main questions:
How does the diet of *P. leopardus* vary ontogenetically?
How does morphology affect this change?

How does the size and behaviour of the prey influence dietary choice in *P. leopardus*?

A list of species of fish prey identified in the diet of *P. leopardus* and their size (where possible) is included here for two reasons. Firstly, prey are identified to just family level in the following three chapters. Secondly, the table indicates proportions of young fish in the diet of *P. leopardus.*

4.2 METHODS AND RESULTS

4.2.1 Collection of *P. leopardus*

Ontogenetic study

To examine ontogenetic patterns in feeding, I examined only those samples of *P. leopardus* collected in summer (November to February, with the exception of a few juveniles which were collected during spring, Gladstone sample, Table 4.1). I pooled the data from several studies where *P. leopardus* were collected during summer months (Doherty unpubl. data; Ferriera unpubl data; Samoilys unpubl data) to obtain a broad range of sizes of *P. leopardus* of sufficient numbers (Table 4.1). Although the majority of specimens were collected from reefs from Townsville to Cairns, some were collected as far north as Lizard Island and a few were collected from the Capricornia Bunker Group (near Gladstone), in the southern GBR (see Chapter 6, Fig. 6.1, Table 4.1). Although most coral trout were collected by spear, some were hooked by handlines, others were captured using fence nets or poisoned with rotenone (Table 4.1).

Size information of prey

Undigested prey (digestion stages 1 & 2) were the only stomach contents that provided accurate measurements of size and weight of prey (see Chapters 2 and 3). As these undigested prey items occurred in small proportions in samples of *P. leopardus*, a very large number of predators were required to obtain reliable measurements of prey size. The data reported here was extracted from all studies of *P. leopardus* (Chapters 2, 5, 6 and 7) as well as from other, smaller samples of *P. leopardus* collected between 1990-92 from reefs off Cairns by personnel of the Northern Fisheries Centre.

4.2.2 Measurement of specimens

Techniques used to measure *P. leopardus* and individual undigested prey were described in the General Methods (Section. 2.2).

Gape size of *P. leopardus*

Coral trout extend their mouth forward to engulf prey. When fully extended, the mouth of this predator is wider laterally than vertically. In order to swallow the largest prey fish possible the widest diameter of the fish must pass through the trouts' mouth laterally. As many prey fish of coral trout are laterally compressed, the prey are swallowed on their side (i.e. at a 90^0 angle to the swimming position of the predator (pers. obs.)). Gape size in *P. leopardus* is defined as the narrowest inside measurement of the mouth/throat area. Gape size, which was always a lateral measurement in trout, was measured to the nearest mm using callipers. The SL and FL (cm) and gape size (mm) were measured in *P. leopardus* of varying sizes (n=64 fish).

Morphometric relationships in *P. leopardus*

The length-weight relationships of *P. leopardus* were used to estimate weight of *P. leopardus* from SL, and SL from FL when SL or weight was not measured. The length-weight relationship was calculated from *P. leopardus* over the size range 4.7 cm SL (5.7 cm FL) to 57.3 cm SL (66.3 cm FL) and over a total wet-weight range of 0.003 to 4.75 kgs (Fig 4.1, Table 4.2). The relationship between FL (cm) and total weight (kg) was similar to other collections of *P. leopardus* from the northern GBR regions (Brown *et al.* 1994). The relationship between SL (cm) and total weight (kg) was used to calculate weights of fish frames (Table 4.2). The relationship between FL and SL was used to calculate SL of *P. leopardus* in cases in which only FL had been measured.

There was a strong linear relationship between fish length and gape width of *P. leopardus*. The gape of the predator increased linearly with fish length (Fig 4.2).

Size classes of predator and prey

Size classes of *P. leopardus* were based on SL (in cm). FLs were converted to SL (Table 4.2). To describe diet, *P. leopardus* were divided into nine size classes <10, 10-14.9, 15-19.9, 20-24.9, 25-29.9, 30-34.9, 35-39.9, 40-44.9 and 45-54.9 and the number of *P. leopardus* in each size class ranged from 36 to 260. As less items were identified from the stomach contents, I used fewer size classes (<15, 15-24.9, 25-34.9, 35-44.9 and 45-54.9) for analyses, with the exception of analyses of family richness of the prey.

Size classes of prey fish were based on SL (in mm) as it was the most appropriate measure of digested prey fishes. Caudal fins were often damaged by digestion.

4.2.3 Ontogenetic changes in the diet of *P. leopardus*

Number of prey

Five categories were used to describe the number of prey (0, 1, 2, 3, ≥4) found in stomachs of *P. leopardus*. In 1072 *P. leopardus* captured during summer, 37.1% of the stomachs were empty, 46.1% contained one prey item and 16.8% had two or more prey items. A total of 950 prey items were found in the stomachs of 674 *P. leopardus*. Categories of number of prey in stomachs of *P. leopardus* varied among size classes (Fig. 4.3). Juveniles ingested prey more frequently than adults. The smallest size class of predator (<10 cm SL) had the lowest proportion of empty stomachs (20.0%) and the highest proportion of stomachs containing numerous prey (43.3% of stomachs had two or more prey items). This pattern of juvenile feeding was seen in the next size class (10-14.9 cm SL) also, with a small proportion of empty stomachs (26.8%) and 19.3% of stomachs containing two or more prey items. In the 15-19.9 cm SL size class, however, *P. leopardus* were eating similar numbers of prey to the larger size classes of *P. leopardus*. The two largest size classes of *P. leopardus* (40-44.9 and 45-54.9) never contained more than two prey items per stomach but did not differ significantly from the other size classes (20-..-39.9, Fig. 4.3).

The major groups of prey

A total of 722 *P. leopardus* contained a total of 1057 prey items that were categorised into three major prey groups: fish (924), crustaceans (101) and cephalopods (7). Twenty five prey items were unidentified. Eight pieces of hard coral and two foraminiferans were found in the stomachs but were considered to have been ingested incidentally along with prey.

The proportion of fish and crustaceans differed among size classes (Fig. 4.4). Juveniles consumed more crustaceans than adults and the smallest size class (<10 cm SL) contained the highest proportion of crustaceans (40.8%, Fig. 4.4). Amongst larger size classes (15-54.9 cm SL), however, there was no difference in the proportion of fish and crustaceans consumed (Fig. 4.4). Six of the seven cephalopods were eaten by the two largest size classes of *P. leopardus* (45-54.9 cm SL). As fish dominated the diet of *P. leopardus* in all size classes (87.4% numerically in diet), the remainder of the results focuses on prey fishes only.

4.2.4 Ontogenetic changes in the size of prey fishes in the diet of *P. leopardus*

Comparison of prey weight and weight of *P. leopardus*

Methods

To determine ontogenetic changes in relative prey weight, I restricted the dietary samples of *P. leopardus* to those containing one or two prey in their stomach. The majority of *P. leopardus* (except juveniles) were found to eat one prey item. Numerous prey would be more likely to have been eaten over a longer time frame and thus digestion stages of individual prey would vary. Accurate weights of prey require relatively undigested prey. Prey weight was thus included in the sample if it was:

1. either a single prey item or the largest of two prey items in the stomach of *P. leopardus*. When two prey items were in the stomach, the weight of the largest prey was between 90 and 99.9% of the total weight of stomach contents in 87% of the samples. The weight of the largest prey was ≥59% of the total weight in the remaining 13% of the samples;
2. in digestion stage 1 or 2 (i.e. mostly undigested: see Chapter 2). The sample size for this study was 155.

Weights of *P. leopardus* were estimated from SL when they were not weighed (45% of the sample, Table 4.2). Relative prey weight was (prey weight/weight of *P. leopardus*)*100.

Results

Of the 155 prey examined, the weight of single prey fish eaten by *P. leopardus* increased with predator weight even though *P. leopardus* of all sizes consumed small prey. The majority of prey consumed by *P. leopardus* (predators < 2 kg) were less than 100 grams. The largest prey item, which weighed more than 400 g, was eaten by a three kg *P. leopardus*.

There were ontogenetic patterns in the relationship between prey and predator weight. Relative prey weight (prey weight/weight of predator*100) increased as the size of *P. leopardus* increased but the relationship was weak ($r^2 = 0.03$, Fig 4.5). The overall mean relative prey weight was 2.8%.

Relationship between prey length and predator length

Each successive size class of *P. leopardus* consumed a significantly wider range of prey sizes, except the two largest (35 to 59.9 cm SL, Fig 4.6 and Table 4.3). *Plectropomus leopardus* of all sizes consumed prey of 30 to 49.9 mm SL. The smallest size class of *P. leopardus* (<15 cm SL) ate the smallest prey (<10 mm SL) with 49.9 mm SL the upper size limit of prey for these predators. All other *P. leopardus* (15 cm SL and larger) consumed prey between 30-99.9 mm SL. Prey in the largest size category (220-229.9 mm SL) were consumed by *P. leopardus* ranging from 35 to 59.9 cm.

Relationship between predator gape and prey depth

Methods

The maximum depth of prey were, with few exceptions, smaller than the maximum gape size of its predator (Fig. 4.2). The ratio of maximum depth of prey to gape size of predator was calculated by dividing depth of prey by gape size. A value of one occurs when the maximum depth of prey equals the gape of the *P. l eopardus* that consumed it and a mean value close to one indicates that the predator is gape-limited (Schael *et al.* 1991). I tested the hypothesis that juveniles were gape-limited by comparing the highest 50% of depth-gape values in five size classes of *P. leopardus*. If juveniles were more gape-limited than adults, then their mean depth-gape ratio would be higher.

Results

There were no gape-related ontogenetic trends in *P. leopardus*. In adult *P. leopardus,* the depth-gape ratio was significantly lower in the largest size class (Fig. 4.7). Either these large *P. leopardus* did not make use of their wide gape to eat deeper-bodied prey, or such prey were not available to them. Gape limitation in *P. leopardus*, if it occurred, would be expected in the smaller predators.

Shape of prey fishes

Methods

Shape of prey was calculated by dividing the SL by the maximum depth. Low values were deep-bodied prey (e.g. Pomacentridae = 2) and higher values were long and narrow fishes (e.g. Synodontidae = 7).

Results

The shape of the prey consumed by five size classes of *P. leopardus* varied significantly (Fig. 4.8). On average, juvenile *P. leopardus* (<15 cm SL) consumed narrower prey than adult *P. leopardus* (Fig. 4.8). Furthermore, the shape of prey in each family varied among the four habitats (Fig. 4.9).

4.2.5 The prey fishes of *P. leopardus*

Abundance of prey in families in the diet of *P. leopardus*

In the diet of *P. leopardus* during summer, 422 prey were classified into 28 families (Table 4.4), and three families (Clupeidae, Pomacentridae and Labridae) accounted for more than 60% of the diet numerically (Table 4.5).

Overall, the families of prey eaten by *P. leopardus* varied ontogenetically (Table 4.5, Fig. 4.10). The abundance of families in the diet differed most among the middle size ranges of *P. leopardus* (Fig. 4.10). There was no significant difference among the three smallest and the three largest size classes of *P. leopardus* (Fig. 4.10). Some families of prey fishes were eaten exclusively by juveniles (e.g. Tripterygiidae and Callionymidae) or mostly by adults (e.g. Atherinidae and Scaridae,Table 4.4, Fig 4.10). Prey in other families were eaten in larger proportions by juveniles (e.g. Gobiidae) or adults (e.g. Pomacentridae Table 4.4, Fig 4.10).

Habitats of prey fishes

Twelve of the 28 families of fishes in the diet of *P. leopardus* during summer were classified as demersal (Table 4.6). Demersal fishes occurred prominently in the diet of all size classes of *P. leopardus* whereas benthic fishes were a major component (59.2%) of only the smallest size class of predator (Fig 4.11). Midwater fishes appeared in the diet of all size classes of *P. leopardus* except for the smallest (<15) and soft sediment fish appeared in the diet of all size classes of *P. leopardus* except for the largest size class (Fig 4.11).

The habitats of prey fishes of *P. leopardus* varied among size classes (Fig. 4.11). Demersal coral reef fishes dominated the diet of adult *P. leopardus* except for the 25-34.9 cm SL size class which consumed more midwater fishes (Fig. 4.11). Midwater fishes associated with reefs were the second largest component of the adult diet. Fishes dwelling on soft sediments around reefs and benthic dwellers on hard coral substrata were eaten least frequently (Fig. 4.11). This pattern differed for juvenile predators in the two smallest size classes (Fig. 4.11). A transition toward adult feeding was evident in the larger of these two size classes (15-24.9 cm SL) because the diet comprised a higher proportion of benthic coral reef dwellers and a lower proportion of pelagic prey than adults.

Predation by *P. leopardus* on different size ranges of prey in families

Methods

To test the hypothesis that dietary composition at the level of prey family is influenced by a positive relationship between the size of the predator and the general size-range of individuals within the family, I examined the size of *P. leopardus* feeding on prey in important families.

To determine which families of prey were important in the overall diet of *P. leopardus*, the % number of prey in each predator size class (% prey number/total number of prey for that size class) was summed across every size class of predator (<15, <25, <35, <45, <55 mm SL) for each family. In 11 families this total was >10%. I categorised the size-range of ten of these families into three general size groups based on prior knowledge of the maximum sizes of species in the whole family; small only, small to large and large only. One family, Blenniidae, was not included in the analysis. These size categories were confirmed by the size range of individuals in each family found in the stomachs of *P. leopardus* even though there was some overlap of sizes between categories (Table 4.7). Families of small prey ranged from 2 to 81 mm SL. Families of large prey ranged from 57 to 177 mm SL while prey in small-large families ranged from 17 to 205 mm SL. The one exception to this was the family Serranidae, which consisted of young, and therefore small, individuals (Table 4.7).

Results

The hypothesis above predicts that families of small prey would be eaten mostly by small *P. leopardus*, families of large prey would be eaten mostly by large *P. leopardus* and *P. leopardus* of all sizes would eat the families with a broad size range. The size-structure of the population of *P. leopardus* consuming prey in each family was examined in each category (Table 4.8). Families of small prey fishes were mostly eaten by small *P. leopardus* (Fig 4.12). Two benthic-dwelling families of prey (Gobiidae and Tripterygiidae) and one demersal family (Plesiopidae) were consumed mostly by the smallest size class (<15 cm) of *P. leopardus*. The size-structure of *P. leopardus* ingesting these three families differed from that ingesting every other family. Clupeidae were consumed by *P. leopardus* of all sizes except the smallest. Families with large individuals, such as Synodontidae, Caesionidae and Scaridae, were consumed mostly by larger *P. leopardus*. The samples of *P. leopardus* consuming prey in 'large' families differed in size-structure from those consuming prey in 'small' families, including the Clupeidae, but were mostly similar to the samples of *P. leopardus* consuming the prey in 'small-to-large' families (Table 4.8). In both the 'large' and 'small-to-large' category the largest number of prey were consumed mostly by the <45 cm SL size class of *P. leopardus*.

Predation on two families with differing shapes

The shape of prey in two common families, pomacentrids and caesionids, that were eaten by large *P. leopardus* (>30 cm SL), were compared. In both families, body depth was closely related to standard length of the prey fish (Fig 4.13). The shape of the prey in the two families differed significantly (Fig 4.13). Pomacentrids were elongate to orbicular, compressed fishes whereas caesionid prey had a slender, cylindrical body (Randall *et al.* 1990). The relationship between the size of the predator and size of prey was compared for both measurements of prey size (length and depth). There was a significant relationship between predator length and size of pomacentrids (both SL and depth of prey Fig 4.14). For caesionids, these relationships were not significant (Fig 4.14). The length of pomacentrid and caesionid prey consumed by *P. leopardus* differed significantly (Fig 4.14a). *Plectropomus leopardus* consumed pomacentrids shorter than caesionids (Fig 4.14a). The depth of prey consumed by *P. leopardus*, however, did not differ between families (Fig 4.14b). Size-related predation by *P. leopardus* on these two families appears dependent on depth of prey rather than SL.

4.2.6 Species composition of the diet of *P. leopardus*

Methods

A total of 908 prey in the diet of *P. leopardus* were identified to one or all of the following: species, genus and family (Table 4.9). For each family, very small fishes were classified as newly settled if they were smaller than twice the size at settlement (SL in mm, Table 4.9). This list of prey is somewhat influenced by the ability to classify the prey into families, genera and species. For example Scaridae are easily classified into family and genera but identification into species is difficult. Pomacentridae are not easily identified to genera and species since many of the morphometrics overlap among species. Labridae, however, are easier to identify into genera because of their dentition.

Results

Overall *P. leopardus* ate 908 prey in 37 families Generally, *P. leopardus* consumed very few newly settled fish (1.3% numerically). In two of the three most abundant families, high species richness corresponded to high abundance of prey in the diet (Table 4.9). Pomacentridae was the most abundant family and the most species rich in the diet with 10 genera and 21 species. Similarly, Labridae was the second most species rich in the diet and the third most abundant. Clupeidae, however, ranked second in abundance with only two species in one genus.

4.3 DISCUSSION

Plectropomus leopardus are one of the major predators of adult coral reef fishes on the GBR. Newly settled fish represented only one percent by number of their diet. After the first year of their life *P. leopardus* are almost entirely piscivorous. As *P. leopardus* are such large predators, few families of fishes on coral reefs would not be available to them as prey because even large adults must pass through smaller size classes. Yet *P. leopardus* appear to be selective feeders at the level of family and species. Many abundant families of fishes on the GBR (e.g. Siganidae, Pomacanthidae and Chaetodontidae) were rarely eaten. Furthermore, of families of prey common in the diet, some prey species were eaten in much higher proportions than expected from their general abundance on reefs (e.g. *Acanthochromis polyacanthus* in Pomacentridae). Other species were eaten in much lower proportions (e.g. *Pomacentrus amboinensis, Pomacentrus moluccensis* and *Pomacentrus wardi,* Williams 1982). *Plectropomus leopardus* also select prey by size. In size-related predation by *P. leopardus,* body depth of prey is more important than length. Size-related feeding patterns do not occur when *P. leopardus* are feeding on small schooling prey fishes or when *P. leopardus* reach a certain size as they continue to feed on the smaller prey fishes that are abundant on coral reefs.

Among fish, ontogenetic changes in resource availability, including food types, are nearly universal (see review by Werner and Gilliam 1984). On coral reefs, many fishes that are midwater piscivores as adults are predators of benthic invertebrates as juveniles (Austin and Austin 1971). *P. leopardus,* like many serranids (Parrish 1987), become more piscivorous with increasing size. Juvenile *P. leopardus* consumed crustaceans and fishes; adults consumed fishes almost exclusively. Ontogenetic shifts in diet similar to those observed for *P. leopardus* have been documented in a few species of tropical serranids (Randall 1965; Harmelin-Vivien and Bouchon 1976). The diet of small (6-9 cm) *Epinephelus merra* contained 35% fish while the diet of larger individuals of the same species (10-24 cm) contained 68% fish

(Harmelin-Vivien and Bouchon 1976). Similarly, large *Epinephelus striatus* and three species of *Cephalopholis* fed more on fish and less on crustaceans as the predators grew (Randall 1965; Shpigel and Fishelson 1989).

Plectropomus leopardus have distinct juvenile and adult diets. As juveniles grow, they progressively eat more fishes until they are eating an adult diet at >20 cm SL in size. The fishes and crustaceans taken by small *P. leopardus* were benthic. Juveniles avoid gape limitation by consuming narrower prey fish (on average) than adult *P. leopardus.* Furthermore, the families of prey fish consumed by juveniles were similar among the juvenile size classes, but different from those consumed by adults. Thus, juvenile *P. leopardus* are not feeding on the smallest individuals (recruits and juveniles) of the same families that adults consume.

The major change in the diet to predominantly piscivorous corresponds to the onset of sexual maturity in *P. leopardus.* Sexual maturity occurs at a minimum size of 20 cm SL on the northern GBR (Ferreira 1993). Major ontogenetic shifts in feeding are often correlated with discrete growth periods in the life history (Werner and Gilliam 1984), but in *P. leopardus* growth remains high until 35 cm FL (Ferreira and Russ 1994). Fishing would have little impact on the ontogenetic shift in diet as it occurs well before *P. leopardus* enter the fishery (currently at 38 cm FL legal minimum size).

Major ontogenetic shifts in feeding of piscivorous fish occur at different sizes for different species. The major change in feeding by *P. leopardus* occurred at a relative smaller size (20 cm SL with *P. leopardus* growing to greater than 60 cm SL) than fishes in the Northwest Atlantic fin fishery (Langton 1982). In this fishery, Atlantic cod, *Gadus morhua*, and silver hake, *Merluccius bilinearis*, showed size-dependent shifts in diet (60-70 cm FL for Atlantic cod which grow to >80 cm in size and 20-25 cm for silver hake which grow to >35 cm in length) from crustaceans to fish (Langton 1982). As *P. leopardus* can attain 20 cm SL in their first year (Ferreira and Russ 1994), this large predator is mostly piscivorous throughout life.

The distinctive diet of juvenile *P. leopardus* is related to differences in their behaviour. Juvenile *P. leopardus* are benthic dwellers, living close to reef substrata (mostly within 30 cm, Goeden 1974). Behavioural observations of juvenile feeding corroborate the results of this dietary study. Goeden (1974) observed that predatory attacks by juvenile *P. leopardus* were in a horizontal or downward direction towards benthic crustaceans and fishes. Furthermore, the transition from a juvenile to an adult diet was observed by Goeden (1974). Feeding behaviour in the youngest age class (equivalent to 10-20 cm SL size class) differed from that of all other ages of *P. leopardus* (Goeden 1974). In the next two age classes (equivalent to 10-20 cm and 19-31 cm SL) feeding behaviour was similar because they preyed upon demersal or demersal-pelagic fishes and some invertebrates. The smaller size class showed greater dependence on benthic prey while the larger size class occasionally took midwater prey (Goeden 1974).

Other differences to adults in feeding by juveniles are the rate of feeding and the relative size of prey consumed. Juveniles eat higher numbers of prey items and therefore feed more frequently than adults. Goeden (1974) observed that the smallest *P. leopardus* (<5.5 cm SL) fed most frequently, attacking prey once every three to five minutes on average. He concluded that either the ration was small or the attempts unsuccessful, but favoured the latter possibility. The results of the present study suggest that both factors play some role. Firstly, relative prey-weight or ration is lower in smaller *P. leopardus*. Secondly, the success rate of strikes can be calculated using information on the number of prey in the stomachs (0 to 7), rate of digestion of prey (approx. 12 hours, Light pers. comm.) and strike rates (mean =15 strikes.hour^{-1}, Goeden 1974). As the contents of a stomach are digested in 12 hours, daily food rations are twice the stomach contents (0-14). Daily feeding, however, occurs over 12 hours during daylight and represents an average 180 predatory strikes. Thus successful strikes range between 0 -

7.7%. Strike rates of adult *P. leopardus* are much lower and therefore their success rate would be expected to be higher (see Chapter 8).

The ontogenetic shift in diet by *P. leopardus* did not correspond to a change in habitat use, unlike for other coral reef predatory fishes such as some lutjanids and carangids (Austin and Austin 1971). Juvenile *P. leopardus* use the same habitat as adults (Ayling and Ayling 1992; Samoilys pers. comm.).

Kingsford (1992) found the proportion of crustaceans in the diet of *P. leopardus* differed between habitats. *Plectropomus leopardus* of all sizes in the lagoon of One Tree Reef (OTR) consistently ate a higher proportion of crustaceans than *P. leopardus* on the reef slope. Similarly, the percentage of crustaceans in the diet of *P. leopardus* of varying sizes differed between OTR and the reefs in this study (Kingsford 1992, Table 4.10). In the smallest size class of the predator (<10 cm SL) in the lagoon of OTR, the importance of crustaceans may have been overestimated because the sample size of trout was small (n=3, Kingsford 1992). In the next size class (10-19.9 cm SL), *P. leopardus* in the two studies had similar proportions of crustaceans in their diet, with the exception of *P. leopardus* from the reef slope of OTR, which consumed more fishes (Table 4.10). Even though *P. leopardus* in the 20-30 cm (SL) size class continued to eat a high proportion of crustaceans (15%) in the lagoon of OTR, *P. leopardus* on the slope of OTR and in my study were feeding like the adult population (Kingsford 1992). The closed structure of the reef at OTR may explain these differences. At OTR movement of *P. leopardus* between the two habitats is restricted during low tide and the reef may constitute a permanent barrier between habitats. Restriction to the shallow lagoon may explain the higher proportion of crustaceans in the diet of adult *P. leopardus* in OTR. In the present study, *P. leopardus* were able to feed across several habitats because the reefs did not have a ponding lagoon like OTR.

Most studies on prey selection in fish have shown a clear tendency for predators to select larger prey as they grow larger (see Gordoa and Macpherson 1990). In other studies, larger *P. leopardus* fed on a wider range of prey sizes and larger fish ate larger prey (Choat 1968; Kingsford 1992). Small and medium sized *P. leopardus* showed such a trend. Prey size range increased in each consecutive size class for the smallest three of the five size classes. Beyond a certain size (35 cm SL), however, an increase in size of *P. leopardus* did not change the size of prey consumed.

Plectropomus leopardus reach a size threshold beyond which there is no change in diet. After 35 cm SL, dietary composition and size of fish prey did not vary, despite the fish spanning 20 cm in length (one third of their maximum size). This explains the lower depth-of-prey-to-gape ratio in the largest size class. As large *P. leopardus* eat a subset of the families consumed by smaller adults, it appears that individuals in these families are not available in correspondingly larger sizes. Prey in these families either cannot attain or seldom grow to such large sizes. Another prey type, however, becomes available to large *P. leopardus*. Cephalopods represented 5% of the diet of the two largest size classes (40-45 and 45-55 cm SL) of *P. leopardus*. Furthermore, cephalopods were not a common prey item in *P. leopardus* less than 40 cm SL (one out of 889 prey items). Other, less piscivorous serranids, such as *Epinephelus merra* eat cephalopods at large sizes (Harmelin-Vivien and Bouchon 1976).

The habitat and habits of the prey fish played some role in ontogenetic differences in the diet of *P. leopardus*. Demersal fishes were the most common prey of *P. leopardus* while fishes from the soft sediment were the least abundant prey. *Plectropomus leopardus* in the middle size ranges (25-34.9 cm SL) consumed the highest abundance of midwater prey fishes. Benthic fishes, as discussed previously, were consumed mostly by small *P. leopardus*. Generally, however, feeding patterns in *P. leopardus* were related to size.

The size of the predators that consumed the three size categories of prey in families indicated that feeding in *P. leopardus* was related to size of prey. Mostly, the size-structure of *P. leopardus* feeding on prey in 'small' families were similar within this category but differed from the size-structure of *P. leopardus* feeding on the two larger prey-size categories. The one exception to this pattern was a small schooling family, Clupeidae. The size-structure of *P. leopardus* feeding on this family of prey was similar to the small-to-large size category. The size-structure of *P. leopardus* feeding on prey in one of the 'large-only' families (Serranidae), was similar to the size-structure of predators feeding on the 'small-to-large' families because *P. leopardus* consumed juvenile Serranidae. Generally, the size range of predators feeding on prey in a family was predictable from the range of prey sizes in that family. Other studies have found that intraspecific variation in diet was caused by anatomical and behavioural differences in both predators and prey (Smale 1987). In other fishes, however, prey selection may be entirely size related. The taxonomic identity of prey was unimportant in largemouth bass as preferences were based on similar body depth (Hambright 1991).

Size-related preferences in feeding may be altered by prey availability, visibility (Main 1985) and movement (Gordoa and Macpherson 1990). Large piscivores consume small schooling fishes when available (Smale 1987; Ursin 1973). *Plectropomus leopardus* is no exception. In one study, a high percentage of atherinids occurred in the stomachs of *P. leopardus* because the specimens were speared from a group which had been clustering around the periphery of schools of *Pranesus capricornesis* (Choat 1968). Similarly, yellowfin tuna, *Thunnus albacares* (over their entire size range 40-140 cm) consume 10 cm engraulids and 20 cm pilchards when available (Smale 1987).

Body depth is the most important prey-related factor physically constraining the consumption of large prey by *P. leopardus*. Prey in two common families of differing shapes, size-related predation occurred when body depth, rather than length, measurements were used. *Plectropomus leopardus* of similar sizes ate orbicular pomacentrids and schooling fusiform caesionids of the same body depth. Predation on two prey species with varying morphology and behaviour has been found to differ (Moody *et al.* 1983). Fusiform fathead minnows (*Pimephales promelas*) which schooled constantly were more susceptible to capture than the deep-bodied, spined bluegill (*Micropterus salmoides*) which remained motionless during threats of predation (Moody *et al.* 1983). Interactions between body-depth of prey and mouth width in piscivore populations explained prey-size distributions in piscivore gut contents (Hambright 1991). Size distributions of gut contents were skewed towards smaller prey in lakes even though smaller prey were less available (Hambright 1991).

The mean prey-depth-to-gape ratio was 0.60 for *P. leopardus*. These predators, however, can eat prey much closer in size to their gape. In feeding experiments in tanks (Chapter 3) an *Amblyglyphidodon curacao* with a maximum body depth of 51 mm was swallowed by a captive 32 cm SL *P. leopardus* with a gape of 54 mm. Werner (1974) determined an optimal size of prey based on predator gape, prey size and handling time which was a prey-depth-to-gape ratio of 0.59 regardless of predator size. Prey to gape size ratios of juvenile and small adult *P. leopardus* were similar to Werner's calculated optimal size. Werner (1974) suggested that small predators need to be very careful in size selection of prey as a small change in size of an item's breadth generates a considerable increase in expended effort. Larger predators, however, can afford to be "less selective". The largest size class of *P. leopardus* (45-59.9 cm SL) appears to be "less selective" because their prey-depth-to-gape ratio drops to 0.47. This drop, however, may simply reflect the high abundance of small prey fishes available on the GBR.

When feeding captive *P. leopardus*, I observed that prey handling time was affected by both depth and length of prey. Deep-bodied prey required more manipulation before swallowing, whereas a long time was required to swallow long prey completely and the caudal fin of the prey protruded from the mouth for up to 30 minutes after it was captured. In contrast, the weight-adjusted handling time for prey of equivalent lengths was found to be lowest for shallow bodied and highest for deeper bodies fishes (Hoyle and Keast 1987). Hard fin spines also increased handling time and caused injury to predatory fish (Hoogland *et al.* 1956; Gillen *et al.* 1981). Many experimental studies have assessed the importance of prey shape in predation (Werner 1974; Moody *et al.* 1983; Hambright 1991). Prey body depth is among the factors affecting predator-prey interactions of largemouth bass (Webb 1986) and a hybrid pike (Moody *et al.* 1983). Shape of prey affects detection, pursuit and handling times in predatory fish (Moody *et al.* 1983; Webb 1986). Body shape is an important factor facilitating escape from predation. Large body-depth often resulted in misdirected strikes from the centre of mass, thus increasing the probability of the prey escaping (Webb 1986; Hambright 1991).

Relative weight of single prey items of *P. leopardus* varied with the size of the predator, and mean percentage of prey to predator weight increased as the size of predator increased. Juveniles and possibly small adults eat smaller rations relative to their size and therefore need to feed more frequently. Although small adults appeared to consume higher numbers of prey than large adults, the results were not significant. These results do not suggest that energetic requirements of larger *P. leopardus* are higher because calculations were done from single prey items and smaller trout eat more frequently. Relative prey weight represents daily consumption in *P. leopardus* because adults digest most of their prey in 24 hours (see Chapter 3) and the majority of these predators eat one prey item daily. Average daily consumption of prey in *P. leopardus* (2.8% of total body weight) is similar to other large tropical predators. Mean daily consumption was 3.6% of body weight in the tropical serranid, *Epinephelus striatus* (Reshetnikov *et al.* 1972), and 3.8% in the tropical lutjanid, *L. russelli*, when fed on pilchards at 26.4 °C (Smith *et al.* 1991). A smaller coral reef piscivore, *Synodus englemani*, ate an average of 12% of its body weight per day in summer (Sweatman 1984). This figure was considered to overestimate consumption because feeding rates may slow in the winter (Sweatman 1984).

Plectropomus leopardus did not show ontogenetic changes in all aspects of feeding. Although some studies have shown an increase in the frequency of empty stomachs as predatory fish get larger (Godfriaux and Hynes 1950 cited in Godfriaux 1969), the proportion of empty stomachs of adult *P. leopardus* does not differ with size of predator.

In conclusion, *P. leopardus* are a major predator of adult coral reef fishes on the GBR. After their first year of life, *P. leopardus* are almost entirely piscivorous. Newly settled fish represented only one percent of their fish diet of all sizes of *P. leopardus*. In *P. leopardus*, the major dietary shift in the type, species composition, length and shape of prey occurred at approximately 20 cm SL and corresponded to the onset of maturity. Juvenile *P. leopardus* consumed a higher proportion of benthic dwelling crustaceans, mostly penaeid prawns. Families of prey fish in the diet varied ontogenetically. This shift in diet was due to a change in feeding behaviour because juvenile *P. leopardus* live in similar habitats to adults. Family richness in the diet did not increase with the size of predator as differences were an artifact of sample sizes of predator size classes. In general, feeding in *P. leopardus* was related to the size of the predator. As the gape of P. *leopardus* limits the size of prey ingested, the critical dimension of the prey is depth rather than length. When feeding on larger prey items, small to medium-sized *P. leopardus* (< 35 cm SL) appear to feed optimally with respect to body-depth of prey (Werner 1974). This size-related feeding did not occur under some circumstances. Size of prey was decoupled from size of predators when either, *P. leopardus* were larger than 35 cm (SL) or the prey were small schooling fishes. It appears that *P. leopardus* switch to feeding on small schooling fishes when they are available.

Table 4.1 Collections of the 1076 *P. leopardus* used in the ontogenetic study.

Size of specimens (SL in cm)	Sample size	Location (nearest town)	Method of collection	Year
5.7-16	240	Cairns	spear	1991+2
6.0-13.0	6	Gladstone	rotenone	1990
12.5-25.5	9	Lizard Is.	fence net	1991+2
10.5-51	520	Innisfail	spear	1992
24.8-52.1	301	Townsville	spear	1991+2

Table 4.2 Morphometric relationships between FL, SL (in cm) and weight (in kg) of *P. leopardus.* Relationships are of the form
$W = a L^{b}$ and FL = a +SL. b, with sample size n and r^2.
Standard errors (SE) are in brackets.

y	x	a	b	n	r^2
log weight	log FL	-11.16 (0.046)	3.00 (0.013)	426	0.99
log weight	log SL	-10.56 (0.028)	2.98 (0.008)	533	0.99
SL	FL	-0.130 (0.130)	0.852 (0.003)	427	0.99

Table 4.3 The results of Jonckheere Terpstra tests (Mehta and Patel 1992) comparing the size structure of the populations of prey fishes (SL in mm) among five sizeclasses of *P. leopardus* (<15, 15-24.9, 25-34.9, 35-44.9, 45-59.9 cm SL). *** = one sided p-value ≤0.001, ns = not significant one-sided p-value=0.394, J T test statistic is in parentheses

Size of *P. leopardus* (SL in cm)	Size of *P. leopardus* (SL in cm)			
	<15	<25	<35	<45
<25	*** (7.662)			
<35		*** (3.748)		
<45			*** (7.472)	
<60				ns (0.269)

Table 4.4 The number of prey in each fish family consumed by nine sizeclasses (<10, 10-14.9, 15-19.9, 20-24.9, 25-29.9, 30-34.9, 35-39.9, 40-44.9, 45-49.9, 50-54.9 SL cm) of *P. leopardus* collected during summer varied ontogenetically (K-W$_{[8]}$=53.75, p-value <0.001).

PREY	**Size of *P. leopardus* (SL in cm)**									**Total**
FAMILIES	**<10**	**<15**	**<20**	**<25**	**<30**	**<35**	**<40**	**<45**	**<55**	
Clupeidae			1	3	22	56	20	5	1	108
Pomacentridae		5	3	8	11	23	28	11	4	93
Labridae		6	3	2	6	20	11	5	4	57
Gobiidae	12	8	1	1		2	2			26
Caesionidae					6	4	8	2	2	22
Scaridae		1			1	2	6	8	2	20
Synodontidae					5	5	9	1		20
Blenniidae	1	4	2		4	2	2			15
Atherinidae						7	3			10
Apogonidae			2	5	1		1			9
Serranidae	1			1	1		3	1	1	8
Acanthuridae	1			1		1	2	2		7
Tripterigiidae	2	3								5
Callionymidae	1	3								4
Engraulidae						1	2			3
Fistulariidae						1		1		2
Nemipteridae						1	1			2
Scorpaenidae					1				1	2
Balistidae						1				1
Chaetodontidae		1								1
Creedidae			1							1
Lutjanidae									1	1
Monacanthidae					1					1
Pinguipidae								1		1
Platycephalidae			1							1
Plesiopidae						1				1
Siganidae			1							1
TOTAL	18	31	15	21	59	127	98	37	16	422
Number of *P. leopardus*	60	93	78	88	157	260	191	113	36	

Table 4.5 The numerical percentage of prey in each family of fish consumed by nine sizeclasses (<10, 10-14.9, 15-19.9, 20-24.9, 25-29.9, 30-34.9, 35-39.9, 40-44.9, 45-49.9, 50-54.9) of *P. leopardus*. The total number of prey families in each sizeclasse of *P. leopardus* is recorded.

PREY	**Size of *P. leopardus* (SL in cm)**									**Total**
FAMILIES	**<10**	**<15**	**<20**	**<25**	**<30**	**<35**	**<40**	**<45**	**<55**	
Clupeidae			6.6	14.3	37.3	44.1	20.4	13.5	6.3	25.6
Pomacentridae		16.1	20.0	38.1	18.6	18.1	28.6	29.7	25.0	22.0
Labridae		19.3	20.0	9.5	10.2	15.7	11.2	13.5	25.0	13.5
Gobiidae	66.7	25.8	6.6	4.8		1.6	2.0			6.2
Caesionidae					10.2	3.1	8.2	5.4	12.5	5.2
Scaridae		3.2			1.7	1.6	9.2	21.6	12.5	4.7
Synodontidae					8.5	3.9	9.2	2.7		4.7
Blenniidae	5.5	12.9	13.3		6.8	1.6	2.0			3.5
Atherinidae						5.5	3.1			2.4
Apogonidae			13.3	23.8	1.7		1.0			2.1
Serranidae	5.5			4.8	1.7		3.1	2.7	6.3	1.9
Acanthuridae	5.5			4.8		0.8	2.0	5.4		1.6
Tripterigiidae	11.1	9.7								1.2
Callionymidae	5.5	9.7								0.9
Engraulidae						0.8	2.0			0.7
Fistulariidae						0.8		2.7		0.5
Nemipteridae						0.8	1.0			0.5
Scorpaenidae					1.7				6.3	0.5
Balistidae						0.8				0.2
Chaetodontidae		3.2								0.2
Creedidae			6.6							0.2
Lutjanidae									6.3	0.2
Monacanthidae					1.7					0.2
Pinguipidae								2.7		0.2
Platycephalidae			6.6							0.2
Plesiopidae						0.8				0.2
Siganidae			6.6							0.2
Number of prey families	6	8	9	7	11	13	14	10	8	
Number of *P. leopardus*	60	93	78	88	157	260	191	113	36	

Table 4.6 The families of prey fishes classified by their association with four broad habitats on the reef. Two habitats are strongly related to the reef substrata, demersal (with loose benthic association) and benthic (closely associated with benthos). The other two habitats are midwater and soft sediment.

DEMERSAL	BENTHIC	MIDWATER	SOFT SEDIMENT
Acanthuridae	Blenniidae	Caesionidae	Callionymidae
Apogonidae	Gobiidae	Clupeidae	Creedidae
Balistidae	Scorpaenidae	Engraulidae	Eleotridae
Chaetodontidae	Tripterygiidae	Fistulariidae	Nemipteridae
Labridae		Sphyraenidae	Pinguipidae
Lutjanidae			Platycephalidae
Monacanthidae			Synodontidae
Plesiopidae			
Pomacentridae			
Scaridae			
Serranidae			
Siganidae			

Table 4.9 All fish prey identified in the diet of *P. leopardus*. Newly settled prey (i.e. settled within one month) are determined by their length. For the purposes of this study newly settled prey are defined as size at settlement * 2. As the majority of reef species settle at 7-12 mm SL (Victor 1991), prey fish less than 28 mm SL were considered to be newly settled, with two exceptions. An *Escenius sp.* that was smaller than 28 mm was considered not newly settled whereas a *Naso* sp. that was larger than 28 mm was considered newly settled as this genus settle at larger sizes (Bellwood pers comm).

FAMILIES OF FISHES	RECRUITS		OTHER		TOTAL
	SL in mm	number	SL in mm	number	
Pomacentridae	**17-28**		36-158		**234**
Abudefduf sexfasciatus			89	1	
Acanthochromis polyacanthus			49-93	29	
Amblyglyphidodon curacao			71-88	5	
Amphiprion sp.			51	1	
Chromis ternatensis			48-79	4	
Chromis weberi			103-117	2	
Chromis xanthochira			81	1	
Chromis xanthura			46	1	
Chromis spp.			44-93	10	
Dischistodus melanotus			96-104	2	
Dischistodus sp.			121	1	
Neoglyphidodon melas			97-134	2	
Neoglyphidodon nigroris			76	1	
Neopomacentrus azysron			36-52	8	
Neopomacentrus cyanomos			45	1	
Neopomacentrus sp.			42	1	
Pomacentrus amboinensis			68	1	
Pomacentrus bankanensis			53	1	
Pomacentrus brachialis			43-75	4	
Pomacentrus chrysurus			42-68	11	
Pomacentrus lepidogenys			68	1	
Pomacentrus moluccensis			29-60	4	
Pomacentrus nigromarginatus			70	1	
Pomacentrus wardi			86	1	
Pomacentrus spp.			49	2	
Stegastes fasciolatus			106-138	6	
spp.	17-28	4	36-158	121	
Clupeidae			**20-95**		**178**
Spratelloides delicatulus			47-64	13	
Spratelloides gracilis			20-64	158	
Spratelloides spp.			67-95	7	
Labridae	**15-16**		**38-262**		**114**
Anampses sp.			89	1	
Cheilinus chlorourus			84-173	2	
Cheilinus diagrammus			170	1	
Cheilinus trilobatus			164	1	
Cheilio inermis				1	
Choerodon schoenleinii			113	1	
Choerodon sp.			143	1	
Cirrhilabrus punctatus				1	
Coris schroederi			70-130	4	
Coris sp.			37	1	
Halichoeres chloropterus			155	1	
Halichoeres hortulanus			156	1	
Halichoeres sp.				1	
Hemigymnus melapterus			136-138	1	
Macropharyngodon meleagris				2	
Stethojulis bandanensis			70	2	

Stethojulis strigiventer			42	1	
Thalassoma halichores			135	1	
Thalassoma jansenii			106-137	4	
Thalassoma lunare			71-84	1	
Thalassoma sp.			137	1	
spp.	15-16	2	38-262	84	
Pempherididae			**33-54**		**66**
Parapriacanthus ransonneti			33-54	66	
Scaridae			**49-194**		**56**
Scarus globiceps/rivulatus			136	1	
Scarus hardwicki			152	1	
Scarus sordidus			49-194	6	
Scarus spp.	22	1	97-159	33	
spp.	15	1	110-162	13	
Caesionidae			**56-187**		**55**
Caesio caerulaurea			57-185	4	
Caesio spp.			90-170	7	
Pterocaesio diagramma			148-154	2	
Pterocaesio trilineata			111-175	7	
Pterocaesio marri			139-152	6	
Pterocaesio spp.			56-177	20	
spp.			135-187	9	
Gobiidae			**15-115**		**34**
Amblygobius phalaena			61-63	2	
Amblygobius sp.			47	1	
Eviota melasma			15-19	4	
Eviota spp.			10-23	8	
Istigobius sp.			27	1	
Macrodontogobius wilburi			29-43	3	
Plurocyloceua sp				1	
Valenciennia strigata			77-115	2	
Valenciennia sp.				1	
spp.			15-81	11	
Blenniidae			**26-150**		**32**
Atrosalarias fuscus			102-103	2	
Escenius spp.			21-80	5	
Salarinii spp.			73-108	5	
spp.			26-99	20	
Synodontidae			**45-150**		**22**
Saurida sp			150	2	
Synodus variegatus			99-128	1	
Synodus spp.			45-133	12	
spp.			58-69	7	
Apogonidae			**22-61**		**15**
Apogon cooki			22	1	
Apogon doederleini			47	2	
Apogon fragilis			41	4	
Cheilodipterus artus			61	1	
spp.			26-40	7	
Serranidae			**105-125**		**14**
Cephalopholis microprion			136	1	
Cephalopholis sp.			133	1	
Plectropomus spp.	25	1	81-125	8	
spp.				2	
Acanthuridae			**54-188**		**13**
Acanthurus spp.			37-98	2	
Naso sp	34	1	176-188	2	
Zebrasoma scopas			88	1	
Acanthurinae spp.			54-99	2	
spp.			57-82	5	
Scorpaenidae			**57-136**		**12**
Scorpaenodes guamensis			87	2	
Scorpaenodes varipinnis			68	2	

Scorpaenopsis diabolus			136	1	
spp.			57-62	8	
Atherinidae			**52-80**		**10**
spp.			52-80	10	
Platycephalidae			**25-36**		**5**
Onigocia oligolepic				1	
spp.			25-36	4	
Tripterygiidae			**17-21**		**5**
spp.			17-21	5	
Callionymidae			**11-20**		**4**
spp.			11-20	4	
Nemipteridae			**113-152**		**4**
Scolopsis bilineatus			113-152	3	
Scolopsis sp.				1	
Sphyrnidae			**206-227**		**4**
Sphyraena flavicauda			206	1	
Sphyraena spp.			220-227	3	
Engraulidae			**40-56**		**3**
Stolephorus spp.			40-56		
Fistulariidae					**3**
spp.				3	
Pinguipedidae			**131-151**		**3**
Parapercis polyopthalma			131	1	
Parapercis hexophtalma			151	2	
Bothidae					**2**
Bothus sp.			84	1	
sp.				1	
Chaetodontidae					**2**
Chaetodon aureofasciatus			59	1	
sp.	27	1		1	
Holocentridae					**2**
spp.			60	2	
Lutjanidae					**2**
Lutjanus sp.	21	1			
sp.				1	
Monacanthidae					**2**
spp.				2	
Mullidae			**110-161**		**2**
Eupeneus sundaicus			110	1	
Parupeneus multifasciatus			161	1	
Siganidae					**2**
spp.	22	1	135	1	
Balistidae					**1**
Balistoides conspicillum			61	1	
Creediidae					**1**
sp.			50	1	
Exocoetidae					**1**
Cypselurus suttoni			103	1	
Muraenidae					**1**
sp.			145	1	
Plesiopidae					**1**
Plesiops corallicola			77	1	
Pomacanthidae					**1**
Centropyge bicolor			78	1	
Priacanthidae					**1**
Priacanthus hamrur				1	
Tetradontidae					**1**
Canthigaster valentini			54	1	
TOTAL PREY					**908**

Table 4.10 Comparison of the percentage of invertebrate prey found in the stomachs of the three smallest sizeclasses of *P. leopardus* from the lagoon (and reef slope) of OTR, Southern GBR (Kingsford 1992) and from the Northern GBR. The numbers in brackets are the percentage of invertebrates in samples from the reef slope. 'n' varies because the exact sample sizes were not stated in Kingsford (1992).

Sample of *P. leopardus*	**Size of *P. leopardus* (SL in cm)**		
	<10	**<20**	**<30**
lagoon (and slope) of OTR, Southern GBR			
% (#stomachs with invertebrates/ total # stomachs with prey)	66 n=3	26 (8) n=13-45	15 (4) n=13-45
Northern GBR			
% (# of invertebrate prey/ total # of prey)	40.8 n=52	29.7 n=111	4.2 n=163

Figure 4.1 The relationship between standard length (SL, in cm) and total wet weight (W, in kgs) for *P. leopardus*. W = (antilog-11.16)$L^{3.00}$, r^2=0.99, n=426.

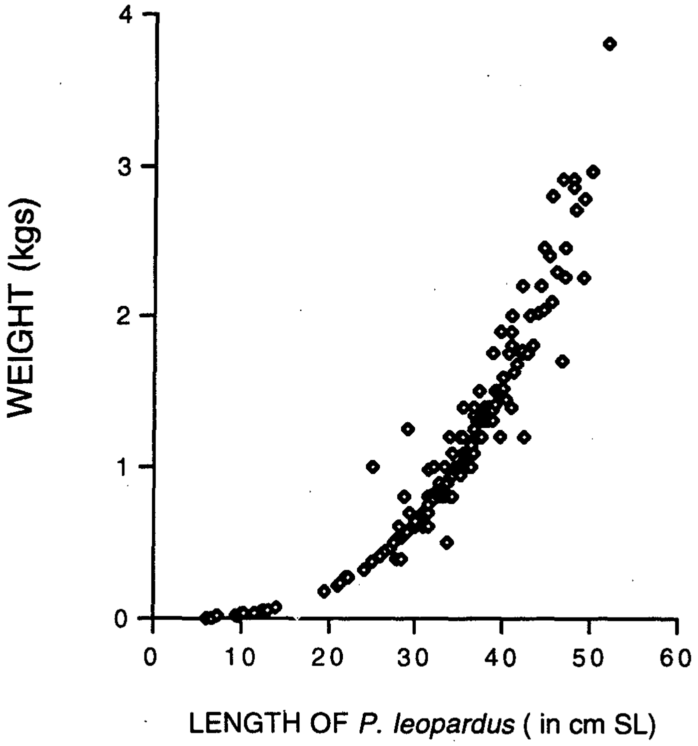


Figure 4.2 Gape width to fish length (SL in cm) relationship for *P. leopardus* (raw data). There was a strong linear relationship between fish length and gape width of *P. leopardus* (Regression $F_{[1,62]}$=1417.42, p<0.01 $\log_{10}$ transformed data). Regression line is $\text{Log}_{10}\text{Gape} = 1.210^{*} \text{Log}_{[10]}\text{SL} - 0.093$ with $r^2 = 0.96$, n = 64. The depth of individual prey is plotted against length (SL in cm) of *P. leopardus*. Each point represents one prey item and may be one of up to 18 prey items in the stomach, but the majority of *P. leopardus* consumed only one prey item.

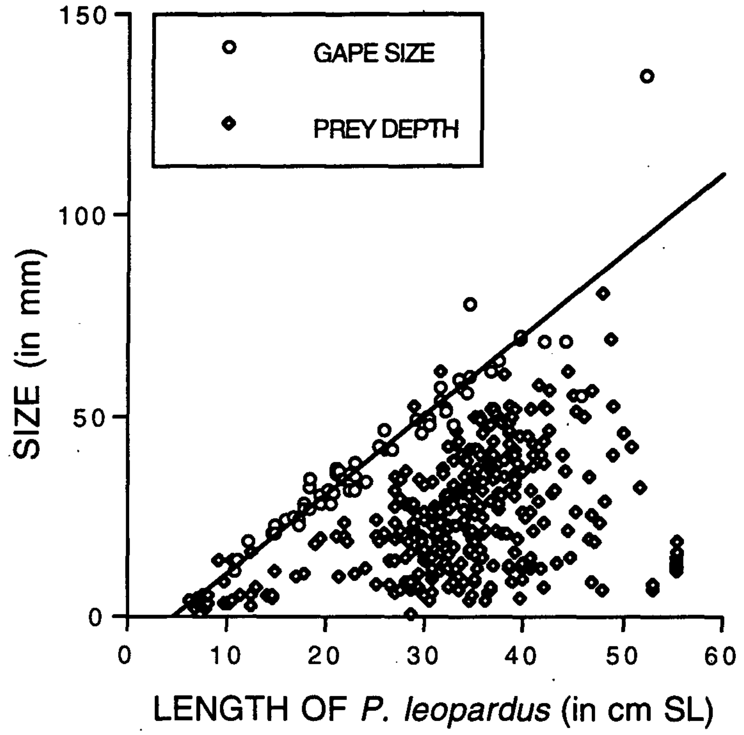


Figure 4.3 Percentage of stomachs in each category of number of prey in the nine size classes of *P. leopardus* (<10 (n=60), 10-14.9 (n=93), 15-19.9 (n=78), 20-24.9 (n=88), 25-29.9 (n=157), 30-34.9 (n=260), 35-39.9 (n=191), 40-44.9 (n=113) and 45-54.9 (n=36)). The number of prey eaten varied significantly among size classes ($KW_{[8]}=33.13$, p-value <0.001) but the number of prey in 'adult' size classes (>19.9 SL) did not vary ($KW_{[6]}=4.588$, p-value =0.593).

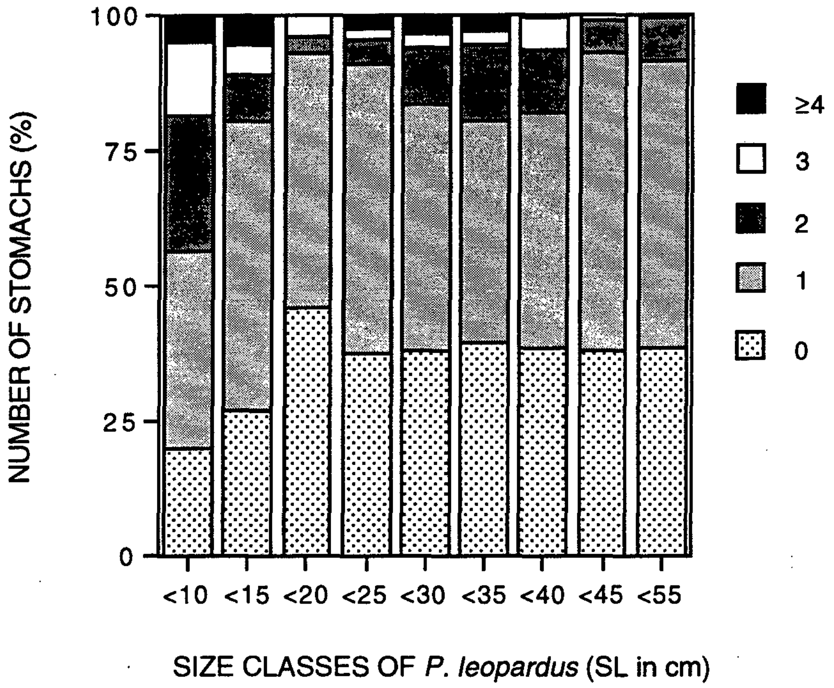


Figure 4.4 Predator-size related changes in gross dietary composition in nine size classes of *P. leopardus* ((n = predator number,p= number of prey), <10 (52,99), 10-14.9(69,115), 15-19.9 (42,50), 20-24.9 (55,69), 25-29.9 (108,154), 30-34.9 (163,270), 35-39.9 (139,201), 40-44.9 (72,82) and 45-54.9 (22,25)) of *P. leopardus* during summer. The major prey groups are fish, crustaceans, cephalopods and unknown. The proportion of fish, crustaceans and cephalopods differed among size classes ($KW_{[8]}$=276.5, p-value <0.001).

There was no difference in the proportion of fish and crustaceans consumed amongst larger size classes (15-54.9 cm SL, $KW_{[6]}$=5.821, p-value =0.433).

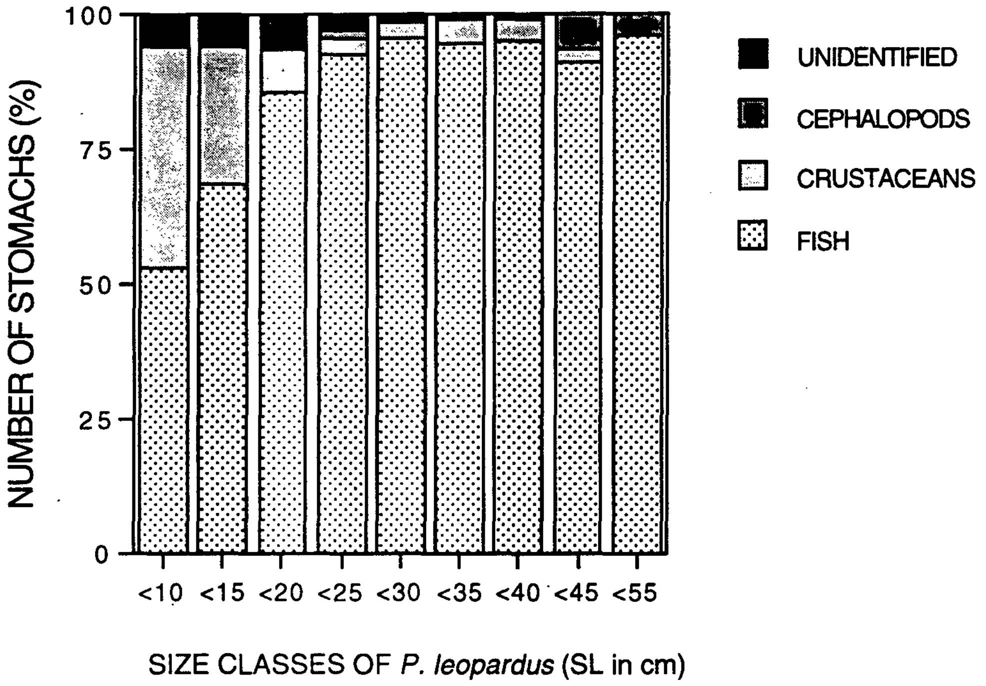


Figure 4.5 Relationship between predator length and relative prey weight. Relative prey weight ((prey weight/predator weight*100), using raw data) of *P. leopardus* increases as the size of predator increases (Regression $F_{[1,190]}=5.281$, $p<0.05$, $r^2 = 0.03$, $\log_{10}$ transformed data).

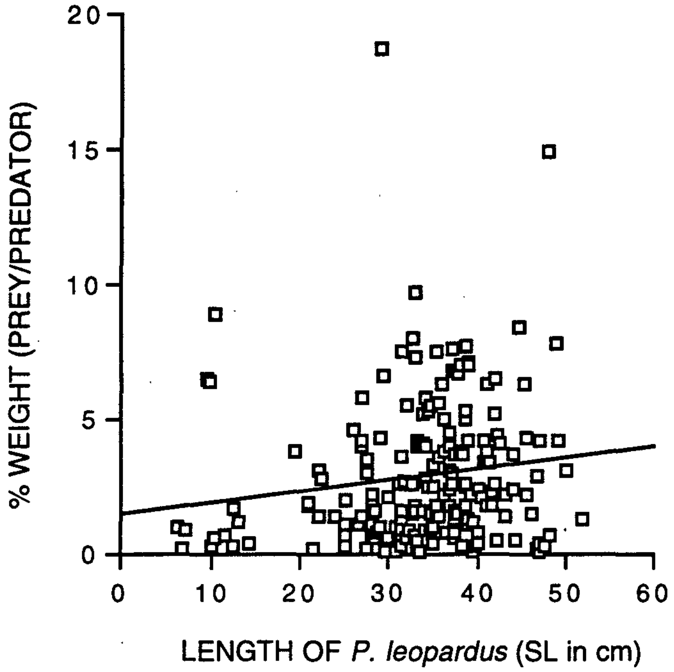


Figure 4.6 Length of prey (SL in mm) consumed by five size classes (<15, 15-24.9, 25-34.9, 35-44.9 and 45-59.9) of *P. leopardus*. Prey are divided into 23 size classes ranging from <10 mm to <230 mm. Each size class of *P. leopardus* ate prey of a different size structure except in the two largest size classes (Table 4.3).

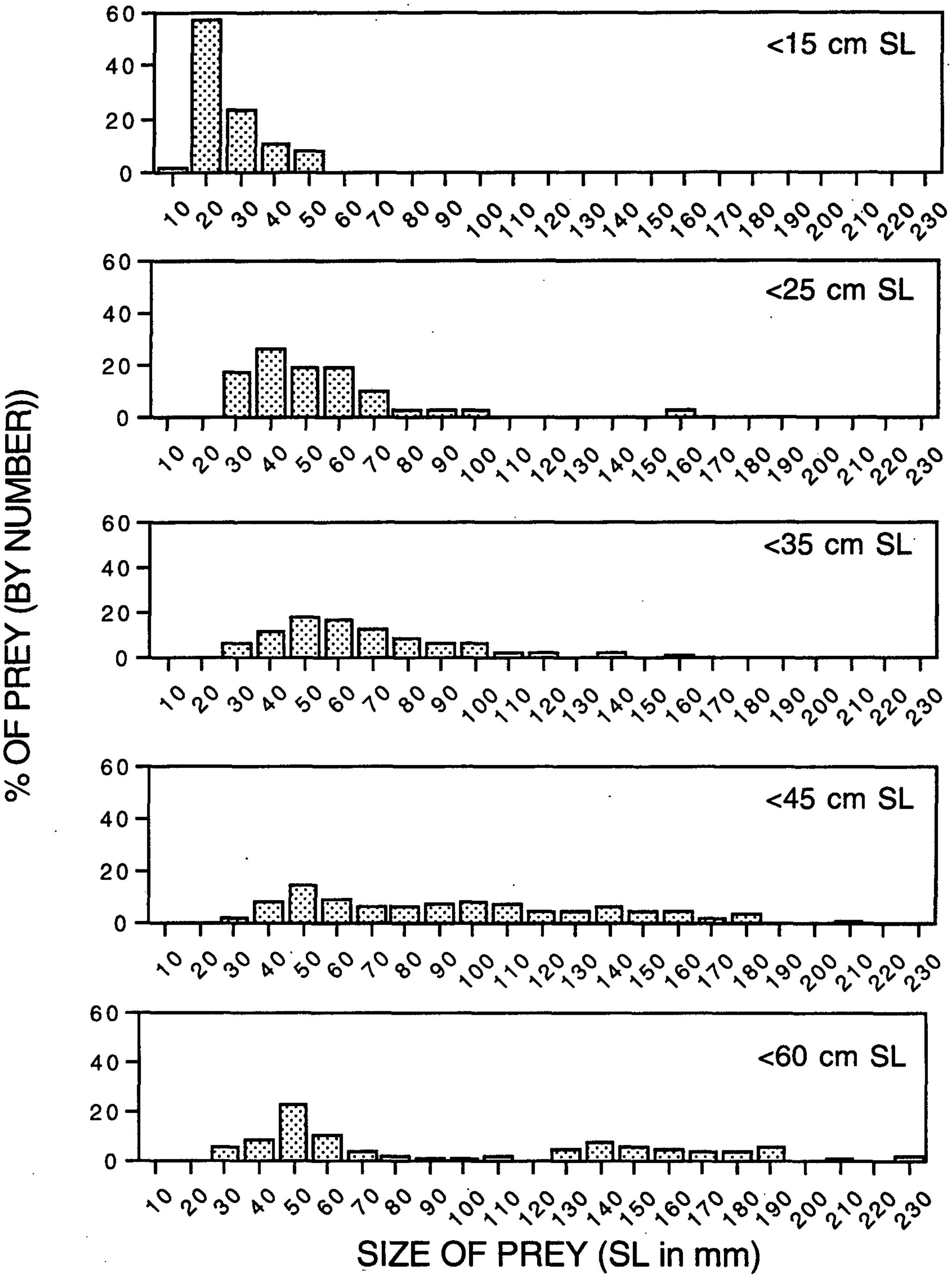


Figure 4.7 The mean ratio (and SE) of maximum depth of prey to gape size of predator for five size classes (<15, 15-24.9, 25-34.9, 35-44.9 and 45-59.9) of *P.leopardus*. Only the highest 50% of the values were used in the analysis. The depth-gape ratio significantly differed between size-classes (ANOVA $F_{[4,176]}$=6.016, p<0.01). The mean depth-gape ratio of the largest size class of *P. leopardus* was significantly lower than the other two adult size-classes (25-34.9, 35-44.9 cm SL, Tukey's pairwise comparisons, p <0.05).

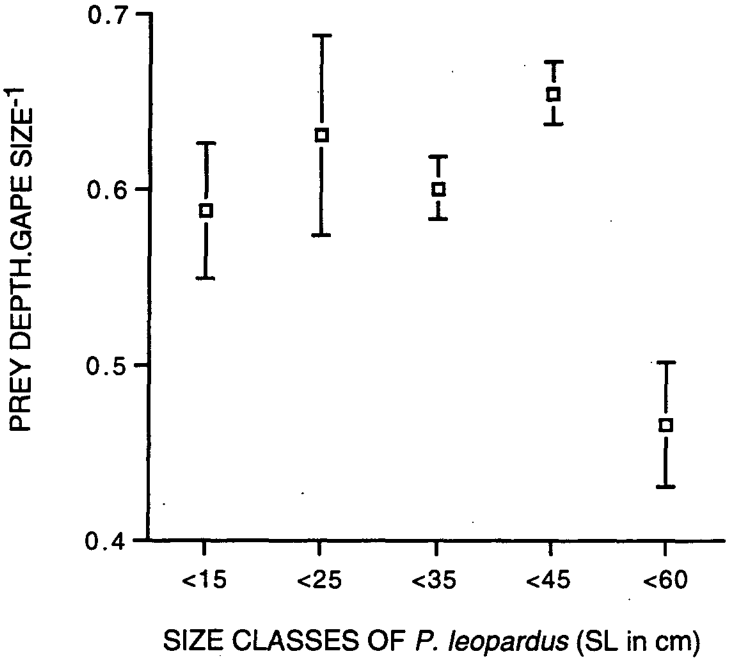


Figure 4.8 The mean (and SE) shape (SL /maximum depth of prey, raw data) of prey of five size classes (<15, 15-24.9, 25-34.9, 35-44.9 and 45-59.9 cm SL) of *P. leopardus* that varied significantly (ANOVA, F=5.607 $_{[4,347]}$, p<0.01 data $\log_{10}$ transformed). Prey of the smallest size class of *P. leopardus* (<15 cm SL) was significantly narrower than prey in any other size-classes (Tukey's pairwise comparisons, p <0.05).

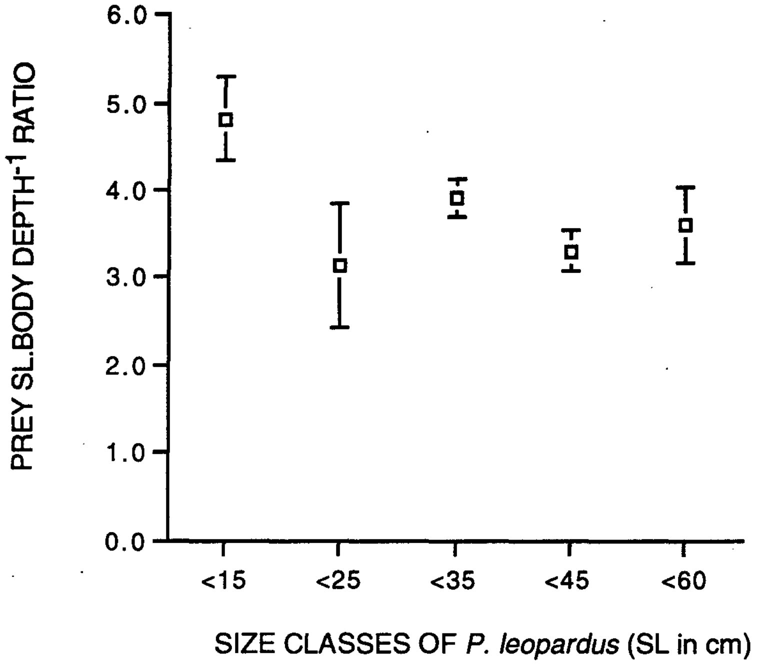


Figure 4.9 The mean (and SE) shape (SL /maximum depth of prey) of the prey of *P. leopardus* living in the four habitats, demersal substrata (D), benthic substrata (B), midwater (M) and soft sediments (S). The shape of the prey differed significantly among habitats (ANOVA, F=2.93 $_{[3,24]}$, p<0.01, data $\log_{10}$ transformed). The shape of the prey in midwater and soft sediment habitats were significantly longer and narrower than prey associated with the demersal reef substrata (Tukey's pairwise comparisons, p <0.05).

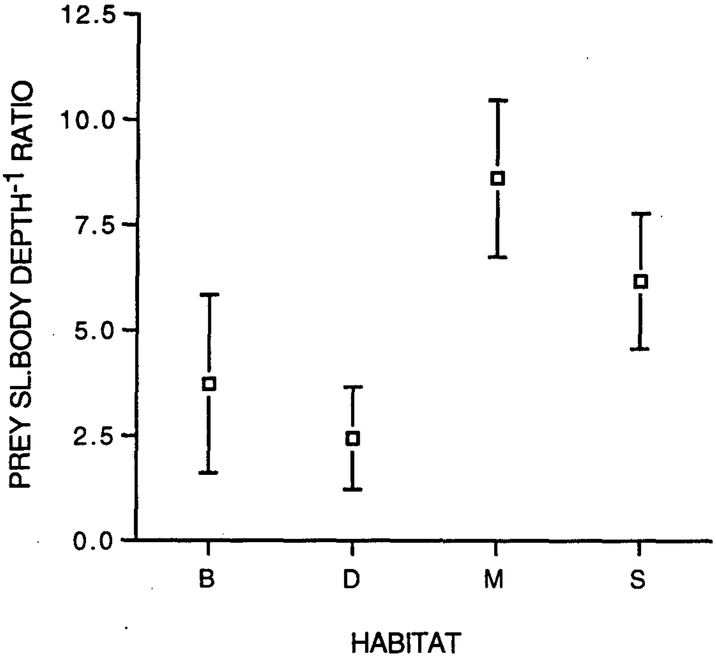


Figure 4.10 The percentage abundance of the most numerous 14 families in the diet of *P. leopardus*. The 14 families are listed in the legend which includes a miscellaneous category of the other families in the diet. The similarity in the diet among size classes of *P. leopardus* is marked by lines below the x axis. All adjacent size classes were tested and only similarity between size classes are shown. The abundance of families were similar among the three smallest size classes (<10, 10-14.9, 15-19.9, $KW_{[2]}$=1.292, p-value =0.529) and the three largest size classes (35-39.9, 40-44.9 and 45-54.9, $KW_{[2]}$=1.50, p-value =0.480). *Plectropomus leopardus* in the mid-range size classes, however, were similar in diet between adjacent size classes only (20-24.9 and 25-29.9, $KW_{[1]}$=1.59, p-value =0.214; 25-29.9 and 30-34.9, $KW_{[1]}$=2.30, p-value =0.127; 30-34.9 and 35-39.9, $KW_{[1]}$=1.23, p-value =0.271).

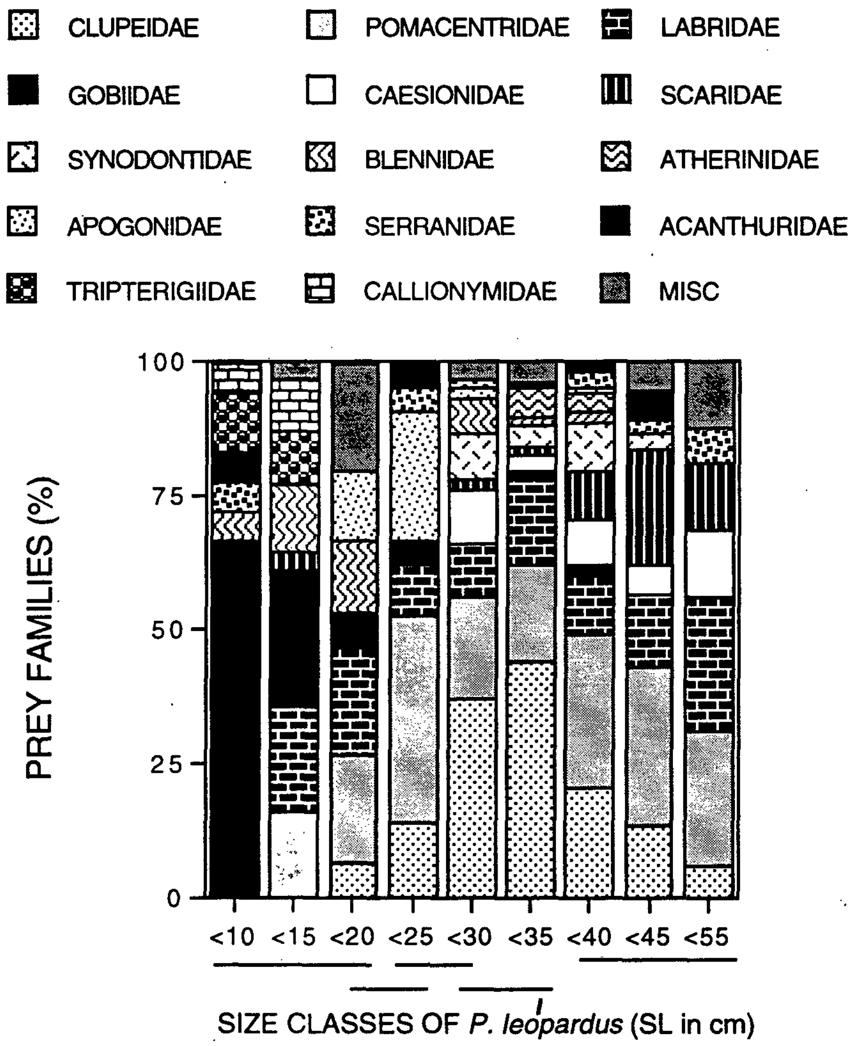


Figure 4.11 The numerical percentage of prey in the four environments, demersal and benthic reef substrata habitats, soft sediment and midwater habitats, that were consumed by five size classes (<15, 15-24.9, 25-34.9, 35-44.9 and 45-54.9) of *P. leopardus*. The habitats of the prey fishes of *P. leopardus* varied among the nine size classes (<10 (52,99), 10-14.9, 15-19.9, 20-24.9, 25-29.9, 30-34.9, 35-39.9, 40-44.9 and 45-54.9, $KW_{[8]}=276.5$, p-value <0.001).

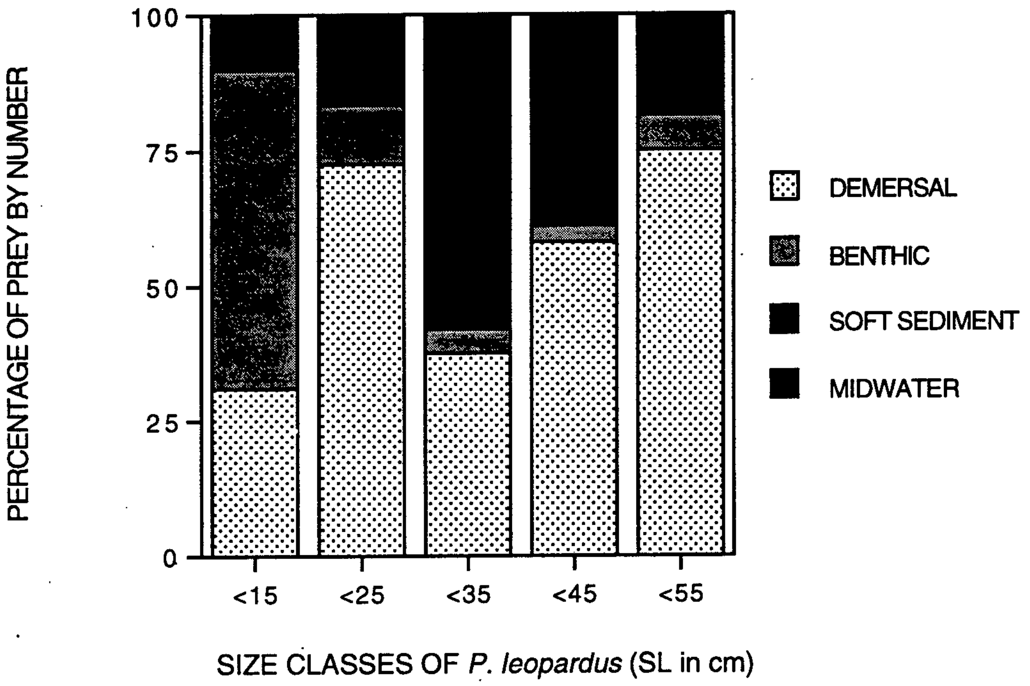


Figure 4.12 The size-structure of the population of *P. leopardus* consuming prey in ten families. Prey in the families Gobiidae, Plesiopidae, Tripterygiidae and Clupeidae were small. Prey in the families Synodontidae, Caesionidae and Scaridae were large, whereas Pomacentridae and Labridae exhibited a wide range of sizes. Surprisingly, the prey size of Serranidae was small (see Table 4.7). The number of identified pey in each size class was 46 in <15, 36 in 15-24.9, 186 in 25-34.9, 135 in 35-44.9 and 16 in 45-54.9.

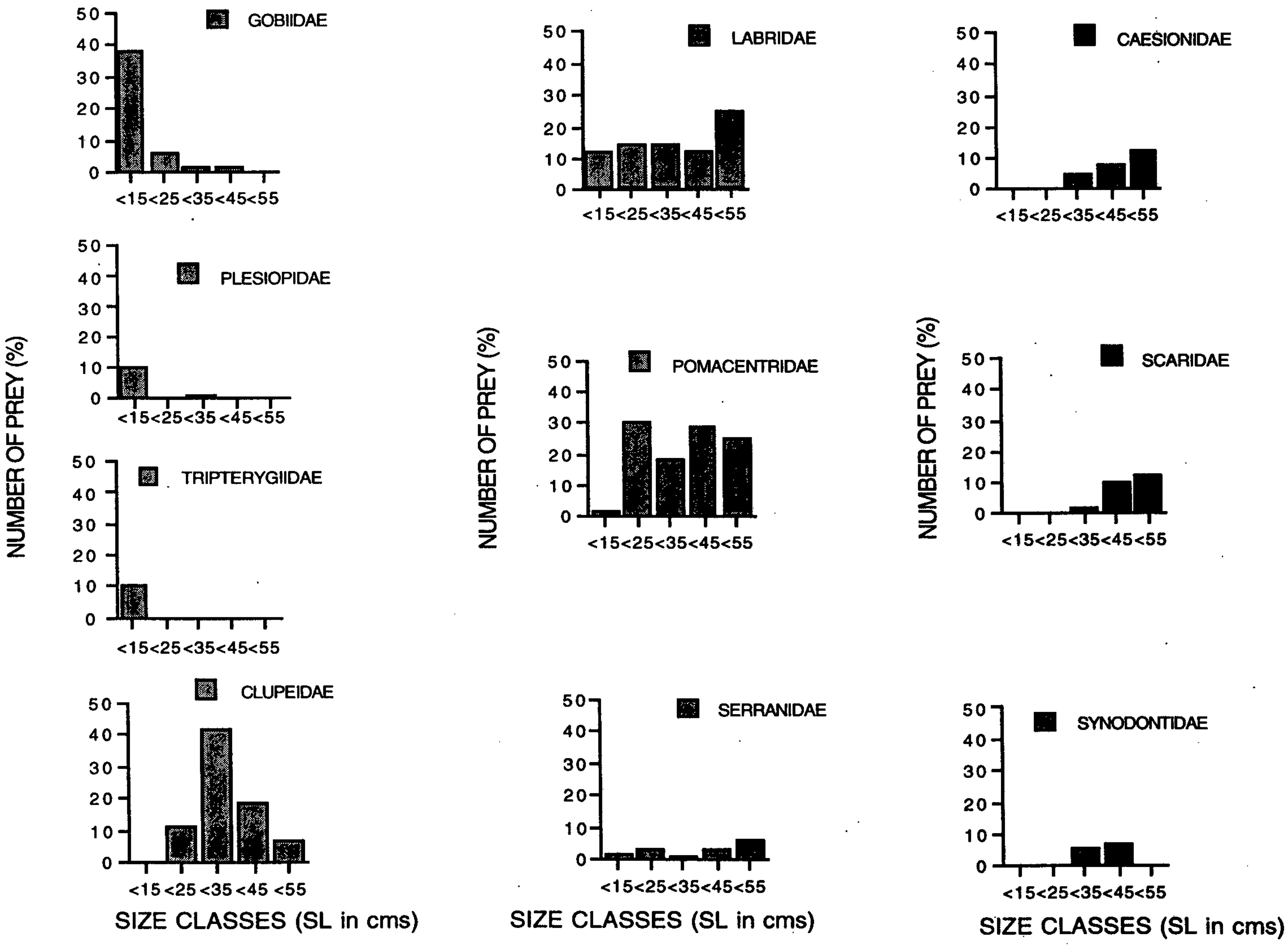


Figure 4.13 The relationship between SL (in mm) and maximum depth (in mm) of prey in two families, Pomacentridae and Caesionidae. In prey in both families, body depth was closely related to standard length (Pomacentridae: Regression $F_{[1,127]}=547.75$, $p<0.01$, $r^2 = 0.81$ and Caesionidae: Regression $F_{[1,25]}=8.156$, $p<0.01$, $r^2 = 0.25$, $\log_{10}$ transformed data for both families). The shape of the prey in the two families differed significantly ($t_{[152]}=3.642$, $p<0.01$).

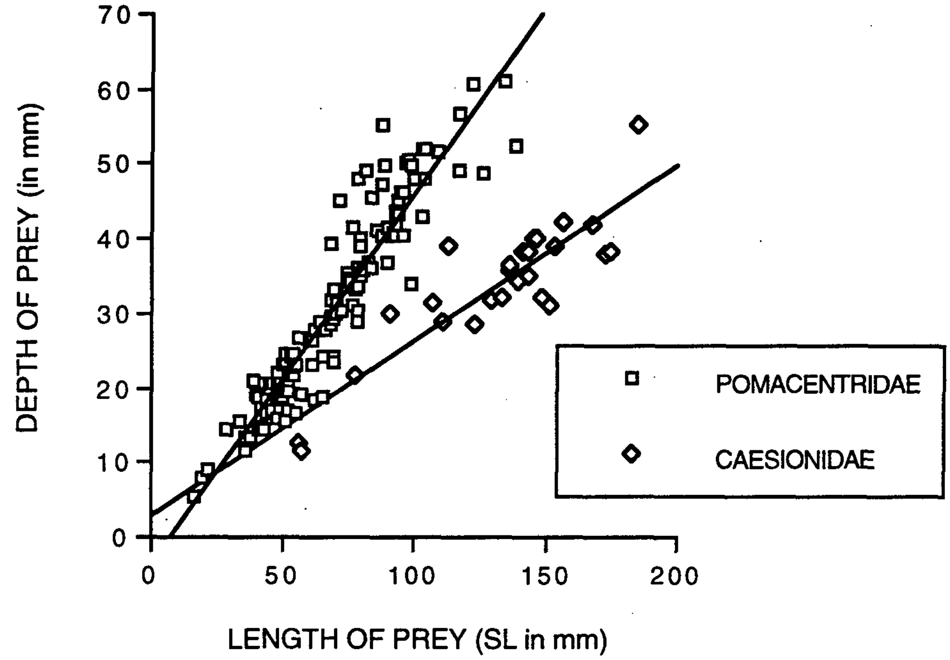
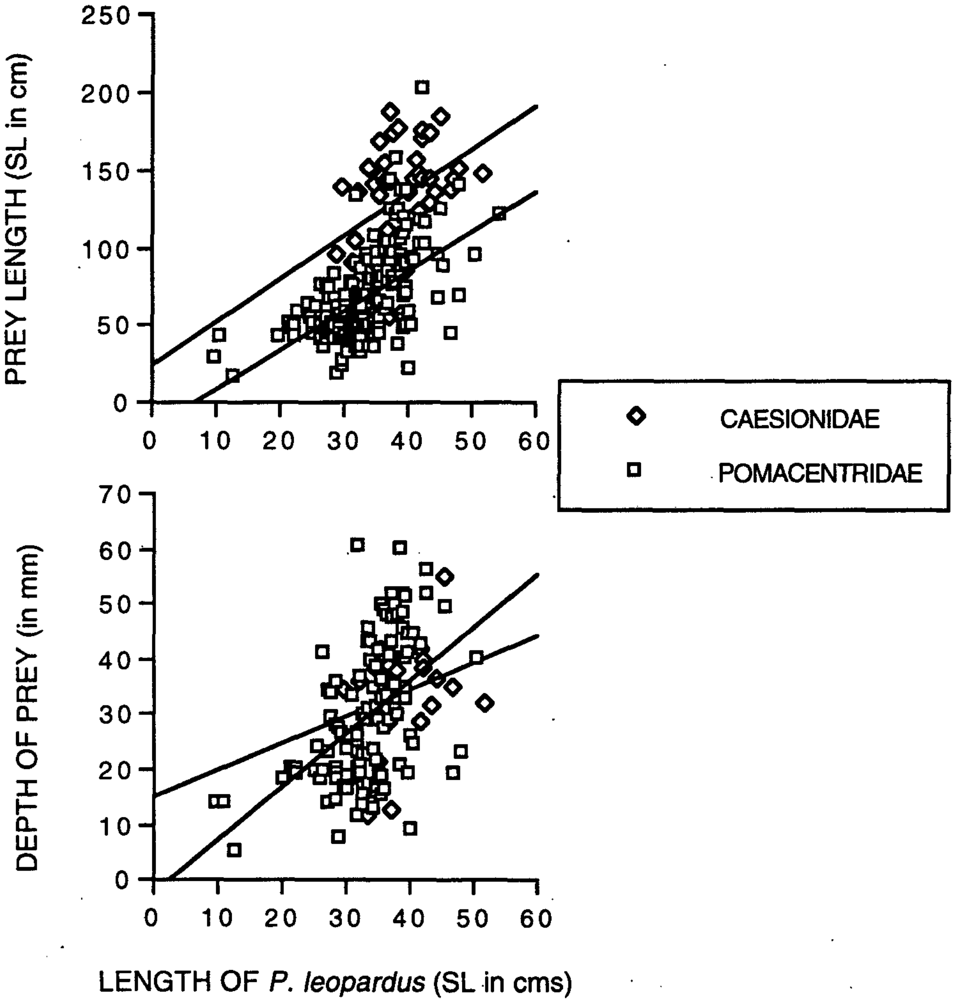


Figure 4.14a The relationship between SL (in cm) of *P. leopardus* and SL (in mm) of the prey it consumed in two families, Pomacentridae and Caesionidae. There was a significant relationship between predator length and SL of pomacentrids (Regression $F_{[1,189]}=68.47$, $p<0.01$, $r^2 = 0.27$ $\log_{10}$ transformed data). For caesionids, this relationship was not significant ($F_{[1,42]}=1.69$, $p=0.201$, $r^2 = 0.04$, $\log_{10}$ transformed data). The length of pomacentrid and caesionid prey consumed by *P. leopardus* differed significantly ($t_{[231]}=2.219$, $p<0.05$, $\log_{10}$ transformed data). *Plectropomus leopardus* consumed pomacentrids shorter than caesionids.

4.14b The relationship between SL (in cm) of *P. leopardus* and maximum depth (in mm) of prey in two families, Pomacentridae and Caesionidae. There was a significant relationship between predator length and depth of pomacentrids (Regression $F_{[1,118]}=27.38$, $p<0.01$, $r^2 = 0.19$, $\log_{10}$ transformed data). For caesionids, this relationship was not significant ($F_{[1,24]}=1.868$, $p=0.184$, $r^2 = 0.07$, $\log_{10}$ transformed data). The depth of prey consumed by *P. leopardus*, however, did not differ significantly between families ($t_{[142]}=0.292$, $p>0.05$, $\log_{10}$ transformed data).



CHAPTER 5

5.0 TEMPORAL VARIATION IN THE DIET OF *P. leopardus* ON THE CENTRAL GBR WITH A COMPARISON TO THE ABUNDANCE OF POTENTIAL PREY FAMILIES

5.1 INTRODUCTION

Seasonal environmental variations which affect the availability of prey are potentially important influences on the structure of fish communities. Evolutionary responses to strong seasonal trends in prey availability include niche segregation of competitors involving seasonal shifts in diet (Desselle *et al.* 1978) as well as diet specialisation among certain piscivorous fishes (Winemiller 1989). Ecological responses of predators to seasonal changes in the availability of prey include corresponding shifts in their diet or foraging locations. On the GBR, coral reef fish communities have very marked annual cycles because of the strong recruitment season (when the young of many species recruit to the reef) in early summer and, to a lesser extent, common spawning seasons (Thresher 1984). In response to annual fluctuations in prey availability, opportunistic piscivores on coral reefs may be expected to exhibit seasonal differences in feeding and this cannot be overlooked when examining their diet.

Variations in prey availability lead to different patterns of feeding by fishes in tropical seas. In a study of 52 piscivorous, tropical estuarine fishes, 37 consumed penaeid prawns when they were abundant; the proportion of prawns in the diet varied seasonally according to the density of prawns in the estuary (Salini *et al.* 1990). Similarly, deep-water snapper, *Pristipomoides filamentosus*, eat more pelagic crustaceans in summer than in winter (Haight *et al.* 1993). On the other hand, tropical snapper, *Lutjanus kasmira,* ate more fish in summer (Oda and Parrish 1981) and *Epinephelus merra* fed mostly on juvenile fishes when they were abundant in summer even though it generally feeds on invertebrates (Randall and Brock 1960). On the southern GBR, seasonal variation in prey availability appears to explain seasonal differences in the diet of *P. leopardus*. *Plectropomus leopardus* consumed mostly pelagic prey fishes (Clupeidae and Engraulidae), which were more readily available in summer, whereas they ate mostly cardinal fishes (Apogonidae) in winter (Kingsford 1992).

Other behaviours, such as spawning, may alter rates of feeding and the diet of *P. leopardus* throughout the year. In another serranid, *Centropristis striata*, a decrease in feeding occurred during the spawning season (Hoff 1970 cited in Hood *et al.* 1994) and a high percentage of empty stomachs (50%) was related to spawning activity (Cupka *et al.* 1993 cited in Hood *et al.* 1994).

On coral reefs the effect of predation as a process structuring reef fish communities is assumed to be uniform throughout the year. Predators are assumed to crop a constant proportion (10%) of the standing crop of the reproductive population (Doherty and Williams 1988). The possibility that predation is seasonally variable has not yet been investigated. Although mortality rates of adult coral reef fishes on the GBR are largely unknown, the only study on seasonal rates of mortality on the GBR provides one piece of indirect evidence for seasonal variation in intensity of predation. At Lizard Island on the northern GBR, the puffer fish, *Canthigaster valentini*, had higher rates of mortality in winter than in summer (Gladstone 1991). The effects of predation on populations of prey could also vary seasonally if piscivores have seasonal differences in rates of feeding, or dietary composition, or both. *Plectropomus leopardus* meets both of these requirements. Firstly, *P. leopardus* have seasonal differences in rates of feeding because daily consumption of food by captive *P. leopardus* was 50% higher in winter than summer (Chapter 3). Secondly, *P. leopardus* have seasonal differences in their diet (Kingsford 1992).

Despite the importance of predation on coral reefs, there have not been sufficient dietary studies of predators to identify the predators of many species of prey (Jones 1991). In addition to knowledge of the diet, information on prey abundance and its vulnerability to predation is required to determine the effects of prey availability on predatory impacts. Such information is very difficult to obtain for large predators on coral reefs because the environment is rich in species of prey. *Plectropomus leopardus* are large, have a piscivorous diet (95.9% fish remains in gut content analysis, Goeden 1978), and they are abundant and widespread of the GBR (Ayling and Ayling 1986). As important predators, *P. leopardus* have the potential to influence the abundance of other coral reef fishes through predation.

Large samples are needed to examine any patterns in the diet of *P. leopardus*. Firstly, approximately one third of collected *P. leopardus* have empty stomachs (Choat 1968; Goeden 1974; Kingsford 1992; see Chapter 4), and most *P. leopardus* have fed on only one prey item (Kingsford 1992; Chapter 4). Secondly, the diet of *P. leopardus* is diverse because it is a generalist predator that lives in an environment characterized by high diversity of prey species. In addition to these sampling problems, inter-reef variability in populations of *P. leopardus* is high. Between reefs, densities differ (Ayling and Ayling 1986) and population length and age structures vary (Ferreira and Russ 1994). Not surprisingly, the diet of *P. leopardus* varied between reefs due to assumed local differences in the availability of specific prey and to differences in reef structure (see Chapter 6). This information suggests that spatial variation should be reduced when examining temporal patterns in feeding of *P. leopardus*. In this study I sampled mostly one reef over time (two reefs were sampled during June). There was no temporal replication of samples because such repeated sampling from one reef was not logistically possible.

The aims of this study were to examine seasonal variations in feeding of a large predatory serranid on the GBR, and compare the overall diet to abundances of families of fishes that were potential prey on midshelf reefs. The specific questions were

1. Does the diet of *P. leopardus* vary temporally on a midshelf reef?
2. Are these differences seasonal?
3. How does the composition of the diet of *P. leopardus* compare with relative abundances of families of potential prey fishes on other midshelf reefs on the Central GBR.

5.2 STUDY SITES, SAMPLING DESIGN AND DATA USED IN THE ANALYSES

Study Sites

The samples were collected from midshelf reefs off Townsville, Little Broadhurst Reef and Big Broadhurst Reef (Fig. 5.1). For the purposes of this study, these two reefs are treated as one called "Broadhurst Reef". Little and Big Broadhurst Reef are about one kilometre apart and their adjoining channel is shallow and may have a live bottom which permits inter-reefal movement (Brown pers. comm.). As *P. leopardus* can move up to 2 km along reefs (Samoilys 1987; Davies 1995), I assumed that some *P. leopardus* may swim between the two reefs. One sample (early winter) included *P. leopardus* from another midshelf reef, Keeper Reef (Fig. 5.1), because the sample size at Broadhurst was lower than other samples (the diets of *P. leopardus* from these two reefs are examined in Chapter 6). All three reefs were zoned General Use B (i.e. all recreational and commercial fishing activities were permitted).

Sampling Design

Plectropomus leopardus were speared by members of the Townsville Skin Diving Club either during day-trips by members (up to 20 spearfishers) or on longer trips by a few club members. All stomachs of *P. leopardus* were fixed within 5 hours of capture. The details of the methods of gut collection and processing are given in Chapter 2.

Fish samples were speared over a two-year period (Table 5.1). Spearfishing requires calm seas (<0.5 m waves). Weather conditions prevented samples from being collected every two months throughout any one year.

Estimating wet weight of prey

Some identified prey were not weighed because they were heavily digested and could not be separated for weighing. In these cases prey weight was estimated from the sample weight, taking into account the digestion stage and the size (when known) of all individuals in the sample. In this study, 20% of weights of prey, which were mostly clupeids, were estimated using this method. The total weight of the prey was unknown in one sample and the mean individual prey weight for the family was used.

The methods of statistical analyses are described in Section 2.5.

5.3 RESULTS

The results are divided into two sections: temporal variation in the diet of *P. leopardus* and a comparison of dietary composition with abundance of potential prey families on the Central GBR.

5.3.1 Temporal variation in the diet of *P. leopardus*

Does the number of prey per stomach vary temporally?

The number of prey per stomach of *P. leopardus* did not vary significantly among the sample months (Fig. 5.2). More than 50% of stomachs contained one prey item in most months except February, where prey items occurred singularly in 33.5% of the stomachs. The presence of small schooling prey fish in the diet of *P. leopardus* was reflected by the proportion of three or more prey per stomach in June (18.8%) and February (12.4%). In August, stomachs of *P. leopardus* contained the smallest number of prey items with 96.3% of the stomachs containing two, one or no prey items.

Can weights of digested prey be used to estimate seasonal consumption?

The proportion of prey in different stages of digestion found in the stomachs of *P. leopardus* did not vary significantly among months (Fig. 5.3). Thus, weights of the digested prey in each sample month were not biased by seasonality in digestion, and any variation among weights of digested prey was attributed to differences in their size. These results justified the use of digested weight of prey as a measure of the diet of *P. leopardus.* The undigested weight of prey was not back calculated from their digested weight because of the scarcity of length-weight information for many species of fishes on coral reefs and the large number of prey species eaten by *P. leopardus*.

Were there temporal differences in the major groups of prey in the diet?

Plectropomus leopardus at Broadhurst Reef ate mostly fish, some crustaceans and a few cephalopods (Table 5.2). Pieces of coral and shell were found in two stomachs, but were not considered prey. The proportions of fish, crustaceans and cephalopods eaten by *P. leopardus* did not vary temporally (Table 5.2). As fish comprised 94.0% of the diet of *P. leopardus* at Broadhurst Reef, the rest of this section focuses on the families and types of prey fish.

Abundance categories of prey fishes

Of the 684 prey fish eaten by *P. leopardus,* 55.9% (382) were identified into 20 families (Table 5.3). *Plectropomus leopardus* ate a wide range of fish species and so families of fishes were classified into four categories: 'Common', 'Occasional', 'Rare' and 'Sporadic'. Three of these categories were based on their frequency of occurrence in the diet of *P. leopardus.* Prey in the 'Common' families occurred in all five months sampled (the mean number of prey in 'Common' families ranged from 2.3-49.3% of the total diet, Table 5.3). Prey in the 'Occasional' families occurred in more than half of the five months sampled (mean number of prey in 'Occasional' families ranged from 0.7-4.8% of the total diet, Table 5.3). Prey in the 'Rare' families occurred in only one of the five months sampled (mean number of prey in the families ranged from 0.7-5.5% of the total diet (Table 5.3). The 'Sporadic' category accommodated the occurrences of schooling, highly mobile prey, that appeared in the diet of *P. leopardus* in large numbers or not at all.

Does family richness of prey fishes vary seasonally?

The family richness in the diet of *P. leopardus* at Broadhurst Reef varied temporally and ranged from eight families in December to 15 in August (Table 5.3). No 'Rare' prey were recorded in either of the summer months (December and February) even though the largest sample of *P. leopardus* was collected in February (n=186).

Differences between measures of diet- % number and % weight

For each family, the total number of individuals in samples ranged from 1 to 79 individuals (max. = Clupeidae, Table 5.3) and the total weight of prey items ranged from 0.33 g to 560.31 g (max. = Pomacentridae, Table 5.4). The proportions of the four categories of prey in the diet of *P. leopardus* at Broadhurst Reef varied depending on the measure (number or weight) used to quantify the diet (Tables 5.3 and 5.4). The two measures, mean percent number and mean percent weight of digested prey differed most between the 'Common' and 'Sporadic' prey categories for the five months sampled. In the 'Common' prey category, the four families represented a mean of 56.0% of the number of fish eaten and 77.4% of the mean weight. In the 'Sporadic' prey category, two families represented 24.4% numerically and only 2.4% of the diet by weight. The 'Sporadic' prey category had the highest variability in the number of prey, as individual monthly means ranged from zero percent in October and December to 68.2% in February. The 'Occasional' and 'Rare' prey categories represented similar proportions in terms of both number and weight. The 'Occasional' prey category included seven families which represented a mean percentage of approximately 16% of the diet by weight and number. Similarly, the 'Rare' category of prey comprised seven families which represented approximately 4% of the diet by weight and number (Tables 5.3 and 5.4).

Habitat categories of prey fishes

The coral reef environment was divided into four broad habitats: soft sediment, midwaters, benthic reef substrata and demersal reef substrata (see Section 2.5). The families of prey fishes were categorised by the habitat in which they were most commonly found (Table 5.5). Prey in six families (and one genus of Gobiidae, *Valenciennia*) lived in the soft sediment habitat. Two habitats, midwaters associated with reefs and the demersal reef environment, both had prey from five different families. Prey in four families dwelled among the benthic hard substrata (Table 5.5). Prey fishes were eaten commonly from two reef habitats. Approximately 80% of prey, measured by number and by weight, lived in the demersal reef and midwater habitats, and prey from the soft sediment and benthic reef habitats represented less than 20% of the diet in both measures (Table 5.5).

There were no seasonal changes in the use of different habitats where *P. leopardus* were feeding. The number of prey from the four habitats varied temporally ($K\text{-}W_{[4]} = 80.91$, Monte Carlo p-value <0.001), but not seasonally because numbers of prey varied between the two months in both seasons (Winter: $K\text{-}W_{[3]} = 16.73$, Monte Carlo p-value $=0.012$ and Summer: $K\text{-}W_{[3]} = 44.18$, Monte Carlo p-value <0.001).

Which families were most important in the diet?

Pomacentridae was the most important family in the diet of *P. leopardus* as it was ranked either first or second in every month by the index of relative importance (see Section 2.5, Table 5.6). The mean IRI of Pomacentridae (29.2%) was more than twice the value of any other family. The next most important prey were in the other three 'Common' families (Caesionidae, Scaridae and Labridae) plus the Clupeidae in the 'Sporadic' family (Table 5.6). Prey in all the 'Common' families ranked in the top four or five IRI, except in February when the Synodontidae in the 'Occasional' category ranked fourth. Clupeidae dominated the diet in June and February but ranked last or were absent in the other three months. Clupeidae were eaten by one third the number of *P. leopardus* that consumed Pomacentridae. A total of 122 clupeids were eaten by 34 *P. leopardus* (3.6 prey/predator) while 103 pomacentrids were eaten by 90 *P. leopardus* (1.1 prey/predator).

What is the degree of dietary overlap between seasons?

Overall, *P. leopardus* showed no obvious seasonal patterns of feeding (Table 5.7). When the abundances of Clupeidae in the 'Sporadic' family were similar, dietary overlap was high. Dietary overlap was high among August, October and December when 'Sporadic' prey were absent from the diet, and between June and February when clupeids were abundant in the diet.

Temporal differences in the numerical composition of the diet

The number of prey fish in each family differed among sample months significantly, but there were no overall seasonal trends (Table 5.3). The largest temporal difference was in the abundance of prey in the 'Sporadic' category, which dominated the diet of *P. leopardus* in June (winter) and February (summer). When the clupeids were removed from the analysis, there were no temporal trends in the abundance of families in the diet (Table 5.3). Of the 20 families eaten by *P. leopardus*, the Synodontidae was the only one that appeared to vary in occurrence seasonally. One synodontid occurred in the two winter samples compared to 10 in the two summer samples (see Table 5.3).

Prey in the 'Common' families dominated the diet in every month on the basis of weight and dominated in three of the five months on the basis of number. The number of prey in the four 'Common' families did not vary significantly among months (Table 5.3). Pomacentridae appeared to be the 'staple diet' of *P. leopardus*, and the total number of the other three 'Common' families, Labridae (30), Scaridae (24) and Caesionidae (23), were similar in the diet.

Summary of temporal variation in the diet

Many aspects of the diet were examined for monthly or seasonal (summer and winter) differences or both (Table 5.8). Seven of the eight aspects of the diet were examined for temporal differences among months. Three did not vary significantly. The number of prey per stomach, the proportion of prey in different stages of digestion in the stomach and proportions of major prey items of *P. leopardus* did not vary throughout the year . When classified by families and by habitats, the diet of *P. leopardus* varied numerically among months (Table 5.8). Also, the relative importance of families of fish in the diet and the weight of the stomach contents in *P. leopardus* varied monthly but not seasonally (Table 5.8). Family richness in the diet varied seasonally as no 'Rare' prey were recorded in winter (Table 5.8).

5.3.2 Comparison of dietary composition with abundance of potential prey families on the central GBR

Williams and Hatcher (1983) measured the abundance (kg/1000 m^2) of families of fishes on the shallow reef slope of one midshelf reef, Rib Reef, on the Central GBR (near Townsville) using explosive collections. The ten most abundant families of fishes by weight each represented more than 1% of the total sample (Table 5.9). The five top ranking families, in terms of biomass of reef fishes, were identical to those recorded in the diet of *P. leopardus* (this study), and represented similar proportions of the total prey biomass, 81.4% and 84.2% respectively (Table 5.9). Caesionidae was the most abundant family on midshelf reefs (50.7% of the total catch). Pomacentridae ranked second in abundance (18.5% of the total catch). Scaridae (5.5%), Serranidae (3.7%) and Labridae (3.0%) ranked third, fourth and fifth respectively, and each family represented less than 6% of the catch. Prey in five of the 10 most abundant families were not eaten by *P. leopardus* on Broadhurst Reef and 16.9% of the total diet (in weight) of *P. leopardus* comprised prey in another 16 rarer families.

The two most abundant families of fish in the diet of *P. leopardus,* Pomacentridae and Caesionidae, were the two most abundant families on the midshelf reefs (see Williams 1982; Williams and Hatcher 1983). Nearly one third of the prey eaten by *P. leopardus* at Broadhurst Reef were pomacentrids (28.1% of the total digested weight) and one fifth of the prey were caesionids (20.7%). On the midshelf reefs, however, caesionids represented over half the biomass of all families of fishes and this abundance was not reflected in the diet of *P. leopardus*. Pomacentrids were recorded slightly more frequently in the diet of *P. leopardus* compared to their relative biomass on midshelf reefs. Scaridae (18.4%) and Labridae (12.8%) were more abundant in the diet of *P. leopardus* than their relative biomass on the midshelf reefs: the abundance of both families in the diet were approximately three times their relative biomass on the midshelf reefs. The family Serranidae was eaten in a similar proportion to it's occurrence on the midshelf reefs (Table 5.9).

5.4 DISCUSSION

5.4.1 Temporal variation in the diet of *P. leopardus*

Plectropomus leopardus on Broadhurst Reef consumed at least 20 different families of fish, which varied widely in size, shape and behaviour. Overall, there were no seasonal patterns in the dietary composition of *P. leopardus*, except in the breadth of the diet. Pomacentridae was the most important family in the diet of *P. leopardus* with monthly IRI's over the year ranging between 14 and 40%. Caesionidae, Labridae and Scaridae were also important in the diet of *P. leopardus*. Clupeids were the dominant prey in a summer and a winter month and accounted for most of the variation between months. Due to differences in the abundances of clupeids, dietary overlap was high among the August, October and December months (when clupeids were mostly absent) and between June and February (when clupeids were abundant).

Seasonal trends occurred in the abundance of prey in only one of the 20 families in the diet of *P. leopardus*. Synodontidae, voracious piscivores dwelling on the sandy-rubble habitat (see Sweatman 1984), were recorded 10 times more often in summer (December and February) than in winter

(June and August). Synodontidae feed on newly settled recruits and juveniles of site-attached species of reef fishes (Sweatman 1984; pers. obs.) and the summer pulses of new recruits provide an abundance of prey for these predators. Synodontids in the stomachs of *P. leopardus* often had fresh or partially swallowed prey fishes in their stomachs, which suggests that Synodontids may be eaten by *P. leopardus* when they are engaged in feeding themselves.

The results of this study suggest that none of the seasonal differences in the diet of *P. leopardus* from the southern GBR (Kingsford 1992) occurred in the central GBR. Kingsford (1992) found seasonal differences in two groups of fishes in the diet of *P. leopardus* at One Tree Reef (OTR). Pelagic fishes (clupeids and engraulids) were recorded more in summer than winter. Apogonids were recorded only in winter, but seven of the 13 apogonids eaten were in one fish only. On the central GBR there were no seasonal differences in the number of clupeids or apogonids eaten by *P. leopardus* throughout the year. Clupeids were eaten in both winter sample months and one summer month. One apogonid each was eaten in four of the five sample months.

Numerically, prey categorised by family and habitat varied monthly, but there were no overall seasonal trends. Monthly differences in the diet of *P. leopardus* were due to fluctuations in the occurrence of one family, the Clupeidae, which were the most commonly occurring family in the 'Sporadic' category. As clupeids were numerically dominant prey in the stomachs of relatively few *P. leopardus,* they were not a highly important component of the overall diet. Thus, the major conclusion of this study is that the diet of *P. leopardus* does not vary significantly throughout the year.

Unlike near-shore environs, midshelf coral reefs are not strongly affected by seasonal tropical rains and related fluctuations in potential prey items such as schooling prawns (Salini *et al.* 1990). While the diet of piscivores in tropical estuaries varied seasonally due to the abundance of suitable food items other than fish (Salini *et al.* 1990), *P. leopardus* were highly piscivorous (94% of the diet by number) throughout the year. Kingsford (1992) also found that the proportion of fish eaten by *P. leopardus* did not vary between summer and winter. The diet of *P. leopardus* differs from the tropical snapper, *Lutjanus kasmira*, and the grouper, *Epinephelus merra*, which consume more fish in summer (Randall and Brock 1960; Oda and Parrish 1981). In summer, *E. merra* fed on the abundant juvenile fishes (Randall and Brock 1960). Both of these predators are less piscivorous than *P. leopardus.* On the GBR, *P. leopardus* rarely feed on juveniles of any species (Chapter 4) and there is no evidence to suggest that they respond to the influx of large numbers of new recruits in summer.

The family richness (or breadth) of the diet of *P. leopardus* was lower in summer regardless of the presence of 'Sporadic' prey. Prey in 'Rare' families, that occurred only once or twice in the diet of *P. leopardus* throughout the year, were eaten only in winter. This increase in family richness in the diet of *P. leopardus* in winter did not result from larger sample sizes, or more identifiable prey in winter. The largest sample occurred in summer (n=186, number of prey = 131), and both a summer (n=51) and a winter (n=54) month had low numbers of prey. Interestingly, the only study on seasonal mortality rates of a coral reef fish agrees with the results of this study. The slow-moving, toxic pufferfish, *Canthigaster valentini,* had a higher mortality rate in winter than in summer in the northern GBR (Gladstone 1991). *Canthigaster valentini* was a 'Rare' prey eaten in winter by *P. leopardus* in the southern GBR (Chapter 6). Prey in 'Rare' families include a wide variety of sizes and behaviours, and they live in numerous types of habitat. For example, Bothidae are a cryptic family which live in sandy habitats, whereas Muraenidae are shy fish that hide amongst coral substrata (Randall *et al.* 1990).

Seasonal differences in the family richness of the diet of *P. leopardus* may be related to seasonal differences in consumption of food (see Chapter 3) rather than seasonal differences in prey availability. 'Rare' prey of *P. leopardus* were eaten only in winter even though they were available throughout the year. As the preference of predators is weaker when they are hungry and their preferred prey are scarce (Murdoch *et. al.* 1975), *P. leopardus* may be less selective about their prey species in winter than in summer because they have higher food requirements. Prey in 'Rare' families included toxic or cryptic species that do not appear to be ideal prey. An alternative explanation for the increase in consumption of 'Rare' prey in winter is that feeding behaviour of *P. leopardus* changes seasonally, but there was no evidence to support this. The number of prey consumed by *P. leopardus* did not vary seasonally in this study and seasonal changes in habitat use have not been documented in the two behavioural studies of *P. leopardus* (Goeden 1974; Samoilys 1987).

Hixon (1991) found that piscivores reduced species richness of local prey on coral reefs. Species richness of assemblages of fishes occupying natural and artificial reefs at St Thomas, U.S. Virgin Islands, decreased as the number of piscivores increased. Hixon (1991) considered that the piscivores in this small coral reef community extirpated the locally rare species. While it is very doubtful that *P. leopardus* would have such an impact on any prey species on the GBR because of the wide variety of prey they consume, *P. leopardus* may affect small populations of rare prey species in winter (such as *C. valentini*).

Plectropomus leopardus do not feed continuously and the results of this study suggest that about 50% of the population of *P. leopardus* at any one time would be capable of feeding. As *P. leopardus* digested, on average, 88.2% (+/. 3.85) of prey in 24 hours (Chapter 3), individuals with empty stomachs were considered not to have eaten 24 hours prior to capture. On Broadhurst Reef 30-42% of the population of *P. leopardus* had not fed for over 24 hours. In addition to these *P. leopardus*, many had only well digested prey items in their stomachs (Digestion Stages 6 and 7, see Fig. 5.3 and Chapter 2) and thus would be able to feed again.

The diet of *P. leopardus* comprises fish in families that live in all four broad habitats on coral reefs: soft sediments, midwaters, benthic reef substrata and demersal reef substrata. The variety of prey fishes in the diet of *P. leopardus* was reflected in the large home ranges of *P. leopardus* (Samoilys 1987), which included several habitats (Goeden 1978; Kingsford 1992). Yet, *P. leopardus* fed most commonly on prey from the demersal reef environment and from midwaters, consuming four times the number of prey that were eaten from the other two habitats. Families of prey that live on or over soft sediments, or dwell among the benthic reef substrata are at less risk of predation by *P. leopardus*. These two habitats contain two of the most diverse and most abundant families of fishes (Gobiidae and Blenniidae).

As encounter rates of predators affect the rate of prey mortality (Shulman 1985), prey in habitats frequented by *P. leopardus* (e.g. demersal reef) should be eaten more than prey in other habitats (e.g. soft sediments). Similarly to *P. leopardus,* predators in other coral reef systems focus on prey in reef habitats. In a study in the Caribbean, tethered prey consistently disappeared from sites close to areas of natural reef rather than from areas of soft sediment (Shulman 1985).

The abundance of small schooling prey fishes, such as clupeids, are spatially (see Chapter 6) and temporally variable in the diet of *P. leopardus.* The abundance of clupeids in the diet affected dietary overlap more than any other family of prey in this study. Clupeids occurred either in large numbers in the diet, or not at all. The presence of caesionids and clupeids in the diet of *P. leopardus* indicated that schooling fishes, which occur in the midwaters, are targeted by *P. leopardus,* and this is corroborated by field observations. Samoilys (1987) concluded that feeding behaviour played a major role in determining movements in *P. leopardus. Plectropomus leopardus* move out of their usual feeding habitat, the demersal reef, to pursue these pelagic prey.

Plectropomus leopardus frequently follow large schools of pelagic planktivores (Goeden 1978; Samoilys 1987) and hover high in the water column only in the presence of pelagic prey (Kingsford 1992). Large schools of pelagic prey fishes, which move slowly along the reef edge while feeding, appear to attract the attention of *P. leopardus* more than the smaller, more mobile feeding aggregations of demersal fishes (e.g. Scaridae pers. obs.). Goeden (1978) watched all *P. leopardus* except the smallest vacate an area to follow a school of Pempherididae. Similarly, the study site of Samoilys (1987) was unusually depauperate of *P. leopardus* after a large school of Clupeidae had passed through the area. Groups of *P. leopardus* feed on schools of midwater fishes with apparent success. In this study caesionids frequently occurred in the stomachs of *P. leopardus* caught near a school of this prey.

5.4.2 Comparison of diet to abundance of potential families of prey fish on the Central GBR

The ideal method to examine feeding behaviour in predators is to compare their diet to the abundance of available prey. Estimates of abundance of potential prey can be related to the diet of the predator, and repeated estimates can be used to determine the effect of predation. Yet, problems of scale in spatial correlations of predators and prey need to be considered (see Rose and Leggett 1980) as well as sampling methods. It would be difficult to compare prey abundance to the diet of *P. leopardus* because of the huge diversity and abundance of prey. Surveying large numbers of different, often highly abundant, species of fishes (in 20 families) in a variety of habitats is problematic. In visual censuses, observers measure abundances of species either with low precision (log-scale abundances, see Williams 1991) over large areas of reefs, or in exact counts on small parts of reefs. Surveying highly abundant schooling fishes, that are transient members of the local prey community, is difficult. Thus, visual censuses were not considered as a method to sample availability of prey of *P. leopardus*. Explosive collections are a more effective method of estimating prey abundances for *P. leopardus.*

This study focused on numerical assessment of the abundance of prey in the diet. The majority of *P. leopardus* eat prey singularly and prey weights were reduced by digestion. The explosive collection used in this comparison measured abundance in terms of biomass. The abundance of digested weight of prey in families in the diet of *P. leopardus* was compared to the standing stock of prey (kg/1000 m^2) on another midshelf reef (Williams and Hatcher 1983).

On Broadhurst Reef *P. leopardus* fed on the most abundant prey fishes. The five most abundant families of fishes in the diet of *P. leopardus* (Pomacentridae, Caesionidae, Scaridae, Labridae and Serranidae, using digested weights as the measure) were the same as the top five ranking families of fishes found on other midshelf reefs (Williams and Hatcher 1983). Furthermore, these five families were represented in similar proportions in terms of biomass, but their rank order was not identical (Table 5.9).

Plectropomus leopardus feed disproportionately on demersal reef fishes on the midshelf reefs. Pomacentridae were consumed more than Scaridae and Labridae, perhaps because they were the most abundant family of demersal prey fish on the midshelf reefs. Caesionids were found in the diet of *P. leopardus* in abundances that were proportionally lower than on reefs. The reversal of ranks of the two major prey species, Pomacentridae and Caesionidae, may be explained by their availability to *P. leopardus.* Pomacentrids are small, benthic dwelling fishes that coexist with *P. leopardus*, whereas caesionids are larger, schooling and more mobile, commonly occurring on the reef edge (Randall *et al.* 1990). Thus, it seems likely that caesionids will not always be available as prey to *P. leopardus.* On Broadhurst Reef, *P. leopardus* did not feed on all families of prey that are abundant on midshelf reefs. Five of the 10 most abundant families of fishes on midshelf reefs were not eaten by *P. leopardus* on Broadhurst Reef.

Furthermore 16.9% of the total diet (in weight) of *P. leopardus* comprised another 16 rarer families of prey fishes. Some of the families abundant on midshelf reefs, such as Haemulidae, have never been found in the diet of *P. leopardus* (Chapter 4).

There are two other explanations for the differences between prey abundance and the dietary composition of *P. leopardus*. First, differences in prey abundance between Broadhurst Reef and Rib Reef may have occurred (see Williams 1991). Second, explosive collections may be more effective in capturing some families of fishes than others, irrespective of their abundance on reefs. Thus, collections might not accurately represent the abundance of fishes available to *P. leopardus* as prey. As explosives kill fish by rupturing their swim bladders, some families of coral reef fishes, which do not have swim bladders (e.g. Gobiidae), are not killed by the explosion. Furthermore, differences in buoyancy among pelagic, demersal and benthic fishes may favour retrieval of the buoyant pelagic species (e.g. Caesionidae) over benthic species (e.g. Scorpaenidae).

5.4.3 Conclusion

The diet of *P. leopardus* on a midshelf reef, Central GBR did not vary among months or seasonally (between summer and winter), except in family richness. Family richness of the diet was higher in winter than in summer. Overall, Pomacentridae was the most important family in the diet of *P. leopardus*, and the next most important families were Caesionidae, Labridae, Scaridae and Clupeidae. Seasonal variation in the number of prey in the diet of *P. leopardus* occurred in only one of the 20 families, Synodontidae. These results differ from Kingsford's (1992) study on the southern GBR which found seasonal variation in the abundance of pelagic fishes (mostly clupeids) and apogonids. The top five ranking families in the diet of *P. leopardus* (ranked by digested weight, Pomacentridae, Caesionidae, Scaridae, Labridae and Serranidae) were identical to the top five families in biomass on nearby reefs (Williams and Hatcher 1983). Furthermore, proportions of total biomass were similar, but prey in families were not eaten in exactly the same ranking as biomass on the midshelf reef. Ranks of the two major prey species, Pomacentridae and Caesionidae, were reversed.

Table 5.1 The collection of samples of *P. leopardus* at Broadhurst Reef, unless specified, for the temporal study. Information on season, month, date and sample size (n) is included.

Season	Month	Reef	Date	n
winter	June		10/6/91	65
winter	June	Keeper	23/6/91	43
winter	August		5-7/8/90	135
spring	October		5-7/10/90	185
summer	December		30/11/91- 1/12/91	128
summer	February		3-5/2/92	186

Table 5.2 The number of prey fish, crustaceans and cephalopods eaten by *P. leopardus* collected in June (6), August (8), October (10), December (12) and February (2). The proportion of fish, crustaceans and cephalopods in the diet of *P. leopardus* did not vary temporally (K-$W_{[4]}$= 0.922, Monte Carlo p-value = 0.925)

PREY	MONTHS					TOTAL
GROUPS	6	8	10	12	2	PREY
fish	123	109	141	104	208	684
crustaceans	4	6	8	5	10	35
cephalopod	1		1	2	3	6
coral & shells			2			2
unknown				2		2
TOTAL PREY	128	115	151	113	221	728
Number of *P. leopardus*	108	135	185	128	186	742

Table 5.3 The number of prey in each family consumed by *P. leopardus* collected in June (6), August (8), October (10), December (12) and February (2). The families are grouped by category ('Common', 'Occasional', 'Rare' and 'Sporadic', defined in Section 5.3.2). For each category, the percentage of prey is calculated for each month (value underlined) and averaged over all months (mean % in second last column and SE bracketed in last column). The number of prey in families in the diet of *P. leopardus* differed significantly among sample months (K-$W_{[4]}$= 49.79, Monte Carlo p-value < 0.001) but, when clupeids were omitted from the analysis, there were no significant differences (K-$W_{[3]}$= 0.367, Monte Carlo p-value = 0.454). Also, the number of prey in the four 'Common' families did not vary significantly among months (K-$W_{[3]}$= 0.364, Monte Carlo p-value = 0.947).

PREY	**MONTHS**					**TOTAL**	**MEAN**	**(SE)**
FAMILIES	**6**	**8**	**10**	**12**	**2**		**%**	**total%**
Common	33.33	66.67	74.60	86.27	19.38	**181**	**56.05**	(12.71)
Pomacentridae	16	20	31	24	12	103		27.0%
Labridae	7	6	6	5	7	31		8.1%
Scaridae	4	4	5	8	3	24		6.3%
Caesionidae	2	6	5	7	3	23		6.0%
Occasional	12.34	20.37	20.63	13.72	12.40	**56**	**15.86**	(1.89)
Blenniidae	4	3	4	3		14		3.7%
Synodontidae		1	1	2	8	12		3.1%
Gobiidae	2	3	1		4	9		2.3%
Scorpaenidae	2	1	4		1	8		2.1%
Serranidae	1	1	2	1	1	6		1.6%
Apogonidae		1	1	1	1	4		1.0%
Pinguipedidae	1	1			1	3		0.8%
Rare	2.50	11.11	4.76	0	0	**12**	**3.66**	(2.06)
Sphyraenidae		3				3		0.8%
Nemipteridae			2			2		0.5%
Platycephalidae		2				2		0.5%
Bothidae	1					1		0.3%
Exocoetidae			1			1		0.3%
Mullidae		1				1		0.3%
Muraenidae	1					1		0.3%
Sporadic	51.85	1.85	0	0	68.21	**133**	**24.38**	(14.78)
Clupeidae	42	1			79	122		31.9%
Atherinidae					11	11		2.9%
Total prey	83	54	63	51	131	382		
Number of families	12	15	12	8	12	20		
Number of *P. leopardus*	108	135	185	128	186	742		

Table 5.4 The weights of each family in the diet of *P. leopardus* collected in June (6), August (8), October (10), December (12) and February (2). The families are grouped by category ('Common', 'Occasional', 'Rare' and 'Sporadic'). In the last two columns, the total weight of each family summed for all months (WT) is expressed as a percentage of the total diet. For each category, the monthly percentage of the diet (underlined) and overall mean percentage (and standard error) of all five months (underlined and in bold) are calculated.

PREY	**MONTHS**					**TOTAL**	
FAMILIES	**6**	**8**	**10**	**12**	**2**	**WT** **MEAN**	**%** **(SE)**
Common	71.57	78.84	84.07	94.41	58.55	**77.40**	**(6.01)**
Pomacentridae	136.22	376.54	560.31	336.40	131.55	1541.0	28.1%
Caesionidae	235.48	266.15	251.76	278.75	83.41	1116.0	20.3%
Scaridae	144.03	201.19	341.47	213.95	109.91	1011.0	18.4%
Labridae	172.59	35.13	163.01	240.61	89.35	700.7	12.8%
Occasional	20.26	6.67	13.10	5.58	32.64	**16.20**	**(5.15)**
Serranidae	11.50	33.64	118.78	18.65	68.23	250.8	4.6%
Pinguipedidae	117.70	22.93			46.82	187.5	3.4%
Synodontidae		3.58	28.52	24.68	83.77	140.6	2.6%
Blenniidae	46.30	2.29	28.72	15.64		92.9	1.7%
Gobiidae	31.57	4.06	8.78		20.21	65.2	1.2%
Scorpaenidae	13.61	7.69	12.65		9.93	43.9	0.8%
Apogonidae		0.56	7.67	4.29	1.94	14.5	0.3%
Rare	5.04	14.91	2.86	0	0	**4.01**	**(2.78)**
Mullidae		89.72				89.7	1.6%
Spyraenidae		186.33				76.8	1.4%
Nemipteridae			129.73			29.7	0.5%
Bothidae	16.83					16.8	0.3%
Exocoetridae			15.01			15.0	0.3%
Muraenidae	5.19					5.2	0.1%
Platycephalidae		0.65				0.6	>0.1%
Sporadic	3.12	0.03	0	0	8.81	**2.39**	**(3.83)**
Clupeidae	30.02	0.33			35.45	35.45	1.2%
Atherinidae					26.90	26.9	0.5%
Total	961.04	1231.0	1666.4	1133.0	707.47	5698.9	
Number of *P. leopardus*	108	135	185	128	186	742	

Table 5.5 The families of prey fishes classified by their association with four broad habitats on the reef. Two habitats are strongly related to the reef substrata, demersal (with loose benthic association) and benthic (closely associated with benthos). The other two habitats are midwater and soft sediment. 'Common' families of prey are denoted by '*', 'Occasional' families of prey are denoted by '.', 'Rare' families of prey are not marked and 'Sporadic' families of prey are denoted by '!'. (See Section 2.5 for definition of these categories) The last two rows of the table are the percentage of prey, by number (#) and by weight (wt), associated with each habitat.

	DEMERSAL	BENTHIC	MIDWATER	SOFT SEDIMENT
	.Apogonidae *Labridae *Pomacentridae *Scaridae .Serranidae	.Blenniidae .Gobiidae Muraenidae .Scorpaenidae	!Atherinidae *Caesionidae !Clupeidae Exocoetidae Sphyraenidae	Bothidae Mullidae Nemipteridae .Pinguipedidae Platycephalidae .Synodontidae
#	44.4%	8.4%	41.9%	5.8%
wt	55.0%	3.8%	23.7%	8.5%

Table 5.6 The index of relative importance (see Section 2.5 for explanation) expressed as a percentage for each family of prey consumed by *P. leopardus* collected in June (6), August (8), October (10), December (12) and February (2). The families are grouped by category ('Common', 'Occasional', 'Rare' and 'Sporadic'). The last column includes the the mean of each family (averaged over the five months) and the total percentage of the IRI for each category (in bold).

PREY	**MONTHS**					**MEAN**
FAMILIES	**6**	**8**	**10**	**12**	**2**	
Common						**66.6%**
Pomacentridae	16.34	35.31	42.22	38.38	13.95	29.2
Caesionidae	13.48	17.42	12.16	19.16	7.06	13.8
Scaridae	9.96	12.68	15.14	17.29	8.93	12.8
Labridae	12.68	7.12	9.98	15.52	9.03	10.8
Occasional						**16.1%**
Serranidae	1.22	2.43	5.47	1.80	5.21	3.2
Blenniidae	4.88	2.88	4.00	3.63		3.1
Synodontidae		1.09	1.71	3.05	9.02	3.0
Pinguipedidae	6.74	1.95			3.70	2.5
Gobiidae	2.91	2.96	1.05		2.98	2.0
Scorpaenidae	1.94	1.27	3.47		1.09	1.6
Apogonidae		0.95	1.02	1.17	0.52	0.7
Rare						**3.8%**
Sphyraenidae		6.20				1.2
Mullidae		4.93				1.0
Nemipteridae			2.51			0.5
Platycephalidae		1.88				0.4
Bothidae	1.49					0.3
Exocoetidae			1.26			0.2
Muraenidae	0.89					0.2
Sporadic						**13.2%**
Clupeidae	27.49	0.94			32.35	12.0
Atherinidae					6.16	1.2
Total number of prey	**83**	**54**	**63**	**51**	**131**	**99.7%**
Number of *P. leopardus*	108	135	185	128	186	

Table 5.7 Values of dietary overlap (Schoener *a*) for each pairwise comparison of the diet of *P. leopardus* in the five months. Values of Schoener *a* are calculated based on proportional values of the index of relative importance (IRI). The values are classified into three groups: <0.30 = low dietary overlap, 0.31-0.60 = medium dietary overlap and >0.60 = high dietary overlap.

MONTHS	AUGUST	OCTOBER	DECEMBER	FEBRUARY
JUNE	0.58 medium	0.57 medium	0.57 medium	0.75 high
AUGUST		0.77 high	0.79 high	0.48 medium
OCTOBER			0.84 high	0.49 medium
DECEMBER				0.44 medium

Table 5.8 Summary of temporal variation in aspects of the diet of *P. leopardus*.

ASPECTS OF DIET	**TEMPORAL VARIATION**	
	Monthly	**Seasonal**
Number of prey per stomach	no difference	not tested
Digestion stages of prey	no difference	not tested
Weight of undigested prey	varied	no difference
Major prey types	no difference	not tested
Fish prey families	not tested	no 'Rare' prey eaten in winter
Index of relative importance of prey families (IRI)	varied	no patterns
Number of prey in families	varied but not when clupeids excluded	no patterns
Number of prey in habitats	varied	no patterns

Table 5.9 A comparison of the relative abundance of the major families of reef fishes on the shallow reef slope at Rib Reef in the Central GBR (kg/1000m^2, from Williams and Hatcher 1983) and the diet of *P. leopardus* from Broadhurst Reef. See Fig. 2.6 for the location of Rib Reef.

PREY	**RELATIVE ABUNDANCE OF PREYFAMILIES**					
FAMILIES	**- ON REEFS**			**- IN DIET**		
	percentage		rank	percentage		rank
Caesionidae	50.7		1	20.3		2
Pomacentridae	18.5		2	28.1		1
Scaridae	5.5		3	18.4		3
Serranidae	3.7	subtotal	4	4.6	subtotal	5
Labridae	3.0	=81.4%	5	12.8	=84.2%	4
Acanthuridae	2.5		6			
Holocentridae	2.4		7			
Chaetodontidae	2.4		8			
Haemulidae	1.7		9			
Lethrinidae	1.2		10			
Miscellaneous	8.5		-	16.9		-

Figure 5.1 Map of the Central Section of the Great Barrier Reef showing Little and Big Broadhurst Reef and Keeper Reef (all zoned General Use B).

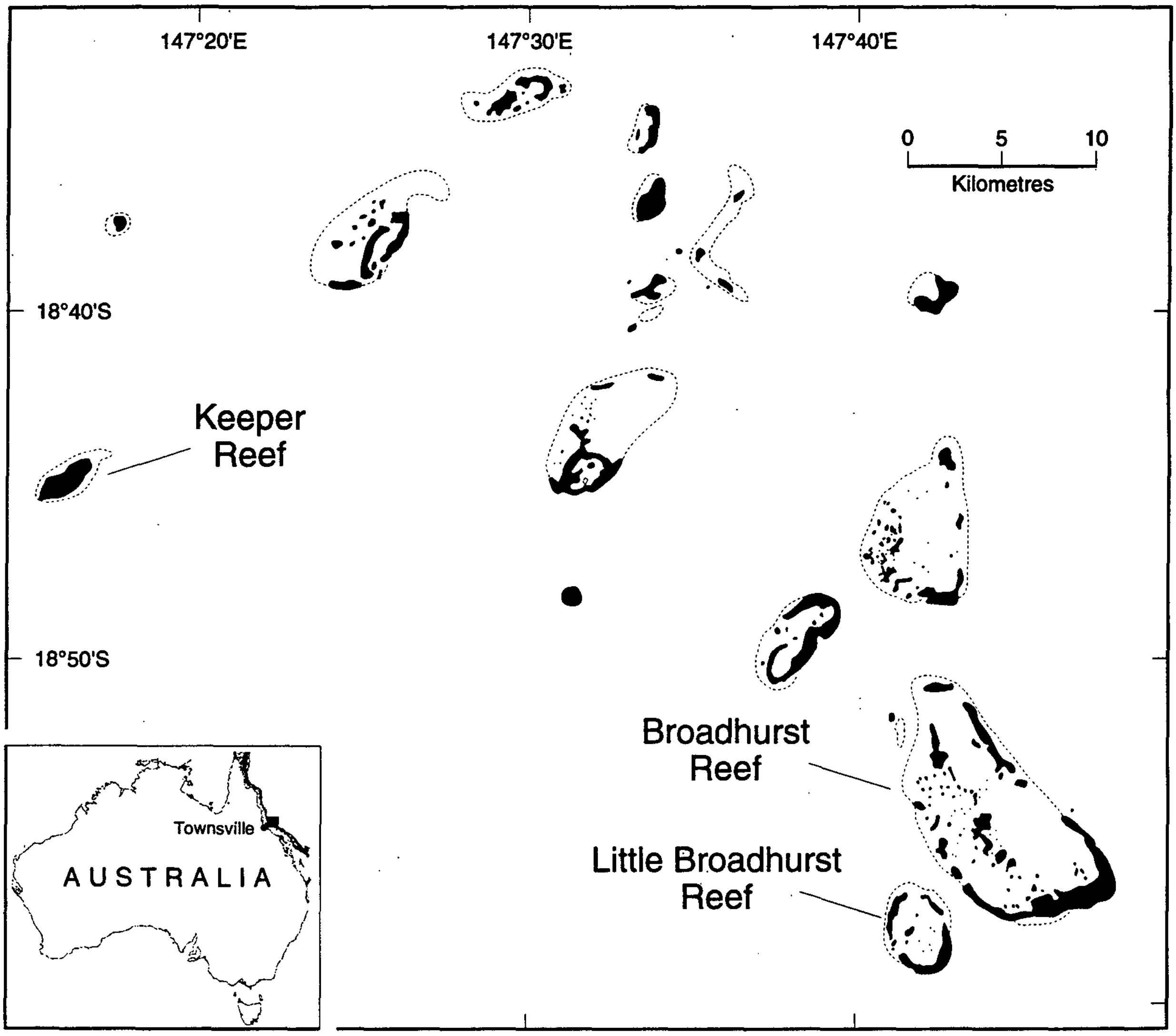


Figure 5.2 The number of prey per stomach of *P. leopardus* from Broadhurst Reefs during the sample months June, August, October, December and February. The number of prey per stomach did not vary among the sample months (K-$W_{[4]}$ = 2.99, Monte Carlo p-value =0.56). See Table 5.1 for sample sizes of *P. leopardus.*

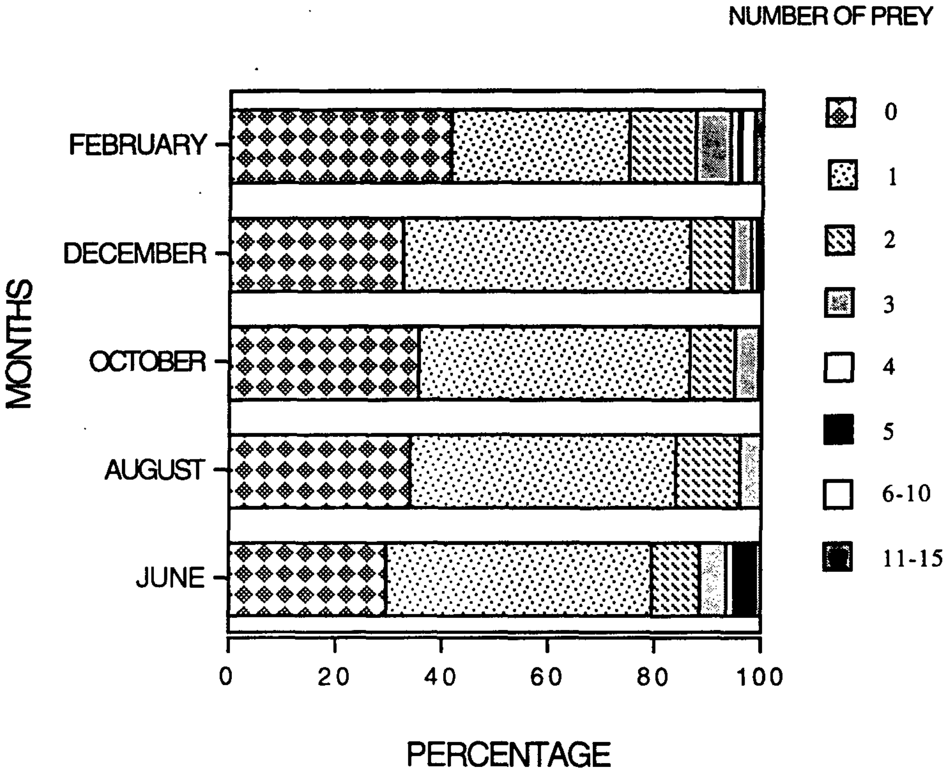
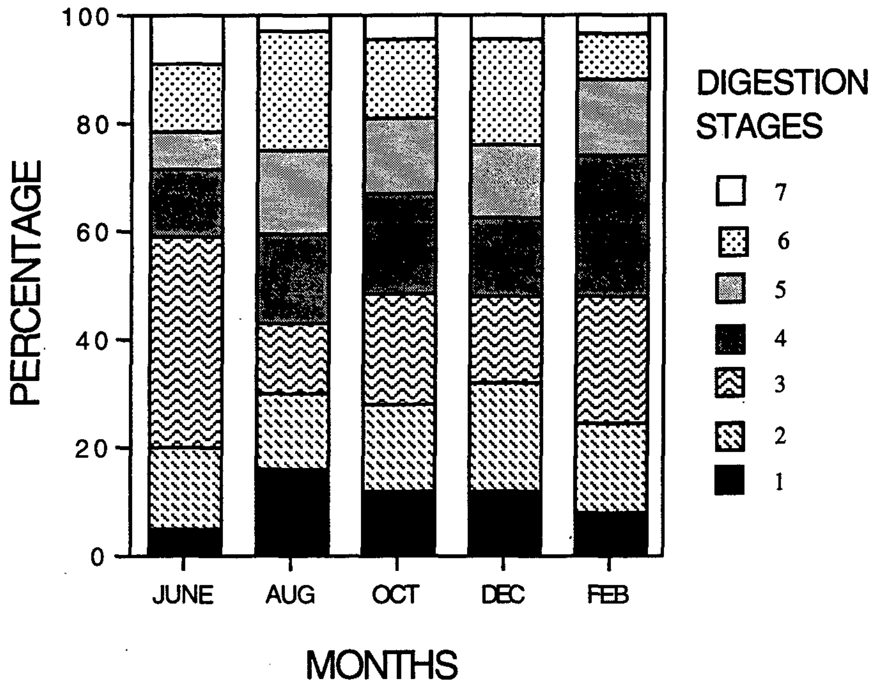


Figure 5.3 The digestion stages of fish prey in the stomachs of *P. leopardus* from Broadhurst Reef during the sample months June, August, October, December and February. The proportion of prey in different stages of digestion did not vary significantly among months (two sided J-T test= -0.702, 5*7 table, Monte Carlo p-value =0.48).



CHAPTER 6

6.0 REGIONAL VARIATION IN DIET OF *P. leopardus*

6.1 INTRODUCTION

Most studies of predation by coral reef fishes describe the diets of one or more piscivores (Hiatt and Strasburg 1960; Randall 1967; Choat 1968; Harmelin-Vivien and Bouchon 1976; Kingsford 1992). A few studies have sampled the whole fish community to relate the diets of piscivores to the abundance of the prey (Chave 1978; Parrish *et al.* 1986). All studies of predatory fishes on coral reefs have usually sampled just a single location or geographic region. The unstated assumption is that piscivory is similar throughout the coral reef community. If piscivory is uniform among regions, then the diet of opportunistic reef piscivores would change only when the availability or behaviour of their prey varied.

The ecology of coral reef fishes vary in most aspects across time and space. Temporal variations in feeding by coral reef fishes has received much attention in both behavioural and dietary studies (Hobson 1972; Goeden 1978; Samoilys 1987; Kingsford 1992). Yet nothing is known about spatial variation in piscivory.

In Australia, the Great Barrier Reef (GBR) extends over 2 300 kilometres of coastline. As the largest coral reef system in the world, the GBR provides an excellent opportunity to examine regional differences in fish populations (Williams 1983).

One of the major reef-dwelling piscivores on the GBR is the coral trout, *P. leopardus,* which is considered to be one of the two most abundant predators on the GBR (Ayling and Ayling 1986). The other predator is the red bass, *Lutjanus bohar,* and it is highly abundant on the outer reefs (Ayling and Ayling 1986). *Plectropomus leopardus* is the most widespread and abundant species of its genus on the GBR (Ayling and Ayling 1986).

Three studies have examined the diet of *P. leopardus* on the GBR (Choat 1968, Goeden 1974, Kingsford 1992). All three studies were done in one small area (near Heron Island on the Southern GBR). Kingsford's (1992) study was not completed when this research began. The combined results of Choat's (1968) and Goeden's (1974) studies on the diet of *P. leopardus* (n=184 fish collected during summer: October-December) differed substantially from samples (n=345 fish) collected from the Central Section of the GBR in July and October 1990 (St. John unpubl.). This study was designed to test whether these preliminary findings were indicative of a real difference in diet of *P. leopardus* on a regional scale. The major aim of this study was to compare diet of *P. leopardus* among three regions on the GBR and between two reefs within each region. Additionally, two spatial patterns at different scales were investigated in greater detail using larger data sets (Choat 1968; Goeden 1974; Kingsford 1992). Two reefs in the southern region were compared using the combined results of four separate studies that span nearly 30 years. This large data set from the southern region was compared to another from the central region (Chapter 5) to investigate regional patterns.

6.2 STUDY SITES, SAMPLING DESIGN AND METHODS

6.2.1 Study Sites

The Great Barrier Reef Marine Park is divided into four sections for management. Within these sections, reefs are zoned for different purposes. In the General Use B Zone, all recreational and commercial fishing activities are allowed. In the Marine Park A Zone limited fishing (no commercial line fishing or spearfishing) is allowed. No fishing is allowed in the Marine Park B Zone. In the Scientific Zone restricted fishing is allowed by permit only.

Plectropomus leopardus were collected from two reefs in each of three Sections of the GBRMP: Southern, Central and Far Northern. I refer to these as the southern, central and northern regions in this study. In the southern region the reefs were Heron Reef (23°27'S 151°52'E, Marine Park A) and One Tree Reef (23°30'S 152°06'E, Scientific Zone). In the central region, the midshelf reefs off Townsville were Broadhurst Reef (Little 18°58'S 147°42'E and Big 18°55'S 147°45'E combined) and Keeper Reef (18°46'S 147°16'E, all zoned General Use B). The reefs of the northern region were Lizard Is (14°38'S 145°28'E, Marine Park A & B) and Eyrie Reef (14°42'S 145°22'E, Marine Park B, Fig. 6.1).

6.2.2 Sampling Design

Plectropomus leopardus were collected between June 10 and July 14, 1991 because schooling fishes, which are the most variable component of prey in the diet (pers. obs.), were considered to be less abundant during winter months (Kingsford pers. comm.). The six reefs were sampled in a factorial design. The factors (and number of levels) were regions (3), and reefs (2). Approximately one third of *P. leopardus* stomachs were empty upon capture (29% - Choat 1968; 36% - Goeden 1974; 29% - Kingsford 1992; 33% - Chapter 2). Of those stomachs with prey, less than half can be expected to have identifiable prey (pers. obs.). Thus, a large number of trout were needed to obtain useful comparative dietary information. Based on the preliminary data of abundance of prey in the major families in the diet of *P. leopardus* (combined results of Choat's (1968) and Goeden's (1974) studies on the Southern GBR, n=184 fish and n=345 fish collected from the Central Section of the GBR, St John unpubl.), and considering the requirements of the Chi Squared test (i.e. expected values to be greater than 5), a minimum of 70 *P. leopardus* from each reef was required for meaningful statistical comparisons between reefs and regions.

In the central region of the GBR, *P. leopardus* were speared by approximately 15 spearfishers during a day-trip to each reef. In the other two regions, *P. leopardus* were speared by one diver. All stomachs of *P. leopardus* were fixed within 5 hours of capture. The details of the methods are given in

Section 2.2.

When highly digested, identified prey could not be weighed; their individual weight was estimated from the total weight of the sample (see Chapter 5).

6.2.3 Intra- and inter-region comparison using other studies

As the three other studies on feeding by *P. leopardus* were all done in the southern region on the same two reefs, I combined the results of all the studies (including this one) to compare two reefs; One Tree Reef and Heron Reef (plus the adjoining Wistari Reef). From reefs near Heron Island, Choat (1968) collected 134 *P. leopardus* during summer months between 1963-1966 and Goeden (1974) collected 50 *P. leopardus* between October - December 1972. At One Tree Reef, Kingsford (1992) collected 270 *P. leopardus* over two summers (1989 and 1991) and two winters (1990 and 1991) from outer reef and lagoon habitats. As these studies did not report weights of prey, the composition of the diet was compared numerically.

These combined results from the southern region are compared to the overall results from a large dietary study done in the central region. At Broadhurst Reef a total of 699 *P. leopardus* were speared in a two year period from August 1990 to February 1992.

The methods of statistical analyses are described in Section 2.5.

6.3 RESULTS

6.3.1 Differences among regions and between reefs in the catch of *P. leopardus*

<u>Does the catch rate of *P. leopardus* vary regionally?</u>

A total of 363 *P. leopardus* were collected from the southern (One Tree Reef n=69, Heron Reef n=67), central (Broadhurst Reefs n=66, Keeper Reef n=43), and northern region (Lizard Is. Reef n=89, Eyrie Reef n=25). The catch rates by spearing by the same spearfisher were different in the northern and southern regions. At Eyrie Reef in the north, each fish took three times longer to spear (1 trout every 16 minutes) than the fish at One Tree Reef in the south (1 trout every 5.5 minutes). These differences in catch rates reflected the time required to search for *P. leopardus.*

Are there regional differences in size structure of *P. leopardus*?

The size structure of the populations of *P. leopardus* varied among the three regions (Fig. 6.2). The two samples of *P. leopardus* in the southern and northern region were compared statistically because the zoning for the four reefs was similar and the same spearfisher collected all the samples. The size of *P. leopardus* differed significantly between the southern and northern region (Fig. 6.2). Although more than half the *P. leopardus* from each region were 35-45 cm (SL) (southern = 55.9% and northern = 61.2%), the upper and lower size classes differed between the two samples. The largest fish (<60 cm) occurred only in the southern region. The smallest fish (<30 cm) occurred only in the northern region. In the central region, a greater proportion of *P. leopardus* were smaller than in either of the other two regions: 44% of *P. leopardus* were less than 35 cm compared to 8.1% in the southern region and 34.5% in the northern region.

6.3.2 Regional diet of *P. leopardus*

Does the number of prey per predator vary within regions?

The numbers of prey per predator differed significantly between reefs in the southern and central regions (see Chapter 5 for Central Region, Fig. 6.3). In the northern region, where the sample sizes were smaller, the result was not significant (Fig. 6.3). These differences between reefs within regions obscured comparisons among regions.

Does the number of *P. leopardus* with empty stomachs vary within regions?

In the southern and northern regions, the major difference between the two reefs within a region was the proportion of empty stomachs (Fig. 6.3). The greatest difference occurred in the southern region, where 29.8% of *P.*

leopardus from Heron Reef had empty stomachs compared to 60.9% from One Tree Reef. In the northern region 35.9% of *P. leopardus* from Lizard Reef had empty stomachs compared to 56.0% at Eyrie Reef.

Are *P. leopardus* equally piscivorous throughout the GBR?

Similar proportions of fish, crustaceans and cephalopods were eaten by *P. leopardus* in every region (Table 6.1). As fish dominated the diet of *P. leopardus* (95.9% by number), the remainder of the results focuses on the prey fish.

Family richness in the diet of *P. leopardus*

Prey in a total of 22 families were eaten by *P. leopardus* from the three regions (Table 6.2). The number of prey in each family ranged from 1 to 67 individuals and the total weight of each family ranged from 1 g to 646 g (latter= 10 Scarids, Table 6.3). In the southern region, prey in 14 families were identified from 114 individuals. In the central region, prey in 12 families were identified from 83 individuals. In the northern region, prey in eight families were identified from 38 individuals .

The number of families eaten by *P. leopardus* appeared to increase in a southward trend. More families were consumed in the southern region (14) than in the central (12) and northern region (8, Table 6.2). This trend did not appear to be the result of regional differences in sample sizes of *P. leopardus* in the southern and northern region When compared to the northern region, the stomachs of only six more *P. leopardus* in the southern region contained prey, but prey in four more families were identified (Table 6.2).

Were genera and species in the families similar among regions?

Families of fish on the GBR often contain many species which are diverse in size and behaviour. To ensure that prey in families in every region included a similar suite of species or genera, prey species and genera in several families were compared between regions. Two genera in two families, *Chromis* and *Pterocaesio*, occurred in the diet of *P. leopardus* in all three regions. Two species, *Acanthochromis polyacanthus* and *Caesio caerulaurea*, and one genus, *Scarus* occurred in the diet of *P. leopardus* in two of the three regions. All of these fishes belonged to three of the four most common families in the entire study (Pomacentridae, Scaridae and Caesionidae). In conclusion, the genera and species of prey from the common families in the diet of *P. leopardus* were similar in every region.

Abundance categories of prey fishes

Prey in families were classified into the four categories used in Chapter 4: Common, Occasional, Rare and Sporadic. 'Common' prey occurred in every region. 'Occasional' prey occurred either singularly at more than one region, or in larger numbers (>1) at one region. 'Rare' prey occurred only once in one region. The 'Sporadic' category included highly mobile prey which occurred in large numbers in the stomachs of *P. leopardus* from one reef. 'Common' prey included 93 individuals in four families. 'Occasional' prey included 20 individuals in seven families, and 9 individuals in 9 families were classed as 'Rare'. Two families which contained 113 individuals were classed as 'Sporadic' (Table 6.2).

'Common' prey represented 39% of the sample of identified prey in number and 72% in weight. 'Occasional' and 'Rare' prey were 8% and 4% respectively of the total sample in number, but were more similar in weight (14% and 11% respectively). The difference between proportions of the sample using number and weight measures was largest in 'Sporadic' prey. 'Sporadic' prey was nearly 50% of the sample in number, but less than 5% in weight (Table 6.2 and 6.3).

Which families were most important in the diet?

In each region, a different family was ranked highest in the IRI (Table 6.4). Prey in two families in the 'Sporadic' category ranked top: pempherids in the southern region and clupeids in the central region. In the north, Pomacentridae ranked just above Caesionidae as the most important family in the diet.

Does the importance of prey in families vary regionally?

The importance of prey in the 'Common' families varied among regions (Table 6.4). In the southern region, scarids ranked second and were almost twice as important as labrids and pomacentrids. Caesionids represented less than 3% of the diet. In the central region, pomacentrids ranked second, followed closely by caesionids, labrids and scarids. In the northern region, the number of families in the diet was two thirds of the other two regions and so comparatively, all the IRI values were high. Pomacentrids and caesionids ranked first and second respectively, and their IRI values were six times higher than any other family.

The importance of prey in the other categories varied among regions (Table 6.4). In the southern region, the Acanthuridae, in the 'Occasional' category, ranked fifth, whereas in the central region one large pinguipedid, in the `Rare' category, ranked sixth.

Does dietary overlap vary regionally?

In paired comparisons of the diet between regions, *P. leopardus* in the central region had medium dietary overlap with both the northern and southern samples (southern-central Schoener $a = 0.37$; central-northern Schoener $a = 0.42$, Table 6.5). The diet of the two most distant populations of *P. leopardus,* southern and northern, had low overlap (Schoener $a = 0.28$, Table 6.5).

Does the numerical abundance of families in diets vary regionally?

The total number of prey in each family varied between regions (Table 6.2). The largest difference among regions was due to prey in the 'Sporadic' category, which made up nearly 50% of the sample in two of the regions. Other regional differences occurred in the 'Common' families. Prey in the

'Common' families represented 72% of the diet by weight (Table 6.3) and 40% of the diet by number (Table 6.2) and were eaten by *P. leopardus* in every region. The percentage of prey in the four 'Common' families varied significantly among regions (Table 6.2). Individual families showed different trends. The percentage of Pomacentridae in the diet increased in a northward trend (Table 6.2, Fig. 6.4). Pomacentridae and Caesionidae were most abundant in the diet in the northern region whereas Scaridae and Labridae were most abundant in the southern region (Table 6.2, Fig. 6.4). Except for Caesionidae, in the central region the number of prey in 'Common' families was intermediate between the southern and northern regions (Fig. 6.4).

Does the size of predators that consumed prey vary regionally?

Between 40% and 70% of *P. leopardus* sampled at each reef had eaten within the last 24 hours. The size structure of these *P. leopardus* varied among regions (southern-central: Dmax = 0.186, K-S $p<0.05$, central-northern: Dmax = 0.172, K-S $p<0.05$ and: southern-northern Dmax = 0.263, K-S $p<0.01$) and was similar to the overall size structure in each region. Large *P. leopardus* (45-59.9 cm SL) made up a higher percentage of the sample in the southern region (30%) than in the central (21%) or northern (4%) regions.

Are prey in each of the 'Common' families consumed by *P. leopardus* of different sizes?

On the GBR *P. leopardus* of different sizes consumed prey in the four 'Common' families (Fig. 6.5). Caesionidae and Labridae were consumed by *P. leopardus* in the middle size ranges (30 - 45.9 cm SL). Pomacentridae were seldom eaten by large *P. leopardus* (>45 cm SL, 4.4% of the sample) whereas Scaridae were not eaten by small *P. leopardus* (<35 cm SL) at all. These size-related feeding patterns may explain the regional differences in diets because the size of predators, that had consumed prey, varied regionally.

Is predation on 'Common' families related to predator size?

This test examined whether prey in each of the 'Common' families were eaten in proportion to the size structure of the population of *P. leopardus* that had fed on the GBR. For each size category of *P. leopardus* (size classes were pooled to meet the requirements of the test), the number of individuals eaten was compared to the expected number. The expected number was calculated by multiplying the proportion of *P. leopardus,* that had fed, in that size-class by the total number of prey in the family. Predation on labrids and caesionids is not related to predator size as both families were consumed in proportion to the number of *P. leopardus* in the size category (Labridae: $X^2_{[2]} = 1.384$, $p>0.05$, Caesionidae: $X^2_{[1]} = 1.384$, $p>0.05$). Therefore, any regional differences in abundance of prey in either labrids or caesionids is not explained by regional differences in size structure of *P. leopardus.* Predation on pomacentrids is related to predator size as smaller *P. leopardus* consumed pomacentrids in significantly higher proportions than expected by chance alone ($X^2_{[3]} = 30.95$, $p<0.01$). Therefore, the higher proportion of pomacentrids in the diet in the northern region may be explained by the higher proportion of smaller *P. leopardus.* Predation on scarids is related to predator size as larger *P. leopardus* ate scarids in significantly higher proportions than expected by chance alone ($X^2_{[1]} = 11.18$, $p<0.01$). Therefore, the higher proportion of scarids in the diet in the southern region may be explained by the higher proportion of larger *P. leopardus.* In conclusion, the regional differences in the abundance of Scaridae and Pomacentridae in the diet of *P. leopardus* may simply reflect the regional differences in the size structures of the predators.

Does size related predation on Pomacentridae and Scaridae vary among regions?

To test the above question, the size structure of *P. leopardus* that had consumed Pomacentridae and the size structure of *P. leopardus* that had consumed Scaridae were examined among regions. As sample sizes were small, *P. leopardus* that had consumed prey in these families were pooled into three categories based on size: small, 25-34.9 cm (SL), medium 35-44.9 cm (SL) and large, 45-54.9 cm (SL).

Pomacentridae occurred in the stomach of *P. leopardus* mostly singly but occasionally in twos or threes. There were regional differences in size-structure of *P. leopardus* that consumed Pomacentridae. Pomacentridae were eaten by a significantly higher proportion of small predators (25-34.9 cm SL) in the central and northern regions than in the southern region ($K\text{-}W_{[2]} = 21.54$, Monte Carlo p-value <0.001). In the southern region, 73% of pomacentrids were eaten by *P. leopardus* of medium size (35-44.9 cm SL) compared to 6.6% in the central and 26% in the north. In conclusion, the northward increase in abundance of Pomacentridae in the diet of *P. leopardus* is not explained by regional differences in size-structure of the predator. Generally, small *P. leopardus* consumed Pomacentridae. Yet, in the southern region, which has a higher proportion of large *P. leopardus,* Pomacentridae were consumed by larger predators.

The size-structures of *P. leopardus* that consumed Scaridae did not differ significantly among regions ($K\text{-}W_{[2]} = 0.980$, Monte Carlo p-value =0.723). This result indicated that the comparatively high abundance of Scaridae in the diet in the southern region may reflect the higher proportion of large predators in this sample.

Does the proportion of Scaridae in the diet vary among regions?

The proportions of *P. leopardus* that had consumed Scaridae were compared among regions. Firstly, *P. leopardus* that had eaten in the two smallest size categories (< 30 and 30 - 34.9 cm SL, Fig. 6.5) were excluded from the analysis because they didn't eat scarids. This removed six *P. leopardus* from the southern region and 29 from each of the central and northern regions. Without these smaller size classes, the size structure of *P. leopardus* that had eaten was similar between the southern and central regions (southern-central: Dmax = 0.053, n = 38, K-S p>0.05). The size structure of *P. leopardus* that had eaten in the northern region, however, significantly differed from the southern and central regions (southern-northern: Dmax = -0.270, n = 52, K-S p<0.01 and central-northern: Dmax = 0.311, n = 38, K-S p<0.01). *Plectropomus leopardus* were divided into two groups: those that had eaten Scaridae, with or without other prey; and those that had eaten other prey only. The proportion of *P. leopardus* that had eaten scarids varied among regions (Fisher's Exact $\text{test}_{[2]}$= 6.569, p=0.04). In the southern region, 18.5% of *P. leopardus* contained scarids compared to 11.8% in the central region and 2.0% in the north. In conclusion, *P. leopardus* consumed scarids proportionally more in the southern region than in the northern region.

Are there intra-region differences in the diet of *P. leopardus*?

The diet of *P. leopardus* showed varying levels of overlap between reefs within the different regions. There was medium overlap in the diet of *P. leopardus* between reefs in the southern region (Schoener *a* = 0.3733). The largest difference between the diets was due to the 'Sporadic' family of pempherids at Heron Reef. Similarly, in the central region, there was a medium overlap in the diet of *P. leopardus* between the two reefs (Schoener *a* = 0.3143). The largest difference between the diets was due to the 'Sporadic' family of clupeids. The northern region, where there was no 'Sporadic' prey fish in the diet, had the highest dietary overlap between reefs within regions (Schoener *a* = 0.5028).

In the southern and central regions the number of prey fish in each family varied between reefs (south: Fisher's Exact $\text{test}_{[13]}$= 60.79, Monte Carlo p-value <0.001, central: Fisher's Exact $\text{test}_{[11]}$= 30.09, Monte Carlo p-value <0.001). Prey in the 'Sporadic' category accounted for most of this variability. When this category was excluded from analyses, there was no difference between reefs in either region (south: Fisher's Exact $\text{test}_{[11]}$= 14.82, Monte Carlo p-value=0.075 and central: Fisher's Exact $\text{test}_{[10]}$= 8.019, Monte Carlo p-value=0.707). In the northern region, where no 'Sporadic' prey were recorded, the number of prey in the diet of *P. leopardus* did not differ significantly between reefs(Fisher's Exact test$_{[7]}$= 8.533, Monte Carlo p-value=0.233). In conclusion, the abundance of families in the diet of *P. leopardus* within regions did not differ significantly when the 'Sporadic' prey were excluded from the diet.

6.3.3 Diet of *P. leopardus* in the southern region

When all four studies of the diet of *P. leopardus* in the southern region of the GBR were combined, 274 prey fish from Heron Reef and 276 prey fish from One Tree Reef were recorded in 250 and 339 *P. leopardus,* respectively. In the southern region, the diet of *P. leopardus* comprised 24 families and family richness was identical between reefs. Prey from each reef (Heron Reef, n=187 and One Tree Reef, n=163) were identified into 17 families (Table 6.6). Each family was classified into one of four categories (see Section 6.3.2). Three families, with a total of 121 fishes, were classed as 'Common' prey. Sixty six prey fish in nine families were classed as 'Occasional' and eight individuals in eight families were 'Rare'. Four families, with a total of 155 fishes, were classed as 'Sporadic' (Table 6.6).

Numerically, prey in the highest ranking families at both reefs were in the 'Sporadic' category; clupeids ranked first at One Tree Reef, whereas pempherids and atherinids ranked first and second at Heron Reef respectively. The next highest ranking prey were in families in the 'Common' category: Scaridae, Labridae and Pomacentridae.

Does the abundance of prey in families differ between reefs?

The abundance of families in the diet of *P. leopardus* differed significantly between the two reefs (Table 6.6). This result was influenced by variations in the numbers of 'Sporadic' prey at each reef. 'Sporadic' prey comprised 44.3% of the diet (Table 6.7) but previous results (see 6.3.2) indicated that in terms of weight, 'Sporadic' prey were not an important component of the diet.

Percentages of prey in the three 'Common' families were similar on both reefs (31.02% at Heron and 38.65% at One Tree Reef). As 'Common' families were the most important components of the diet by weight (see previous results in 6.3.2), I compared the numbers of prey in the three 'Common' families between reefs. There was no difference between the numbers of prey in the 'Common' families on Heron and One Tree Reef (G = 2.992, $X^2_{[2]}$ p>0.05).

6.3.4 Diet of *P. leopardus* in the southern and central regions

The diet of *P. leopardus* from larger data sets in two regions were compared to determine whether they corroborated the findings of the present study. The fish diet of *P. leopardus* in the southern region (all four studies, see above) was compared with the fish diet of *P. leopardus* from Broadhurst and Keeper Reef in the central region (see Chapter 5). This test was not completely independent because both regions included the results of the present study. Overall, a total of 30 families were consumed by 1331 *P. leopardus*. Fourteen families were common to both regions (Table 6.8). There were more families of prey fish in the diet of *P. leopardus* from the southern region (n=24) than the central region (n=20) despite a higher number of *P. leopardus* collected in the central region (Table 6.8). Two 'Sporadics', Engraulidae and Pempherididae, were not recorded in the diet in the central region (Table 6.8). The higher family richness in the southern region corroborates the smaller regional study which found a southward trend of increasing family richness in the diet of *P. leopardus*.

Of the five top ranking families, three of the four 'Common' families, Pomacentridae, Scaridae and Labridae were considered to be the most important prey in the diet of *P. leopardus* . Clupeidae and Pempherididae, were small fishes and thus were only numerically important (Table 6.8).

<u>Does the abundance of prey in families differ between regions?</u>

The abundance of families in the diet of *P. leopardus* varied significantly between the two regions (Table 6.8). Furthermore, the abundance of prey in the four 'Common' families, that are important in the diet by weight, differed regionally (Fisher's Exact test$_{[3]}$= 38.19, Monte Carlo p-value <0.001). These results corroborate the trends detected for three of the four 'Common' families in the regional study. Firstly, the northward trend of increasing abundances of Pomacentridae and Caesionidae in the diet of *P. leopardus* was evident in this larger comparison. Pomacentridae were less abundant in the diet in the southern region (14%, smaller study=10%) than in the central region (32%, smaller study=18.5%). Caesionidae were consumed in fewer numbers than Pomacentridae. Caesionidae were seldom recorded in the southern region (0.5% of the diet, smaller study=0.9%) but increased in the diet in the central region (6%, smaller study=2.5%). Second, the southward trend of increasing abundances of the Scaridae and Labridae in the diet of *P. leopardus* was detected only for Scaridae (Table 6.9). Scarids comprised 13% of the diet in the southern region (smaller study=9%) and 6% in the central region (smaller study=5%). There was no difference in the abundance of Labridae in the diet of *P. leopardus* between regions (Table 6.9).

6.4 DISCUSSION

Along the entire GBR, *P. leopardus* is highly piscivorous (numerically 95.9% fish in the diet). Prey in 22 families, which varied widely in size, shape and behaviour, were eaten by *P. leopardus* in the three regions of the GBR sampled. The families could be compared among regions because three of the common families contained similar genera and species in the different regions. These families were divided into categories of prey fish which varied in their importance in the diet of *P. leopardus*. Prey in 'Common' families provided the basis for the diet of *P. leopardus* because of their large size and abundance in the diet. Prey in the 'Occasional' families were supplementary as they occurred in low but consistent numbers in the diet. 'Rare' prey were in the families seldom eaten by *P. leopardus* and included families which have anatomical features to deter predation (e.g. toxic tetraodontids). Prey in 'Sporadic' families were small fishes which form large single-species schools and were eaten intermittently in high numbers by *P. leopardus*. Prey in 'Sporadic' families were significant in the diet numerically, but were much less important in terms of prey weight.

The composition of the diets of *P. leopardus* varied regionally. This variation was not due to the presence of highly variable 'Sporadic' prey in the diet alone. The abundance of the four 'Common' families, which were the most important component in the diet, also varied among regions. Most of these regional differences in the diet were corroborated by the results of larger combined studies of 1331 *P. leopardus* in two of the three regions. These regional patterns in abundance of 'Common' prey were consistent between reefs within regions despite the high variability in the diet within regions.

Within regions, differences in the diet of *P. leopardus* between reefs were often associated with the presence of 'Sporadic' prey. When 'Sporadic' prey were removed from the analyses, there were no differences within regions (between reefs) in the composition of the diet of *P. leopardus*. The results of the larger combined studies on the two reefs in the southern region corroborated this conclusion. Also, the number of prey per individual predator significantly varied between reefs within regions since reefs with small schooling prey fishes (the 'Sporadic' category) had the highest numbers of prey items per stomach. Other aspects of feeding by *P. leopardus,* that were not related to the presence of sporadic prey, differed between reefs. The proportion of empty stomachs in the population of *P. leopardus* differed between reefs within regions and were not related to predator density (suggested by catch rates). The two reefs with the highest proportion of empty stomachs had the most and least abundant population of *P. leopardus* (One Tree Reef and Eyrie Reef respectively).

There were latitudinal trends in the diet of *P. leopardus*. Firstly, the overall diet of *P. leopardus* (determined by the IRI) was more similar between populations located near to each other (southern-central and central-northern) than the two most distant samples (southern-northern). Second, there was a southward increase in family richness in the diet of *P. leopardus*. This increase was corroborated by the comparison between the two larger studies that had higher numbers of *P. leopardus* and thus a higher family richness in the diet. In the larger study, family richness in the diet of *P. leopardus* in the southern region was identical between reefs. In total, four more families were prey to *P. leopardus* in the southern region than in the central region, despite a smaller sample size (total numbers of *P. leopardus* were 153 fewer in the south). Thirdly, there were latitudinal trends in abundance of three of the four 'Common' families in the diet of *P. leopardus*. Regional trends in abundance of caesionids and pomacentrids in the diet of *P. leopardus* were opposite to the trend in abundance for Scaridae, which were eaten more in the southern region. For Pomacentridae and Scaridae the numbers of individuals in the central region fell between those in the northern and southern regions. The number of Caesionidae in the diet of *P. leopardus* in the central region was similar to the southern region. These trends in abundance were supported by the larger studies in the southern and central regions. Even though the numbers of the 'Common' families were low, the latitudinal trends in their abundances in the diets of *P. leopardus* appeared to be real.

Latitudinal trends in abundance of prey in the most common families in the diet of *P. leopardus* are not surprising as populations exhibit several other latitudinal gradients along the GBR. Firstly, spawning in *P. leopardus* occurs earlier in the south than in the northern GBR (Brown *et al.* 1994). Second, the density and size of populations of *P. leopardus* increases southward. Collection of samples by the same spearfisher suggested that *P. leopardus* were less abundant in the northern region than in the southern region. At Eyrie Reef each fish took three times longer to spear (1 trout every 16 minutes) than the fish at One Tree Reef (1 trout every 5.5 minutes). Furthermore, the sampled *P. leopardus* were smaller in the northern region. The average size of individuals in populations of *P. leopardus* increased in a southward trend: the SL of the largest individuals increased by one 5 cm size category in each region. These latitudinal trends are corroborated by visual census surveys of coral trout along the GBR: populations of *P. leopardus* are larger and occur in higher densities in a southward trend along the GBR (Ayling 1986) and this latitudinal gradient along the GBR appears independent of current fishing pressure (Russ 1991).

Regional differences in size-structure of *P. leopardus* did not explain the regional trends in abundance in two of the 'Common' families in their diet. The abundance of Caesionidae and Pomacentridae in the diet of *P. leopardus* increased in a northward trend. There were no predator-size-related feeding patterns on Caesionidae. Caesionids, which are a slender, streamlined fish that grow up to 25 cm TL (Randall *et al.* 1990), were eaten one at a time by *P. leopardus* of all sizes. Despite their large size, most caesionids were eaten by *P. leopardus* in the northern region, where the two largest size classes of *P. leopardus* were absent in the population. This suggests that the high abundance of caesionids in the diet of *P. leopardus* in the northern region was not related to regional differences in the size-structure of *P. leopardus* . Overall, pomacentrids were eaten mostly by *P. leopardus* in the smaller size ranges, 25-35 cm (SL). This trend, however, was not consistent among regions. In the southern region, where *P. leopardus* were larger, pomacentrids were eaten by larger *P. leopardus* in much higher proportions than in the central or northern regions.
Scaridae increased in abundance in the diet of *P. leopardus* in a southward trend. Overall scarids were eaten by large *P. leopardus* and this was consistent among regions. Thus, the abundance of scarids in the diet of *P. leopardus* in the southern region may be related to the larger size of the predator in the south. Even when the smaller size classes of *P. leopardus* (that did not eat scarids) were removed from the analysis, regional differences in the proportion of *P. leopardus* containing scarids were confounded by regional differences in the size structure of *P. leopardus* .

Although most studies which find regional trends in the diet of fishes link dietary differences to variation in prey availability (Godfriaux 1969), other studies have found regional differences when food items were available but not eaten (Allen and Aron 1958). Evidence for regional abundances of prey in the three families (Scaridae, Pomacentridae and Caesionidae) is sparse but does not seem to account for regional variation in feeding by *P. leopardus*. Latitudinal abundances of Scaridae and Pomacentridae do not vary significantly (Williams and English in prep, cited by Williams 1991). In the diet of *P. leopardus.*, however, Pomacentridae increased in abundance in a northward trend. Choat (1991) suggested that the abundance of Scaridae decreases in a southward trend along the GBR although he did not present data for the southern region. In contrast, Scaridae increased in abundance in a southward trend in the diet. Although Caesionidae are more abundant on reefs in the central than in the southern region (Russ pers. comm.), this prey family increased in abundance in the diet of *P. leopardus* in a northward trend. In conclusion, information on prey abundances to date, cannot account for regional differences in abundances of families in the diet of *P. leopardus*.

As prey availability and size of predator does not explain the regional trends in feeding by *P. leopardus* clearly, feeding behaviour may explain these differences. Predatory behaviour of *P. leopardus* is complex; this fish must use different strategies to accommodate varying prey behaviours and sizes, as well as develop new strategies for larger prey as they grow (see Chapters 3 and 8). Adaptive strategies for predators include two important aspects of foraging behaviour; learning and memory (Marcotte and Browman 1986). Serranids are considered to have well developed learning capabilities (Diamant and Shpigel 1985). All feeding strategies of *P. leopardus* must be learned either individually or from other conspecifics. Yet, the results of a behavioural experiment on *P. leopardus* suggest that successful predatory behaviour is not learned alone because familiarization with the prey over time did not improve the success of predators in a predation experiment (Chapter

8). Generally *P. leopardus* are considered to forage alone (Goeden 1974), but underwater observations of fishing reveal that *P. leopardus* appear to watch their conspecifics carefully during feeding (pers. obs.). Smaller *P. leopardus* mimic the predatory behaviour of slightly larger conspecifics which appear to be hunting (pers. obs.). Also, *P. leopardus* engage in intraspecific following behaviour (Goeden 1974; Samoilys 1987).

Following behaviour in interspecific fishes is well documented as a means to increase foraging success by the follower. The follower has a greater chance of capturing escaping prey (Strand 1988). Even though the reasons for intraspecific following behaviour are unclear in *P. leopardus*, this behaviour is a potential vehicle for learning predatory strategies. Thus, common predatory strategies may be learned actively by smaller conspecifics following and copying predatory behaviour of slightly larger individuals in their home ranges. Strategies could also be learned passively by watching predatory behaviours and events. In this way, populations of *P. leopardus* could develop behavioural strategies which favour the capture of prey in certain families over others. Thus, regional differences in behavioural patterns of feeding may explain regional trends in the diet of *P. leopardus*. A behavioural gradient of feeding by *P. leopardus* may occur along the GBR. If the diet of *P. leopardus* is influenced by predatory strategies learned from larger conspecifics, drastic reductions of fishable *P. leopardus* may interfere with the predatory behaviour and success of the following generations of *P. leopardus*. Predatory behaviour of *P. leopardus* is discussed in Chapter 8.

'Sporadic' prey accounted for much of the variation in the diet of *P. leopardus* although, in contrast to the temporal study, it did not account for all regional variation in the diet of *P. leopardus*. As discussed in Chapter 5, *P. leopardus* actively target 'Sporadic' prey when they are available. The high numerical variability of 'Sporadic' prey in the diet of *P. leopardus* at the scale of reefs suggests that this component of the diet of *P. leopardus* will always be temporally and spatially variable because it reflects the local abundances of pelagic prey.

The results of this study suggest that tide or day did not appear to affect rates of feeding by *P. leopardus.* Reefs in the southern region were sampled on consecutive days; *P. leopardus* from Heron Reef were caught both before and after the One Tree Reef sample was taken. Yet *P. leopardus* from these reefs had the highest and lowest proportion of empty stomachs. At one site on One Tree Reef, the spearfisher noticed a large *P. laevis* which may have inhibited feeding in the smaller *P. leopardus* .

This study examined diets of *P. leopardus* at two spatial scales, regions and reefs. Habitats within reefs were not examined. To date only one study has examined the diet of *P. leopardus* in two habitats at One Tree Reef, which has a closed system of lagoons which flood at high tide (Kingsford 1992). Kingsford (1992) caught all of his samples at high tide and found differences in the abundance of some groups in the diet of *P. leopardus* from lagoon and reef slope samples at One Tree Reef. Most pelagic prey (Clupeids and Engraulids) were eaten on the reef slope whereas Blenniidae were eaten only by *P. leopardus* within the lagoon. The structure of this unusual reef may prevent *P. leopardus* from moving between slope and lagoonal habitats frequently. Thus confinement to one habitat may explain the abundance of Blenniidae in the diet. This lack of movement by *P. leopardus* at One Tree Reef appears to be supported by the distribution of the predator. At One Tree Reef *P. leopardus* are more abundant on reef slopes and edges than in the centre of the lagoon (Kingsford 1992). Yet, on reefs which are more open in structure (e.g. Broadhurst Reef), *P. leopardus* may have more habitat types within their home range, since they can swim distances of up to 2 km (Davies 1995) and have large home ranges which are over 1 hectare in area (Samoilys 1987, see Chapters 4 and 5).

The marine park zoning of the reefs may have contributed to the regional differences in size-structures of *P. leopardus* because fishing reduces the number of larger *P. leopardus* on reefs (Craik 1981; Ayling and Ayling 1986). Fishing was restricted on the reefs sampled in the northern and southern regions. The highest proportion of small *P. leopardus* (<30 cm SL) occurred in the central region, where both reefs were open to fishing. Alternatively, differences among spearfishers may have influenced the size of the catch as *P. leopardus* were speared by one spearfisher in the southern and northern regions and by a group of spear fishers in the central region. Most spearfishers will choose a larger trout in preference to a smaller one but the ability to estimate legal sizes accurately varied between the spearfishers (pers. obs.).

Latitudinal gradients in the importance of the major families in the diet of *P. leopardus* along the GBR suggest that southern and northern populations of *P. leopardus* may be ecologically distinct. Thus, *P. leopardus* may have varying predatory impacts on populations of prey throughout the GBR. Caley (1991) found that more predation occurred on juvenile and small prey on small patch reefs at Lizard Is. in the northern region than at One Tree Reef in the southern region. The study by Caley (1991) and the present study suggest that predation is not a uniform process, and the impact of predation on prey communities may vary along the GBR. Future studies on predation or diets of predators need to consider regional differences as conclusions from isolated studies may not be applicable to the whole GBR.

In conclusion, latitudinal gradients in feeding of *P. leopardus* suggest that these predators are not a homogenous pool of piscivores feeding in the same way. For purposes of management, the trout fishery is not dependent on one prey group and depletion of one species of prey from a reef or region might not affect the trout fishery. Drastic reductions in abundance of *P. leopardus* due to fishing, however, may interfere with the predatory behaviour and success of following generations of *P. leopardus*. Furthermore, regional differences in the diet of *P. leopardus* mean that studies of the diet of *P. leopardus* from one reef cannot be applied uncritically to the rest of the GBR.

Table 6.1 The number of fish, crustaceans and cephalopods consumed by *P. leopardus* from the three regions, southern (S), central (C) and northern (N). The proportions of fish, crustaceans and cephalopods were similar among regions (K-W$_{[4]}$=0.305, Monte-Carlo p-value =0.86). The table includes the total number of prey and the number of *P. leopardus* with prey (i.e. trout with empty stomachs excluded).

PREY GROUPS	**REGIONS**			**TOTAL**
	S	**C**	**N**	
fish	140	123	86	349
crustaceans	6	4	3	13
cephalopods	1	1		2
total prey	147	129	89	364
number of *P. leopardus* with prey	74	77	68	359

Table 6.2 The number and numerical percentage of prey in each family in the diet of *P. leopardus* from the three regions, southern (S), central (C) and northern (N). The number of prey fish in each family varied among regions (Fisher's Exact test$_{[42]}$ =235.4, Monte-Carlo p-value <0.001). The families are grouped by category ('Common', 'Occasional', 'Rare' and 'Sporadic'), and the total percentage of each family and each category (in bold) is included in the last column. Numbers of prey in the four 'Common' families varied significantly among regions (Fisher's Exact test$_{[6]}$ =23.83, Monte-Carlo p-value <0.001). The total number of identified and unidentified prey fish and the number of *P. leopardus* with prey are recorded for each region.

PREY	**COUNT**			**PERCENTAGE**			
FAMILIES	S	C	N	S	C	N	TOTAL
Common							**39.1**
Pomacentridae	11	15	19	9.6	18.5	50.0	19.3
Labridae	11	6	2	9.6	7.4	5.3	8.1
Scaridae	10	4	1	8.8	4.9	2.6	6.4
Caesionidae	1	2	9	0.9	2.5	23.7	5.1
Occasional							**8.5**
Blenniidae		4	1		4.9	2.6	2.1
Apogonidae			4			10.5	1.7
Acanthuridae	2		1	1.7		2.6	1.3
Bothidae	1	1		0.9	1.2		0.8
Gobiidae		2			2.5		0.8
Holocentridae	2			1.7			0.8
Scorpaenidae		2			2.5		0.8
Rare							**3.8**
Lethri/Lutjanid			1			2.6	0.4
Monacanthidae	1			0.9			0.4
Muraenidae		1			1.2		0.4
Pinguipedidae		1			1.2		0.4
Serranidae		1			1.2		0.4
Siganidae	1			0.9			0.4
Sphyraenidae	1			0.9			0.4
Synodontidae	1			0.9			0.4
Tetraodontidae	1			0.9			0.4
Sporadic							**48.5**
Pempherididae	67			58.8			28.7
Clupeidae	4	42		3.5	51.8		19.7
total	114	83	38				
total fish prey	140	124	86				
number of prey families	14	12	8				
number of *P. leopardus*	74	77	68				

Table 6.3 The summed and percentage weights of each family of prey in the three regions, southern (S), central (C) and northern (N). The families are grouped by category ('Common', 'Occasional', 'Rare' and 'Sporadic'), and the total percentage of each family and each category (in bold) is included.

PREY	**WEIGHT**			**PERCENTAGE**			
FAMILIES	S	C	N	S	C	N	TOTAL
Common							**71.8**
Scaridae	646.01	144.03	59.85	35.6	15.0	8.3	24.3
Pomacentridae	261.11	136.22	209.51	14.4	14.2	29.2	17.4
Caesionidae	23.50	235.48	317.58	1.3	24.5	44.2	16.5
Labridae	273.70	172.59	26.62	15.1	18.0	3.7	13.5
Occasional							**13.6**
Acanthuridae	270.25		50.00	14.9		7.0	9.1
Blenniidae		46.30	11.67		4.8	1.62	1.6
Gobiidae		32.2			3.3		0.9
Bothidae	5.66	16.83		0.3	1.7		0.6
Holocentridae	21.07			1.2			0.6
Scorpaenidae		13.61			1.4		0.4
Apogonidae			6.13			0.8	0.2
Rare							**10.6**
Pinguipedidae		117.70			12.2		3.4
Siganidae	66.19			3.6			1.9
Monacanthidae	61.19			3.4			1.7
Sphyraenidae	60.19			3.3			1.7
Lethri/Lutjanid			36.56			5.1	1.0
Serranidae		11.50			1.9		0.3
Tetraodontidae	9.60			0.5			0.3
Muraenidae		5.19			0.5		0.1
Synodontidae	1.00			<0.1			>0.1
Sporadic							**4.10**
Pempherididae	108.77			6.0			3.1
Clupeidae	4.54	30.02		0.3	3.1		1.0
total	1812.8	961.7	717.9				
number of *P. leopardus*	74	77	68				

Table 6.4 The index of relative importance (IRI), expressed as a percentage for each family of prey, and their rank in the three regions, southern (S), central (C) and northern (N). The families are grouped by category ('Common', 'Occasional', 'Rare' and 'Sporadic').

PREY	IRI					
FAMILIES	S		C		N	
Common						
Caesionidae	1.08	11	13.48	3	33.96	2
Labridae	12.37	3	12.68	4	4.49	6
Pomacentridae	12.03	4	16.34	2	39.59	1
Scaridae	22.20	2	9.96	5	5.48	4
Occasional						
Acanthuridae	8.33	5			4.80	5
Apogonidae					5.69	3
Blenniidae			4.88	7	2.13	8
Bothidae	0.59	13	1.49	10		
Gobiidae			2.91	8		
Holocentridae	1.46	10				
Scorpaenidae			1.94	9		
Rare						
Lethri/Lutjanid					3.86	7
Monacanthidae	2.13	7				
Muraenidae			0.89	12		
Pinguipedidae			6.74	6		
Serranidae			1.22	11		
Siganidae	2.26	6				
Sphyraenidae	2.10	8				
Synodontidae	0.47	14				
Tetraodontidae	0.70	12				
Sporadic						
Clupeidae	1.88	9	27.49	1		
Pempherididae	32.39	1				

Table 6.5 Values of dietary overlap (Schoener *a*) for each pairwise regional comparison of the diet of *P. leopardus*. Values of Schoener *a* are calculated based on the proportion of the index of relative importance (IRI) for each region. The values are classified into three groups: <0.30 = low dietary overlap, <0.60 = medium dietary overlap and >0.60 = high dietary overlap.

REGIONS	CENTRAL	NORTHERN
SOUTHERN	0.38 medium	0.28 low
CENTRAL		0.42 medium

Table 6.6 The number of prey in the diet of *P. leopardus* from the combined results of four studies in the southern region at two reefs, Heron and One Tree. Published data for Heron and Wistari Reefs come from Choat (1968) and Goeden (1974) and for One Tree Reef from Kingsford (1992). The total number of prey fish in each family varied between the two reefs (Fisher's Exact test$_{[23]}$ =189.2, Monte-Carlo p-value <0.001). The families are grouped by category ('Common', 'Occasional', 'Rare' and 'Sporadic'). Totals of prey fish (identified, unidentified and grand) and sample sizes of *P. leopardus* (including predators with empty stomachs) for each reef are included.

PREY FAMILIES	Heron Reef	One Tree Reef	TOTAL
Common			
Pomacentridae	26	19	45
Scaridae	18	27	45
Labridae	14	17	31
Occasional			
Blenniidae	4	24	28
Apogonidae		13	13
Gobiidae	2	6	8
Pinguipedidae	4		4
Synodontidae	3	1	4
Acanthuridae	2	1	3
Caesionidae	2		2
Holocentridae	2		2
Siganidae	1	1	2
Rare			
Bothidae	1		1
Congridae		1	1
Monacanthidae		1	1
Mugiloidae		1	1
Scolopsidae	1		1
Serranidae		1	1
Sphyraenidae	1		1
Tetraodontidae		1	1
Sporadic			
Pempherididae	68		68
Clupeidae	9	39	48
Atherinidae	29	3	32
Engraulidae		7	7
total	187	163	350
unidentified fish	87	113	200
grand total of prey fish	274	276	550
number of *P. leopardus*	250	339	589

Table 6.7 The numerical percentage of prey in the diet of *P. leopardus* from combined results of the four studies in the southern region of the GBR at two reefs, Heron and One Tree. See caption in Table 6.6 for information about the published data and the categories of prey fish.

PREY FAMILIES	Heron Reef	One Tree Reef	TOTAL
Common	**31.0%**	**38.6%**	**40.3%**
Pomacentridae	13.9	11.6	12.8
Scaridae	9.6	16.6	12.8
Labridae	7.5	10.4	8.8
Occasional	**10.7%**	**28.2%**	**16.6%**
Blenniidae	2.1	14.7	8.0
Apogonidae		8.0	3.7
Gobiidae	0.1	3.7	2.3
Pinguipedidae	2.1		1.1
Synodontidae	1.6	<0.1	1.1
Acanthuridae	0.1	<0.1	<0.1
Caesionidae	0.1		<0.1
Holocentridae	0.1		<0.1
Siganidae	<0.1	<0.1	<0.1
Rare	**1.6%**	**3.1%**	**2.3%**
Bothidae	<0.1		<0.1
Congridae		<0.1	<0.1
Monacanthidae		<0.1	<0.1
Mugiloidae		<0.1	<0.1
Scolopsidae	<0.1		<0.1
Serranidae		<0.1	<0.1
Sphyraenidae	<0.1		<0.1
Tetraodontidae		<0.1	<0.1
Sporadic	**56.7%**	**30.1%**	**44.3%**
Pempheridae	36.4		19.4
Clupeidae	4.8	23.9	13.7
Atherinidae	15.5	1.8	9.1
Engraulidae		4.3	2.0
identified total	187	163	350
unidentified fish	87	113	200
grand total of prey fish	274	276	550
number of *P. leopardus*	250	339	589

Table 6.8 Number of prey in families in the diet of *P. leopardus* from the southern region (from the four studies at Heron and One Tree Reef) and the central region (from Broadhurst and Keeper Reefs in Chapt. 5). The abundance of families in the diet of *P. leopardus* differed significantly between regions (Fisher's Exact test$_{[29]}$ =231.7, Monte-Carlo p-value <0.001). Published data for Heron and Wistari Reef come from Choat (1968) and Goeden (1974) and for One Tree Reef from Kingsford (1992). Totals of prey fish (identified, unidentified and grand) and sample sizes of *P. leopardus* (including predators with empty stomachs) for each reef are included .

PREY FAMILIES	REGIONS		TOTAL
	SOUTHERN	CENTRAL	
Clupeidae	48	122	170
Pomacentridae	45	103	148
Scaridae	45	24	69
Pempherididae	68		68
Labridae	31	31	62
Atherinidae	32	11	43
Blenniidae	28	14	42
Caesionidae	2	23	25
Apogonidae	13	4	17
Gobiidae	8	9	17
Synodontidae	4	12	16
Scorpaenidae		8	8
Engraulidae	7		7
Pinguipedidae	4	3	7
Serranidae	1	6	7
Sphyraenidae	1	3	4
Acanthuridae	3		3
Bothidae	1	1	2
Holocentridae	2		2
Nemipteridae		2	2
Platycephalidae		2	2
Siganidae	2		2
Congridae	1		1
Exocoetidae		1	1
Monacanthidae	1		1
Mugiloidae	1		1
Mullidae		1	1
Muraenidae		1	1
Scolopsidae	1		1
Tetraodontidae	1		1
identified total	350	382	
unidentified fish	200	302	
grand total of prey fish	550	684	
number of *P. leopardus*	589	742	1331

Table 6.9 Percentages and ranks of six families of prey in the diet of *P. leopardus* in the larger studies from the southern and central regions.

PREY FAMILIES	**REGIONS**			
	SOUTHERN		**CENTRAL**	
	percentage	rank	percentage	rank
Clupeidae	13.7	2	31.9	1
Pomacentridae	12.8	3.5	27.0	2
Labridae	8.8	6	8.1	3
Scaridae	12.8	3.5	6.3	4
Caesionidae	>0.1	>12	6.0	5
Pempherididae	19.4	1		-
number of *P. leopardus*	589		742	

Figure 6.1 Map of the Great Barrier Reef showing the two reefs in each of the three regions. The reefs were Heron and Wistari Reefs combined (Marine Park A) and One Tree Reef (Scientific zone), Southern Section; Little and Big Broadhurst Reef combined and Keeper Reef (zoned General Use B), Central Section; Lizard Reef (Marine Park A & B) and Eyrie Reef (Marine Park B), Far Northern Section.

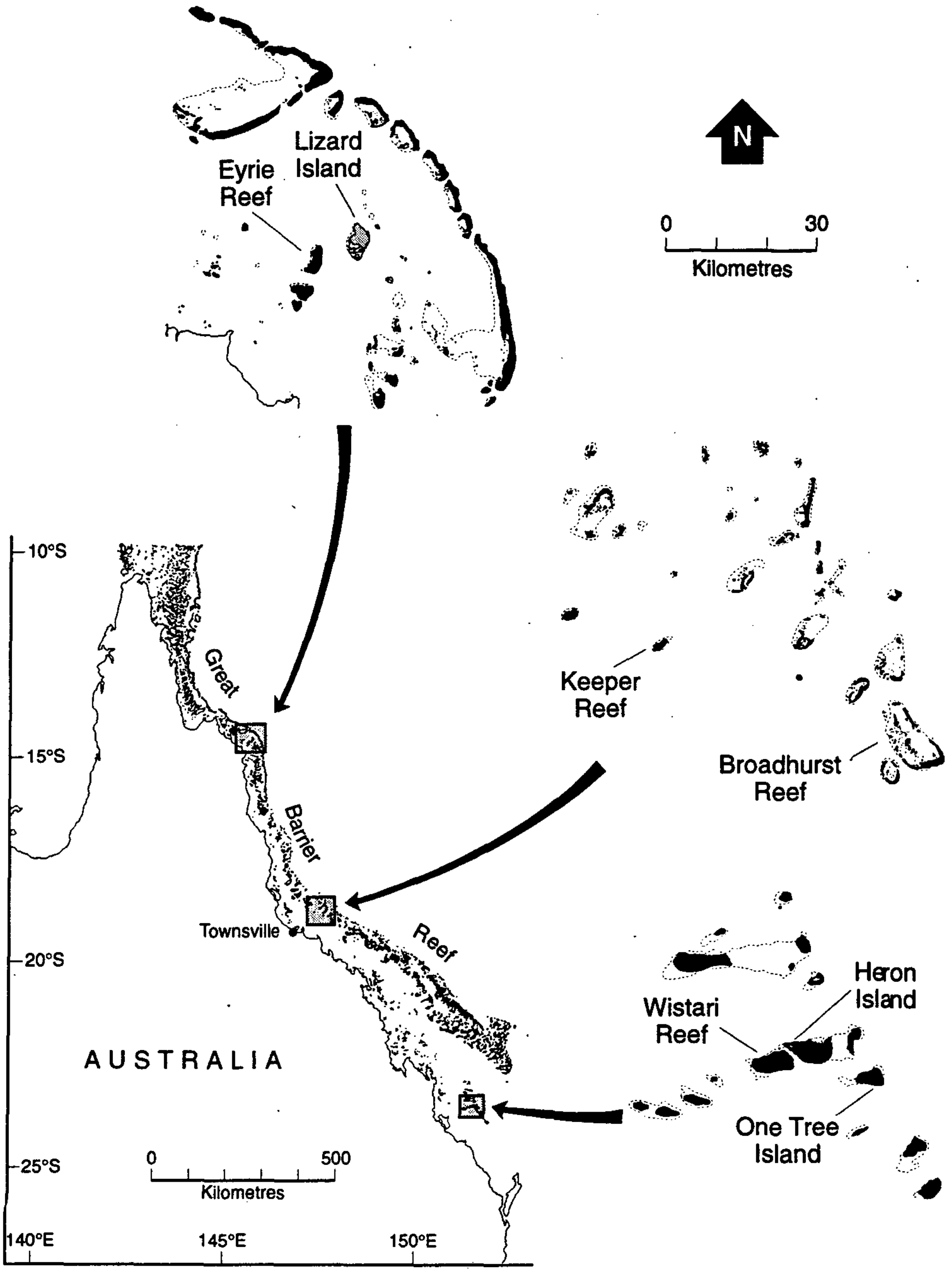


Figure 6.2 The length frequency of the samples of *P. leopardus* collected from each region, southern, central and northern GBR. The samples from each geographic region are divided by reefs: Heron Reef (n= 67) and One Tree Reef (n= 69) in the southern region, Little and Big Broadhurst Reef (n= 66) and Keeper Reef (n= 43) in the central region, Lizard Reef (n= 89) and Eyrie Reef (n= 25) in the northern region. The size of *P. leopardus* differed significantly between the southern and northern region (Dmax= 0.317, K-S p<0.01).

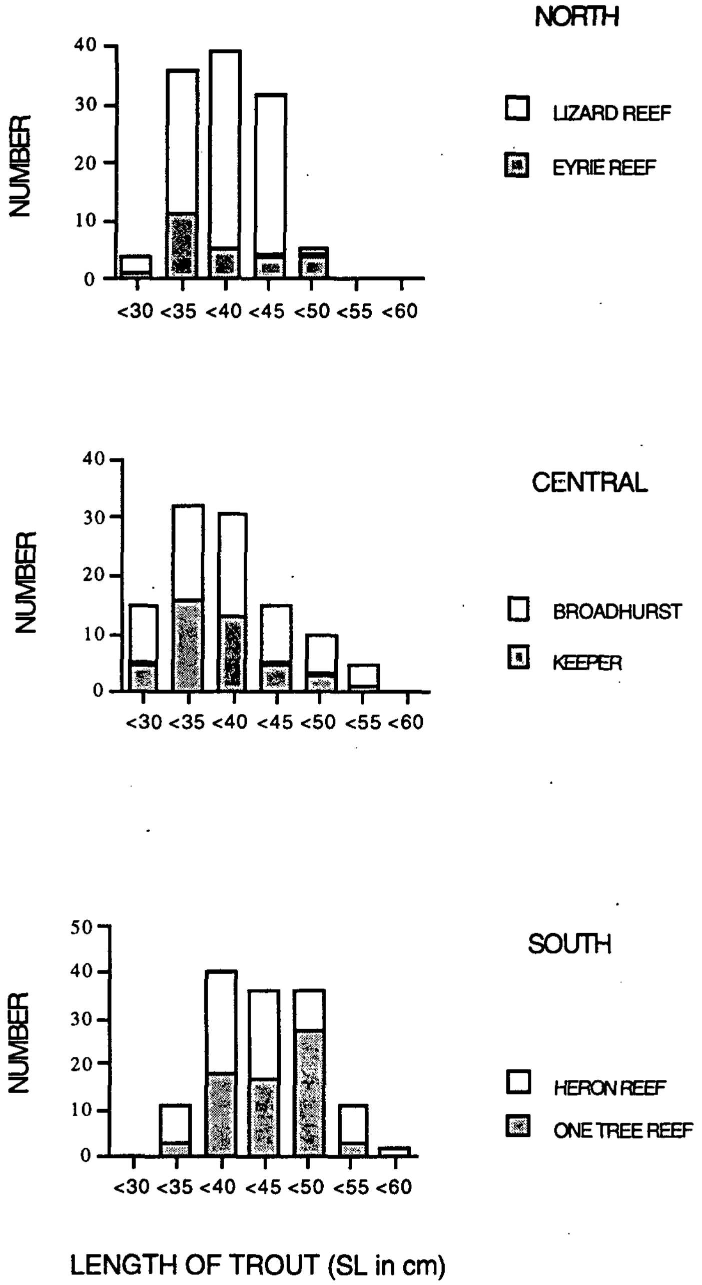


Figure 6.3 The number of prey found in the stomachs of *P. leopardus* at each reef in the three regions, southern, central and northern GBR. The reefs are Heron Reef and One Tree Reef in the southern region, Little and Big Broadhurst Reef and Keeper Reef in the central, Lizard Reef and Eyrie Reef in the north. The number of prey per predator differed significantly between reef within regions (southern $K\text{-}W_{[1]} = 15.0$, Monte Carlo p-value =0.001, central $K\text{-}W_{[1]} = 4.00$, Monte Carlo p-value =0.047, northern $K\text{-}W_{[1]} = 3.43$, Monte Carlo p-value =0.066).

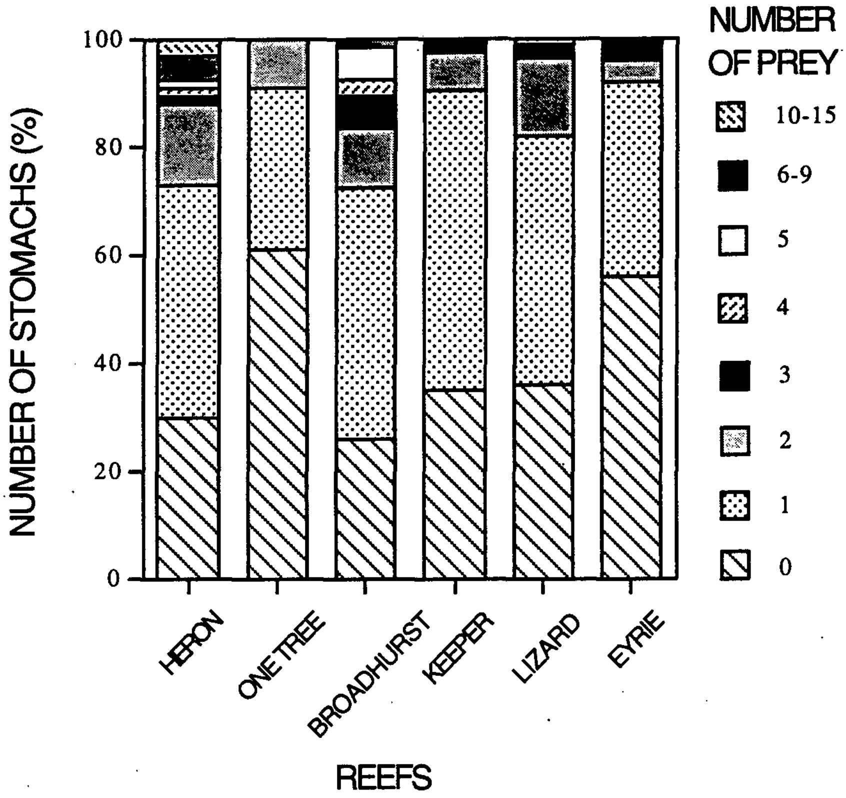


Figure 6.4 Regional differences in the number of prey in the 'Common' families expressed as a percentage of the identified prey in the diet of *P. leopardus*.

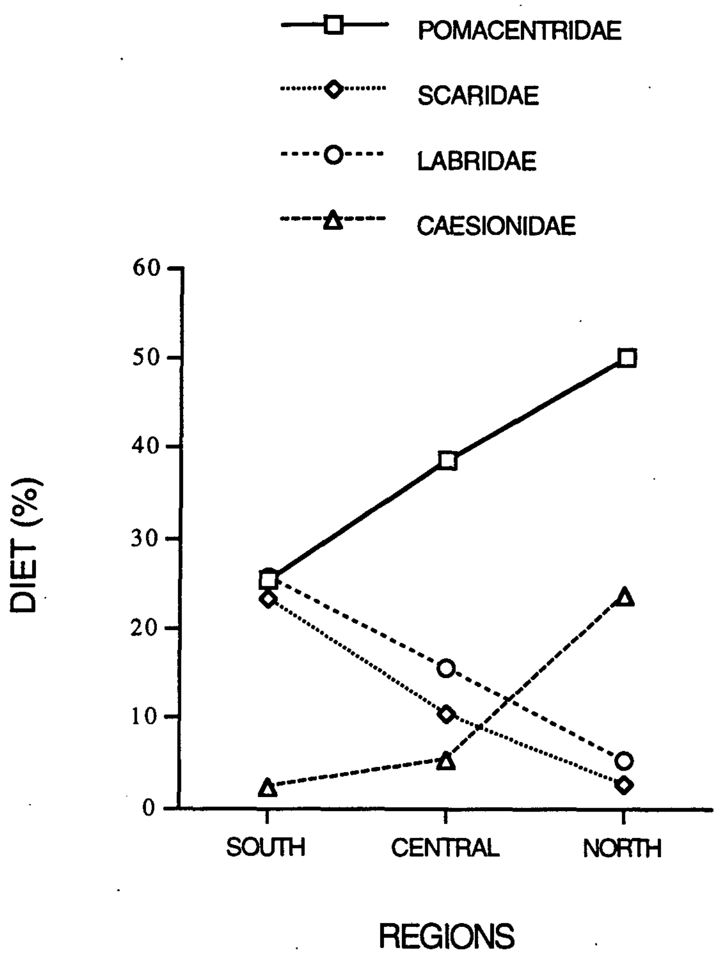
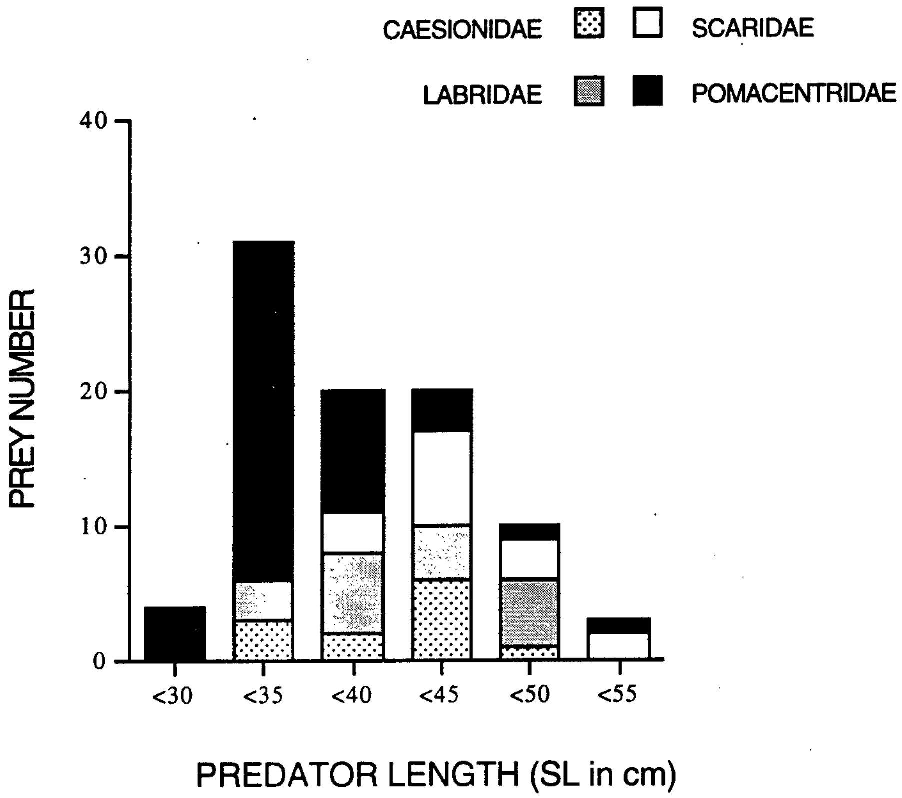


Figure 6.5 The numbers of prey in the four 'Common' families eaten by *P. leopardus* in six size-classes. Prey in the four 'Common' families, pooled across regions, were consumed by *P. leopardus* of different sizes (K-$W_{[15]}$ = 33.36, Monte Carlo p-value <0.001).



CHAPTER 7

7.0 THE EFFECT OF PROTECTION FROM FISHING ON THE DIET OF *P. leopardus*

7.1 INTRODUCTION

Large carnivorous and piscivorous coral reef fish such as lutjanids, serranids and lethrinids are favoured target species of fishers (Bohnsack 1982; Randall 1987; Russ 1985; Koslow *et al.* 1988). Even light to moderate fishing pressure is considered to modify the abundance of these large predatory species. Large piscine predators are vulnerable to overfishing due to their life history characteristics such as slow growth, higher longevity, low rate of natural mortality, limited adult mobility and often late maturity (Bohnsack 1982; Russ 1991). The maintenance of these stocks is considered important to fisheries and thus is of significance to management of coral reefs.

Strategies of coral reef management include the closure of reefs to all forms of exploitation. This strategy is designed to protect reef fish stocks and habitats (Bohnsack 1991; Williams and Russ 1994). Protection of reefs from fishing enables populations of reef fishes to regain or maintain natural levels of abundance and perhaps enhance yields of fishes from areas adjacent to the protected areas (Russ 1985; Alcala and Russ 1990). Since the establishment of the GBR Marine Park (GBRMP) in 1981, the major management strategy has been partitioning of reefs into six main zones that permit different types of fishing. For large piscivores such as coral trout, these zones allow three levels of fishing activities:

General Use 'A' and 'B' Zone- all fishing activities allowed
Marine National Park 'A' Zone- recreational line fishing only (no commercial fishing and no spearfishing. The latter is a recreational sport allowed only on snorkel)
Marine National Park 'B' Zone- no fishing of any kind.

For the areas that are of relevance to this study, the maximum durations of closure to line fishing were eight years for the Cairns Section and four years for the Central Section (Williams and Russ 1994).

Although multispecies fisheries generally predominate in the tropics, the GBR supports a line fishery dominated by a few genera (Russ 1991). The coral trout fishery is the most valuable commercial fin-fishery in Queensland, with a current value of $10 million. The value of this fishery is expanding rapidly with the recent advent of the "live export" market to SE Asia, and on the Australian market coral trout bring a consistently high price (currently about $20/kilogram retail for fillet). In Queensland, coral trout are the fish most targeted when handlining and spearfishing recreationally (Beinssen 1989). Of the three main species of coral trout on the GBR, *Plectropomus leopardus* is the dominant component of catches by both commercial and recreational line fishers (Williams and Russ 1994) and spearfishers (StJohn unpubl. data). Therefore, *P. leopardus* are an important renewable resource which add considerable economic, recreational and environmental value to the area.

The fishing community and fisheries and park managers have already detected a decline in the abundances of *P. leopardus* in some parts of the GBR, particularly close to centres of human population (Craik 1981). The growth rate of the tourist industry on the GBR is high and will continue to increase the recreational fishing pressure on this species. Depleting the abundance of *P. leopardus* may irreversibly alter the structure of the community of coral reef fishes (Goeden 1974). Yet, there is no information on their predatory impact on assemblages of coral reef fishes. To understand the impacts of these predators on the reef fish community, rates of consumption and selectivity of feeding in *P. leopardus* are required, as well as information on the composition and vulnerability of assemblages of prey.

Populations of coral reef fishes vary in abundance in time and space. Two mechanisms, recruitment pulses (settlement) and post-settlement survival, are important to subsequent recruitment to the fishery. In exploited stocks, consecutive cohorts of juveniles do not necessarily contribute equally to population biomass (Nikolskii 1991). The early life history is important in the replenishment of several fisheries, as the size or strength of the 0+ cohort remains in proportion throughout the subsequent age classes (Gulland 1982; Doherty and Fowler 1994). The supply of new piscivorous fishes into the fishery may also depend on post-settlement mortality rates, which are highest in juvenile coral reef fishes (Doherty and Sale 1985; Shulman and Ogden 1987; Meekan 1988; see review by Hixon 1991). Studies of predation on coral reef fishes on patch reefs suggest that small recruits and juveniles undergo 50% to 65% mortality in their first year (Sweatman 1984; Williams 1979), but the rates of recruitment and mortality of the 0+ year class of most piscivorous fishes on the GBR are not known.

On coral reefs, rates of settlement are assumed to be largely independent of local spawning events (but see Meekan unpubl. obs. in Doherty 1991; Doherty *et al.* 1994), as larvae from reef populations are likely to disperse over tens or hundreds of kilometres (Doherty and Williams 1988). Studies on pre-settlement *Plectropomus* spp, using light traps and nets, as well as studies of age and time of settlement, have found differences in patterns of settlement both temporally and spatially. The timing of settlement for *Plectropomus* varies locally and seasonally on the GBR. Whereas *Plectropomus* larvae have been found in reef-associated waters around Lizard Island in every month from October to January (Doherty pers. comm.), replenishment of *P. leopardus* on Green and Arlington Reefs (near Cairns) was restricted to a single three week period (Doherty *et al.* 1994). The spatial pattern of recruitment by *P. leopardus* may be similar among some reefs. Doherty *et al.* (1994) found consistent differences in larval supply between adjacent reefs which he related to reef topography or different dispersal paths to those reefs. On midshelf reefs off Townsville, which are separated by distances of up to 10-30 kms, simultaneous recruitment pulses of *P. leopardus* strongly influenced the age-structure of populations at two of four reefs examined (Ferreira 1993) and strong recruitment pulses of other reef fishes occurred concurrently (Williams 1991).

On the GBR, *Plectropomus* larvae settle at about 20 mm TL (Leis 1987) in rubble areas of back reefs (Doherty pers. comm.), and on midshelf reefs, the density of *P. leopardus* is 70% higher on back than on fore reefs (Ayling and Ayling 1992). *Plectropomus* recruits settle in the same habitat as adult *P. leopardus* (Ayling and Ayling 1992) and may be subject to predation by them (Ayling *et al.* 1991).

Fishing removes the larger individuals from a population and a reduction in the proportion of larger size classes in the population may lead to an increase in the growth rates of the remaining individuals (Russ 1991). An increase in growth rates of individuals in these populations would suggest that feeding behaviours or opportunities could differ between fished and unfished reefs. Differences in the diet of *P. leopardus* on reefs of different fishing pressures may be caused by variation in either abundances of prey or behaviours of the predator. Although the depletion of top predators results in an increase in the abundance of prey in closed systems such as tropical lakes (Pauly 1979; Jones 1982), the evidence for this occurring on coral reefs is inconclusive (Russ 1991). There is little evidence for massive increases in densities of prey species following a reduction of densities of piscivores by fishing. Thompson and Munro (1983) found an increase in abundance of prey fish on reefs where densities of large serranids had been reduced by trap fishing. A small labrid was found to be twice as abundant on a reef subjected to spearfishing than on protected reefs (Bohnsack 1982). Reduction of natural mortality in prey fish through selective fishing of predatory species was considered to be the reason for large numbers of holocentrids at Pedro Cays in Jamaica (Wyatt 1983). Knowledge of the diet of the exploited piscivore is the first step in determining any relationship between fishing and corresponding increases in certain potential prey species.

Any changes in the feeding behaviour of *P. leopardus* on reefs that are fished may be directly or indirectly caused by fishing. As a direct result of line fishing, coral trout may be attracted to popular fishing areas by bait and burley, which could supplement their diet. Dumping bait in the water to attract *P. leopardus* to a fishing area could alter their natural movement patterns or feeding areas. It could also reduce rates of predation because uncaught fish have fed on bait. Indirect effects of line fishing on feeding behaviour include the effects of decreases in the density and increases in the mean size of individual *P. leopardus* in populations. Reducing the density of piscivores may alter feeding patterns of smaller predators, which may be influenced by larger conspecifics. Smaller fishes may learn predatory behaviour by passive observation of larger fish or via following behaviour (see Chapter 6). If fishing changes the size structure of the population, the diet of *P. leopardus* might vary naturally due to ontogenetic differences (see Chapter 4). The presence of larger fish may inhibit feeding in smaller fishes that are chased away from good feeding sites (Samoilys 1987). As the feeding biology of *P. leopardus* has been used to explain changes in catchability and CPUE (Beinssen 1989), information on feeding in *P. leopardus* in different fishing zones will expand our knowledge of the effects of fishing on the GBR.

The stomach contents of samples of *P. leopardus* collected by Brown *et al.* (1992) were examined in this study. These samples provided a unique opportunity to examine the diet of *P. leopardus* on reefs where the age structure was known and independent estimates of densities of adults, recruits and some prey were available. The diet of *P. leopardus* captured by two methods, line and spear, were compared and the possible effects of providing bait to the fish were examined. Also, the rate of predation on and annual losses of the 0+ age class of *Plectropomus* were related to adult densities on reefs.

The major aims of this study were

1. to compare the diet of *P. leopardus* at two fishing zones in the GBRMP (no fishing and all fishing),
2. to compare the diet of *P. leopardus* at reefs within these two fishing zones (see above),
3. to examine predation on *Plectropomus* recruits on reefs in two fishing zones,
4. to compare rates of predation by *P. leopardus* on some prey species (calculated from dietary composition) to the densities of those prey, and
5. to compare the diet of *P. leopardus* caught by line and spear.

7.2 STUDY SITES, SAMPLING DESIGN AND METHODS

7.2.1 Background to this study

As the effects of fishing on the GBR is of major importance to the GBRMPA, a large scale experiment for measuring the effects of fishing on the GBR was designed recently in a proposal by Walters and Sainsbury (1990). Walters and Sainsbury suggested sampling reefs that had been previously closed prior to such an experiment. These reefs were then to be opened at the start of the experiment. Two studies preceded the rezoning of the Cairns Section on the GBR. Ayling and Ayling (1992) visually surveyed a range of species on a selection of reefs in two zones (GU 'B' and MNP 'B'). The species surveyed included coral trout and some of their potential prey. During these surveys, Ayling and Ayling (1992) estimated the total length of all fish (minimum TL for coral trout = 6 cm) In a separate study, Brown *et al.* (1992) collected samples by spear and hook and line of several large commercial fish species, including coral trout, from four of the reefs (in two fishing zones) surveyed by Ayling and Ayling (1992) and compared size and age structure, and catch per unit effort (CPUE) among reefs and levels of fishing pressure.

7.2.2 Source of specimens

The samples of coral trout for this study were part of a larger study done by Brown *et al.* (1992) from the Southern and Northern Fisheries Centre, Queensland Department of Primary Industries (QDPI). This study was one of several which aimed to examine the effect of fishing on some large, commercially fished species. All of the studies, which were funded by the GBRMPA, aimed to assess the density, size-, age- and sex-structure of target species on some reefs before, and after, their zoning was changed.

Ayling and Ayling (1992) surveyed the same reefs visually for many species of fishes including coral trout and some species of Pomacentridae. Data from their report was also used in this chapter.

7.2.3 Collection of samples from different fishing zones and locations

Study Sites and Sampling Design from Brown (1991) and Brown *et. al.* (1992)

Two pairs of mid-continental shelf reefs at the southern end of the Cairns Section of the GBR Marine Park near Innisfail were sampled in January and February, 1992. Each pair comprised one reef which was closed to fishing for eight years (Marine National Park (MNP) 'B') and the other which was open to commercial and recreational fishing activities (General Use (GU) 'B'). A northern pair comprised Wardle Reef (MNP 'B') and Nathan Reef (GU 'B'). The southern pair comprised Noreaster Reef (MNP 'B') and Potter Reef (GU 'B', Fig. 7.1). The two pairs of reefs were approximately 30 kilometres apart and the reefs within pairs were within 10-15 km of each other. The size of the reefs ranged from 12.8 km^2 (Wardle Reef) to 38.9 km^2 (Noreaster Reef, Fig. 7.1). The northern pair of reefs were sampled in January (Nathan Reef 20-22/1/92 and Wardle Reef 23-25/1/92) and the southern pair were sampled in February (Noreaster Reef 24-26/2/92 and Potter Reef 24-26/2/92).

Study Sites and Sampling Design

To compare the diet of *P. leopardus* between fishing zones and locations, the results of this study were compared with the February 1992 sample of *P. leopardus* speared from Broadhurst Reef off Ingham (see Chapter 5).

Broadhurst Reef, approximately 200 kms south of the other four reefs, is in the Central Section of the Marine Park and is zoned General Use 'B'. Thus, like Nathan and Potter Reefs, Broadhurst Reef has been open to all forms of commercial and recreational fishing. Although the Cairns Section of the Marine Park has been zoned for eight years, the Central Section has been zoned only for four, but the difference in duration of zoning does not affect this study because Broadhurst Reef has been fished for many years. Populations of coral trout on protected reefs near Broadhurst in the Central Section would be less likely to differ from the population on Broadhurst Reef because they have had only four years of protection, which is a relatively short period of closure for fish that can live for more than fourteen years (Ferreira 1993).

Methods of capture in the field from Brown (1991) and Brown *et. al.* (1992)

Two teams of experienced fishers collected fish by spear and line during daylight hours (0600-1800). The spearfishing team worked in two pairs from one small boat. The spearfishers snorkelled along the reef edge in one direction (with the boat) doing a series of 'swims'. One pair dropped the others in the water and moved the boat ahead to a predetermined 'swim' distance where they anchored the boat and began their 'swim'. When the first pair completed their 'swim' and reached the boat, they would move the boat again down the reef and begin another 'swim'. Divers kept individual tallies of the number of coral trout observed but not captured during each 'swim'. The coral trout were divided into two size classes, <40 cm and >40 cm (TL). The line fishing team worked in pairs from two small boats, and used single hook rigs with Western Australian pilchards (*Sardinops neopilchardus*) as bait.

The aim of the field work was to collect 120 coral trout from each reef (at Nathan Reef an additional 70 coral trout were collected as part of another study). To attempt to sample the actual population of coral trout, spearfishers were deliberately not size selective. Thus, spearfishers hunted each fish immediately it was seen and, if two or more coral trout were spotted simultaneously, the choice of the target was not based on size. This sample of coral trout differs from the samples reported in Chapters 5 and 6, where the majority of the coral trout were above the then legal size limit (>35 cm TL). All samples were stored on ice in the small boats and frozen on board the mother ship (up to several hours later).

Processing the specimens

Processing of coral trout and stomach samples was similar to previous chapters (see Chapter 2 for details), but SL was not measured for every fish, and smaller fish were weighed whole.

Measures of wet weight

When the weights of individual identified prey were unknown, their weights were calculated from the total weight of the stomach sample (see Section 5.2). Prey weights were estimated for less than 14% of the prey in the sample.

Definitions of size of trout

In this study, *P. leopardus* of different ages are referred to as

1. recruits ≤5 months,
2. juveniles 0+ year age class and
3. adults ≥1 year.

Calculations of feeding by *P. leopardus*

Calculations of feeding were based on one main assumption; the contents of the stomach represented daily feeding in *P. leopardus* as prey items are mostly digested after 24 hours (Chapter 3). Other specific methods are described below in the appropriate sections.

Analyses used in this study are described in Section 2.5.

7.3 RESULTS

7.3.1 The catch of coral trout from reefs within the two zones

Species of *Plectropomus* in the catch

A total of 387 coral trout were caught from the two fished reefs and 347 coral trout from the two unfished reefs (Table 7.1). *P. leopardus,* which represented 91.5% of the total catch by number, was the most common species captured by both spear and line. *P. laevis* was caught much less frequently (7.4% of the total catch by number), and *P. areolatus* was caught rarely (1.1% of the total catch by number). The proportion of the three species of *Plectropomus* in the catch varied significantly between unfished reefs but not between fished reefs (Table 7.1).

The percentage of *P. leopardus* in the catch was higher in the fished reefs (mean= 95.4%, SE=1.3) than in the unfished reefs (mean= 87.6%, SE=0.9, $t_{[2]}$= 4.89, $p<0.05$). *Plectropomus leopardus* appeared to be the most susceptible of the three species to line fishing. Thirteen percent of the catch of *P. leopardus* was caught by line compared to 3.7% of the catch of *P. laevis* and none of the *P. areolatus* catch, although the sample sizes were small in the latter two species.

Size-structure of *P. leopardus* collected by spear

The size-structure of populations of *P. leopardus* speared on the two unfished reefs, Wardle and Noreaster Reefs did not differ significantly (Fig 7.2). Yet, the size structure of the speared *P. leopardus* from the two fished reefs, Nathan and Potter Reef, differed significantly (Fig 7.2). *Plectropomus leopardus* from Nathan Reef had two large modal size classes, 20-24.9 and 45-49.5 cm FL, whereas *P. leopardus* from Potter Reef in the south had a large single modal peak at 35-39.5 cm FL (Fig 7.2).

7.3.2 Differences between samples of *P. leopardus* caught by line and spear

Size of *P. leopardus*

At three of the four reefs, Wardle, Potter and Noreaster Reefs, the size frequencies of the line-caught and speared *P. leopardus* were not significantly different (Fig. 7.2). At Nathan Reef, a greater proportion of larger *P. leopardus* was caught by line than by spear (Fig. 7.2).

Number of *P. leopardus* caught by line

The percentage of line-caught fish in the total catch of *P. leopardus* was significantly higher in the fished reefs (15.2%) than in the unfished reefs (9.6%, Table 7.1) but these proportions were similar at the two southern reefs (12.9% at Potter and 12.7% at Noreaster Reefs respectively). More importantly, there was a significant correlation between the percentage of line caught fish at each reef and the percentage of empty stomachs in the speared catch (Fig. 7.3).

Differences in the diet of *P. leopardus* caught by line and spear

The proportion of natural prey in the diet of *P. leopardus* caught by the two methods of fishing differed within the two fishing zones. A similar pattern occurred at both fished reefs. Line-caught *P. leopardus* contained significantly less natural prey (33.3% and 39.1% at Nathan and Potter Reefs respectively) than those speared (Nathan Reef=53.8%, Fisher's Exact test$_{[1]}$ = 4.54, $p \leq 0.016$; Potter Reef=58.1% Fisher's Exact test$_{[1]}$ = 2.868, $p \leq 0.042$). There was no such pattern at reefs in the unfished zone. The proportion of natural prey was higher in line-caught *P. leopardus* at Wardle Reef as natural prey occurred in all of the 10 fish caught by line (Fisher's Exact test$_{[1]}$ = 4.74, $p \leq 0.028$). The proportion of natural prey did not differ at Noreaster Reef (Fisher's Exact test$_{[1]}$ = 4.54, $p \leq 0.17$). Sample sizes of line-caught *P. leopardus* were very small at all reefs.

The composition of the fish diet of *P. leopardus* caught by line differed significantly from the diet of the speared catch (Table 7.2). In line-caught *P. leopardus,* there were proportionally less Pomacentridae and Labridae but more schooling pelagic prey (Clupeidae) in the diet. The diet of the line-caught *P. leopardus* may be unrepresentative due to their small sample size (n=85 predators or 21 prey items).

7.3.3 Effects of line fishing on the diet of *P. leopardus*

Fish were caught by line and spear from separate sites on the reefs, and thus all coral trout with bait in their stomachs were speared at sites where line fishing had not occurred. I assumed the bait in the stomachs of speared *P. leopardus* was stolen from hooks or burley. When each reef was fished (by a daily average of four people fishing during daylight hours), a total of 5 bait fish (pilchards) were found in the diet of *P. leopardus* speared all four reefs. These bait fish represented, numerically, 1.5% of all food (fish crustaceans, cephalopods and bait) consumed daily. Assuming that speared *P. leopardus* were a representative sample of the remaining population on the reef, line fishing had a negligible effect on the wild population by providing only 1.5% of their daily prey.

7.3.4 Variation in the diet of *P. leopardus* between reefs within different fishing zones

The major groups of prey

Plectropomus leopardus on the four reefs fed mostly upon fish, some crustaceans and a few cephalopods (Table 7.3). Coral, which was found in at least one stomach of *P. leopardus* from most reefs, was assumed to be swallowed incidentally with prey. The proportions of fish, crustaceans and cephalopods in the diet of *P. leopardus* did not vary significantly among the four reefs (Table 7.3). As fish comprised 95.7% of the diet of *P. leopardus* (excluding corals and unidentified stomach contents), the rest of this section focuses on prey fish only.

Family richness in the diet

Of the 468 prey fish in the diet of *P. leopardus,* 39.74% were identified into 22 families (Table 7.4). The family richness of the diet of *P. leopardus* on the fished and unfished reefs ranged from seven families at Noreaster Reef to 15 at Nathan Reef. There was no detectable difference in the number of families in the diet between fishing zones($t_{[2]}$= 1.380, $p>0.05$, $1 - \beta < 0.33$). The number of 'Occasional' families in the diet of *P. leopardus* varied among fishing zones. Prey belonging to all six 'Occasional' families were eaten by *P. leopardus* at both of the fished reefs. Prey in only three 'Occasional' families were in the diet of *P. leopardus* at both of the unfished reefs.

At each reef, the number of prey in a family ranged from 1 to 17 individuals (Table 7.4) and the total prey weight for a family ranged from 0.12 g to 235.09 g (the latter=12 pomacentrids, Table 7.5). Prey in families were classified into four categories based on their numerical abundance in the diet (see Chapter 5 for details): 'Common' (mean number of prey per reef in each family ranged from 3 - 11.7, i.e. total number of prey in a family/number of reefs), 'Occasional' (mean range 1- 2.5), 'Rare" (mean range 0.25 - 0.75) and 'Sporadic' (mean range 0.75- 7.7).

The mean percentage of the four categories of prey in the diet of *P. leopardus* ('Common', 'Occasional', 'Rare' and 'Sporadic') at all four reefs were calculated for two measures, number and weight (see Tables 7.4 and 7.5). In contrast to Chapters 5 and 6, these two measures were similar in three of the four categories. In the 'Common' prey category, three families represented a mean of 53.0% of prey numerically and 61.7% of prey by weight. The 'Occasional' prey category included prey in six families which represented a mean percentage of 21.6% of prey numerically and 29.9% of prey by weight.

The 'Rare' category of prey comprised 11 families which represented 7.5% of the diet numerically and 6.6% of the total diet by weight. Measures of the 'Sporadic' prey category differed most as two families represented 17.8% of prey numerically and only 1.8% of the diet by weight.

Abundance of families of prey

The abundance of prey in families in the diet of *P. leopardus* varied significantly among the four reefs (Table 7.4). The diet of *P. leopardus* was more similar when reefs were grouped by location (North and South) rather than by zone (fished and unfished reefs, Table 7.4). More than half of the diet comprised of prey in the 'Common' families (Tables 7.4 and 7.5). A total of 47 *P. leopardus* ate 47 pomacentrids and 36 *P. leopardus* ate 37 labrids from the four reefs.

Variation in the composition of the diet of *P. leopardus*

Dietary overlap was high in both fished reefs and unfished reefs (Table 7.6). The 'Common' family, Pomacentridae, was the most important prey in the diet of *P. leopardus*. In terms of the IRI, Pomacentridae ranked highest at three of the four reefs, Nathan, Wardle and Noreaster, and second at Potter Reef (Table 7.7). Another 'Common' family, Caesionidae, ranked first in the diet at Potter Reef. All the 'Common' families ranked in the top four, except Caesionidae, which was absent or low ranking in the northern reefs (Nathan and Wardle Reefs). One 'Occasional' family, Scaridae ranked in the top four at three of the four reefs and one 'Sporadic' family, Clupeidae ranked fourth, fifth or sixth at every reef.

Habitats of prey fishes

Families of prey fishes were categorised by the habitat in which they were most commonly found (see Chapter 2). Eight of the families of prey fishes lived in the demersal reef environment, whereas only four families dwelled among soft sediments (Table 7.8). Two habitats, midwaters associated with reefs and benthic hard substrata, were each associated with five families of prey fishes (Table 7.8). Prey were eaten mostly from two reef habitats: 59.7% of prey by number from the demersal reef habitat and 26.9% from the midwaters (Table 7.9). Prey from the soft sediment and benthic reef environment represented 7.0 and 6.4% of the sample respectively. *Plectropomus leopardus* fed in different habitats among reefs but not between fishing zones (Table 7.9).

7.3.5 Further comparison of the diet of *P. leopardus* between fishing zones

The diet of *P. leopardus* was compared among two fishing zones (fishing and no fishing) and a similar fishing zone (fishing allowed) and season from a different location (the February sample of *P. leopardus* from Broadhurst Reef, see Chapter 5). Reefs in each fishing zone were pooled as dietary overlap of *P. leopardus* in reefs zoned the same was high (0.68 for both zones). In summary, in this part of the study dietary comparisons were among

1. Cairns Section - no fishing (MNP 'B', Wardle and Noreaster Reefs)
2. Cairns Section - all fishing (GU 'B') which included all recreational and commercial fishing activities (Nathan and Potter Reefs) and
3. Central Section - all fishing (GU 'B', Broadhurst Reef).

Of the three paired comparisons, dietary overlap was high in two: no-fishing and fishing zones in the Cairns Section, and fishing zones in the Cairns and Central Sections (Table 7.10). Dietary overlap was lowest in the unfished zone (Cairns Section) and the zone open to all fishing activities in the Central Section.

The size distributions of the populations of *P. leopardus* amongst fishing zones were not compared because in the northern study spearfishers were not size selective, whereas at Broadhurst Reef spearfishers were targeting fish of legal sizes (≥35 cm TL).

7.3.6 Pomacentridae as prey of *P. leopardus*

Pomacentridae were the most important prey in the diet of *P. leopardus* at the four reefs. Of the 47 pomacentrids identified in the diet of *P. leopardus,* 23 were classified into 10 species (in seven genera) and prey in two genera were not identified to species (Table 7.11). The most common species in the diet of *P. leopardus* was *Acanthochromis polyacanthus* followed by *Pomacentrus* spp.

The pomacentrids were eaten by all sizes of *P. leopardus* (20.5-58.5 cm FL) except for the smallest size class (<20 cm FL). There was no detectable difference in the proportion of pomacentrids eaten by *P. leopardus* in the two fishing zones (Table 7.11). Ten percent of *P. leopardus* with prey in their stomachs at fished reefs had fed on pomacentrids compared to 14% at the unfished reefs.

Of a total of 468 prey fish in the diet of *P. leopardus*,186 were identified, and 47 of these were pomacentrids If pomacentrids were present in all the prey fish in similar proportions to those that were identified, then a total of 118 pomacentrids would be eaten by the sample of 672 *P. leopardus* (i.e. 47/(186/468)). Thus for every 100 *P. leopardus* on the reef between 15 and 21 pomacentrids (mean = 17.6) could be consumed daily (Binomial Pr. =0.1756, 95% CI=0.1476-0.2065).

7.3.7 Juvenile *Plectropomus* in the diet of *P. leopardus*

A total of four juvenile *Plectropomus* spp. were eaten by *P. leopardus*: two in the January sample and two in the February sample. Three of the four recruits were eaten at fished reefs. Both *Plectropomus* recruits were smaller in the February sample (81 and 87 mm SL) than in the January sample (90 and 107 mm SL).

Brown *et al.* (1992) aged most of the specimens examined in this study. Histograms of the age structure of the speared sample of *P. leopardus* from each reef are shown in Figure 7.4. The proportions of one year olds on the fished reefs were large compared to those on the unfished reefs. The four year old age class was the most dominant of the older age classes of *P. leopardus*. Fish of this age are potential predators on *Plectropomus* recruits.

The size of the four *P. leopardus* that had consumed *Plectropomus* spp. were 34, 40.5, 41 and 43 cm FL. As the mean length of four year old *P. leopardus* from both Townsville and Lizard Is. regions is 41 cm FL (Brown *et al.* 1994), the majority of these predators were probably about four years old. The proportion of one year olds in the age structures were negatively correlated with the proportion of four year olds in the populations of *P. leopardus* (Fig. 7.5). One data point in this correlation is very influential and thus, the results must be treated with caution. All immature *Plectropomus* spp. are vulnerable to predation by adult populations of *P. leopardus*, and annual predation on *Plectropomus* spp. is discussed later using another data set.

The density of *Plectropomus* recruits on each reef was surveyed by Ayling and Ayling (1992) a few days prior to the collection of the samples of *P. leopardus.* The percentage of *Plectropomus* recruits in the diet was positively correlated ($p<0.06$) with the density of recruits on each reef (Fig. 7.6), which suggests that *Plectropomus* recruits may be eaten in proportion to their abundance on reefs. Nathan Reef, which was open to fishing, had the highest recruitment during 1992 (Ayling and Ayling 1992).

Information on the density of adult and recruit *P. leopardus* (from Ayling and Ayling 1992, see Table 7.12) on the four reefs enabled a calculation of the overall proportion of the recruit population potentially eaten daily by *P. leopardus* (Binomial Pr. =0.01488, 95% CI=0.007158-0.02719, see Section 2.5.3 for explanation of binomial tests). Assuming that *Plectropomus* juveniles (n = 4) occurred in similar proportions in the diet as unidentified fish (i.e. number of unidentified fish/total number of fish), then a total of 10 *Plectropomus* juveniles would be eaten by the sample of 672 *P. leopardus* (i.e. 4/(186/468), see Section 7.3.6). Daily predation on juvenile *Plectropomus* was extremely high (7.4% calculated by 1.09*0.01488/0.22 i.e. mean adult density*Binomial pr. of predation/mean recruit density from Table 7.12). As the absolute sample size of *Plectropomus* recruit prey was small, this estimate may be poor.

Throughout the year, three out of 621 *P. leopardus* from Broadhurst Reef ate three *Plectropomus* recruits and juveniles. The three *P. leopardus* ranged in size from 46.4 to 55.3 cm FL and the *Plectropomus* recruits and juveniles ranged in size from 105 to 125 mm (SL). As 382 fish were identified from 684 prey fish, actual numbers of *Plectropomus* juveniles in the diet was estimated to be five. Therefore, an adult *P. leopardus* at Broadhurst Reef eats an average of nearly three (mean = 2.94, with a range of 2.6-9.9) age 0+ year class of *Plectropomus* spp. annually (Binomial probability =0.008052, 95% CI=0.00262-0.0187). All of the *P. leopardus* which ate *Plectropomus* spp. were within the fishing size range (34 cm FL is approximately 35 cm TL, the previous legal minimum size). Thus fishing removes potential predators of juvenile *Plectropomus* spp.

Summer-time and annual rates of predation on *Plectropomus* spp. can be compared using probability values of daily consumption. The probability of daily predation on *Plectropomus* recruits (81 - 107 mm SL) was much higher in summer at the four reefs in the Northern GBR (Binomial Pr. =0.015, 95% CI=0.007-0.027) than the annual predation on *Plectropomus* recruits and juveniles (105 - 125 mm SL) at Broadhurst Reef (Binomial Pr. =0.008, 95% CI=0.003-0.019).

7.4 DISCUSSION

Overall, there was little difference in the diet of *P. leopardus* from reefs in the two fishing zones. The diet was most similar between the two fishing zones (i.e. fishing and no fishing for eight years) at the same location than between reefs with identical zoning (GU 'B') at different locations (Northern and Central Sections). The results of this study suggest that, at current levels of fishing intensity, fishing pressure does not affect the feeding behaviour of *P. leopardus.* Although the diet of *P. leopardus* varied among fishing zones, these differences were relatively small when compared to natural variation among *P. leopardus* on the GBR. There was less similarity in the diet among regional populations of *P. leopardus* (see Chapter 6) and at one reef sampled over time (see Chapter 5) than among different fishing zones.

The lack of difference in the diet of *P. leopardus* between fishing zones is not surprising since other aspects of the populations of *P. leopardus* did not differ (Brown *et al.* 1992; Ayling and Ayling 1992). Brown *et al.* (1992) found no overall effects of fishing on age structure, size structure and catch rate data, although their visual census data detected a greater density of larger trout on unfished reefs. In visual surveys of *P. leopardus,* Ayling and Ayling (1992) found no differences in the density, average length and recruitment of *P. leopardus* among reefs in the two fishing zones. This suggests that there were no effects of fishing zones on populations of *P. leopardus* on these reefs. Two reasons may account for an absence of the effects of fishing on populations of *P. leopardus* on these reefs. Firstly, 'unfished' reefs could have been fished illegally over the eight years. Such violations are thought to be relatively common. Secondly, fishing pressure may be low on midshelf reefs but it is difficult to measure. Commercial fishers take more than half the coral trout caught in the GBR region (Blamey and Hundloe 1991; Trainor 1991). Only a small percentage of recreational boats fish on midshelf reefs (1-2% in most areas and 25% in the Cairns area, Blamey and Hundloe 1992) as boats have to travel between 40 and 80 kms to reach the main clusters of midshelf reefs in the Central and southern Cairns section of the GBRMP (Williams and Russ 1994). The number of vessel-visits, however, is unlikely to be strongly correlated to actual fishing pressure.

Fishing did not affect the diet and feeding behaviour of *P. leopardus.* Dietary overlap was high in reefs of similar fishing zones in the Cairns Section, and the unusually consistent, low numbers of clupeids in the diet of *P. leopardus* at all four reefs contributed to this similarity. The species richness of the diet of *P. leopardus* at each reef did not vary between fishing zones. Although line fishing may attract fish to a particular site, it does not appear to affect feeding areas of *P. leopardus* permanently because the proportion of prey from different reef habitats did not vary among the four reefs.

In the Cairns Section the composition of the diet of *P. leopardus* varied between reefs and was not related to fishing zones. *Plectropomus leopardus* from the two northern reefs consumed more small schooling fishes, Clupeidae and Engraulidae, from the 'Sporadic' family. A large, schooling prey, Caesionidae, were eaten mostly by *P. leopardus* at the two southern reefs. Furthermore, 'Rare' prey were eaten more at the two northern reefs than at the southern pair. This similarity in the diet of *P. leopardus* between reefs of different fishing zones may be attributed to location of the reef or the time of sampling as each zone included one reef from a pair located within 15 kms of the other and each pair of reefs was sampled one month apart.

Brown *et al.* (1992) calculated total mortality of fish >3+ year class and found no differences in overall mortality between the two fishing zones. They suggested that natural mortality may be higher on unfished reefs than on open reefs, thus compensating for fishing mortality. Sharks were more abundant on the unfished reefs at the time of sampling (seen by the spearfishers) and were considered potential predators (Brown *et al.* 1992). Dietary analyses of *P. leopardus* revealed that adults were predators of *Plectropomus* recruits and juveniles. Furthermore, calculations based on densities of adults and recruits indicated that adult *P. leopardus* consumed an extremely high proportion of the recruit population daily throughout summer. Summer months of recruitment were considered to be from November to March because larvae occur in waters around Lizard Island from October to January (Doherty *et al.* 1994) and one *Plectropomus* recruit was eaten in November (at Broadhurst Reef) and in late February (this study). Although predation should be higher in summer, when small *P. leopardus* are most abundant, the calculated rate of predation is not sustainable as it indicates that predation by *P. leopardus* would eliminate the total recruit population in 25 days. Clearly this does not occur. There are at least four possible explanations for this high figure. Predation rates may be artificially high for two reasons: firstly, if the assumption that the proportion of recruits in the identified prey fish was similar to the unidentified prey was incorrect or secondly, if the estimates of recruit *Plectropomus* by Ayling and Ayling (1992) were too low. The second reason is more likely because Ayling and Ayling (1992) did not count *Plectropomus* recruits less than 6 cm (TL) and small fish are easy to miss in counts. Thirdly, the predation rate may be realistic but subject to large fluctuations throughout summer. In this study, there was some evidence to suggest that predation on recruits may be density dependent. Thus, rates of predation would decline as the density of recruits declined. Fourthly, if the predation estimate was realistic and constant throughout summer, then the seasonal rates of recruitment are very high to compensate for this high mortality. Yet regardless of whether these extremely high rates of predation are real or artificial, adult *P. leopardus* may be important predators of juvenile *Plectropomus*. Abundances of adults on the four reefs appear to influence the survivorship of juveniles as the proportion of four year old *P. leopardus* was significantly negatively correlated to the proportion of one year olds in the populations. This conclusion is tenuous as the results are based on a limited data set and the correlation may relate primarily to cycles of recruitment success.

Both of the *P. leopardus* recruits eaten on the southern reefs in February were smaller than the two eaten on the northern reef Nathan in January. These slight differences in size were confounded by the time of sampling and may have been caused by short term temporal variation in recruitment pulses between Nathan and the southern reefs. Alternatively, recruits at both of the southern reefs may have grown more slowly.

Predation on the 0+ year class did not cease after summer. On Broadhurst Reef *Plectropomus* recruits occurred in the stomach samples of *P. leopardus* in June 1991, October 1990 and December 1991 (n=1 for each month) and calculations suggested that every adult *P. leopardus* consumed between 2 and 10 (mean = 3) juvenile *Plectropomus* annually on Broadhurst Reef. These rates of predation at Broadhurst Reef are on an unknown density of *Plectropomus* juveniles at the time of sampling. If predation rates on juveniles are density-dependent, then rates of predation will vary annually according to the abundance of the 0+ age class.

Despite temporal and spatial variation in settlement of *Plectropomus* spp. (Doherty *et al.* 1994) Ayling *et al.* (1991) found that the number of recruits and juvenile coral trout (<35 cm TL) were consistently higher on fished reefs than on protected reefs in the Cairns Section of the GBRMP. Ayling *et al.* (1991) identified this pattern as an effect of fishing. There are three possible explanations for this pattern:

1. open reefs have consistently higher recruitment than unfished reefs because of individual reef topography etc, which was caused by chance or by biased selection of reefs by management.
2. higher densities of adult *P. leopardus* on a reef inhibit settlement of recruits. In one pomacentrid genus, at a much smaller spatial scale, the presence of adults of one species inhibit the settlement of recruits from another species (Sweatman 1985).
3. Cannibalism is higher on unfished reefs.

The third reason seems the most plausible. When fishing decreases the density of adult *P. leopardus,* newly settled recruits may have a higher rate of survivorship on open reefs than on unfished reefs.

The two adjacent fished reefs, Nathan and Potter Reefs, had a very strong pulse of recruitment that did not appear in the unfished reefs. Assuming recruitment was similar to all four reefs, the abundance of the one year age class (1 year =<20-25 cm TL, in Ferreira 1993) on each reef could be explained by the predation by *P. leopardus* greater than three years old (3 years = 30-45 FL cm, in Ferreira and Russ 1994). Four year olds were the most abundant age class of *P. leopardus* on all four reefs and the results of this limited data suggest that the proportion of one year olds was negatively correlated with the proportion of four year olds in the population. In contrast, predation did not modify the relative strength of pulses of recruitment significantly in a study on recruitment of other coral reef fishes (Doherty and

Fowler 1994)

Generally, the major processes which structure populations of *P. leopardus* are considered to be recruitment or fishing or both (Doherty and Williams 1988; Ferreira and Russ 1995). Fishing may play more than one role in structuring populations of *P. leopardus* on the GBR. As well as increasing adult mortality directly, the results of this study suggest tentatively, that fishing may reduce juvenile mortality indirectly.

Pomacentrids were the dominant family in the diet and were consumed by *P. leopardus* of every size group except the smallest. Fishing did not affect the proportion of pomacentrids in the diet of *P. leopardus.* Overall 47 pomacentrids were eaten by *P. leopardus*, and the most numerous species was *Acanthochromis polyacanthus.* Also, the genus *Pomacentrus* was common in the diet. At summer rates of predation one *P. leopardus* would consume between 54 and 75 pomacentrids annually, and nearly 20% of these could be *A. polyacanthus. Acanthochromis polyacanthus* is a unique pomacentrid because parents brood their young. Thus, adult *A. polyacanthus* would be more vulnerable to predation in summer when both parents continually guard a large brood. A study at One Tree Reef on the southern GBR concluded that *P. leopardus* was a predator of *A. polyacanthus* (Thresher 1983a). Thresher (1983a) noted that over a one year period adult *A. polyacanthus* disappeared on three out of four reefs where *P. leopardus* occurred compared to one out of 20 where the piscivore was absent. Furthermore, a significant inverse relationship between the abundance of *P. leopardus* and abundances of the planktivorous pomacentrid *A. polyacanthus* (and a group of four nocturnally active apogonids) were found at 26 patch reefs (Thresher 1983a). Other results in Thresher's study appeared contradictory (Hixon 1991) since he found no correlation between the abundance of potential prey and the total abundance of all piscivores on the reefs. Also, percentage mortality of 27 broods of juvenile *A. polyacanthus* over 30 days was positively correlated with the mean total of all fish present but not correlated with the number of piscivores (Thresher 1983a). Feeding behaviour by *P. leopardus* could partly explain these contradictory patterns. As *P. leopardus* ate mostly adult pomacentrids, this piscivore would probably not affect the mortality of broods of juvenile *A. polyacanthus.*

Generally, depletion of a large number of carnivorous species has not led to detectable increases in abundance of prey species on coral reefs (Bohnsack 1982; Russ 1985, 1991; Hixon 1991; Koslow 1991). To examine the effect of removal of predators, it is important to know which prey species are important in the diet of these large predators. Ayling and Ayling (1992) chose five species of Pomacentridae to be potential prey of *P. leopardus.* Four of these five species counted by Ayling and Ayling (1992), were not recorded in the diet of *P. leopardus* at these reefs (but see Chapter 4 for a complete list of prey species eaten by *P. leopardus*). One species, *Pomacentrus moluccensis,* was eaten once by *P. leopardus* in this study. Another species, *Amblyglyphidodon curacao*, occurred in the diet of *P. leopardus* in another region (see Chapter 4).

Sampling biases of species of *Plectropomus* occurred between the two methods of fishing. Assuming that catchability of *Plectropomus* by line fishing was not density dependent, line fishing was not a good indicator of natural populations of all species of *Plectropomus* because *P. leopardus* was more susceptible to line fishing than *P. laevis.*

Dietary composition of *P. leopardus* in this study indicated that line fishing plays a minor role in reducing predation on prey indirectly by feeding predators. Approximately 1.5% of the diet of *P. leopardus* may be substituted by bait and burley. Commercial fishing would probably supplement feeding by *P. leopardus* more. Twenty percent of coral trout caught by commercial fishers contained bait compared to 11.8% of those caught recreationally (see Table 2.2).

Use of two methods of fishing simultaneously provided some insights into the relationship between feeding biology of *P. leopardus* and methods of capture. Firstly, dietary composition varied between samples collected by the two methods. Line-caught *P. leopardus* had a much higher proportion of pelagic or 'Sporadic' prey than the speared sample. Thus results of dietary analyses from line-caught *P. leopardus* only, would be misleading. Although fishing competitions are a useful method to collect information on species (Rawlinson 1989), the biological data from these collections, such as dietary information, may be biased depending on the methods of capture used. Blaber *et al.* (1990) used fishing competitions as a means of collecting specimens to determine the predators of tuna baitfish and examine the trophic effects of baitfishing on the subsistence fishery. The 18 *P. leopardus* examined in their study comprised 41.9% (dry weight) baitfish prey (including *Stolephorus spp, Spratelloides* and Caesionidae, Blaber *et al.* 1990). This proportion of baitfish in the diet was similar to the numerical proportion of Clupeidae in the diet of *P. leopardus* caught by line in this study, but very different from the overall results. When different fishing methods are used to collect specimens, the method of capture must be specified clearly as it may have affected the results. Secondly, the relative proportions of bait in the diet of *P. leopardus* differed between the two fishing methods at three of the four reefs. At the fished reefs, line-caught *P. leopardus* provided less information about their natural prey than those caught by spear because they contained lower proportions of natural prey. At the unfished reefs the results differed. The relative proportions of bait in the diet of *P. leopardus* was probably influenced by concurrent fishing using the two methods, whereby the amount of bait in the speared trout was increased by line fishing. This is suggested by an earlier pilot study because a significantly higher proportion of bait occurred in the diet of line-caught *P. leopardus* when a larger number of specimens were fished, either by line or by spear, from different reefs (see Table 2.2 Chapter 2).

The history of fishing on reefs may influence behaviour in *P. leopardus* (Russ 1991). Spearfishing has been suggested to change the behaviour of coral trout in the presence of snorkellers (unpubl. GBRMPA workshop) and baited lines may alter long-term feeding behaviour. The results of this study suggest that a prior history of line fishing at a reef did not affect the proportion of fish captured by each method: similar proportions of *P. leopardus* were caught by line in reefs in both fishing zones (two open reefs and one closed). Therefore, the behavioural response of *P. leopardus* to line fishing with bait did not vary among reefs with different histories of line fishing.

CPUE (fish per person-hr) of the line fishers indicated that *P. leopardus* were more abundant on the open reefs, but this was opposite to the conclusion from their visual surveys (Brown *et al.* 1992). Brown *et al.* (1992) could not explain their result. In the present study the percentage of empty stomachs in the speared catch at each reef was correlated with the percentage of line caught fish. When a greater proportion of the population of *P. leopardus* were hungry, more fish were caught by line regardless of the zone of the reef.

Since the 1960's dietary studies using line caught fish have suggested that line fishing contributed to the large number of empty stomachs in fish because it selects for hungry fish and prey is regurgitated during capture (Randall and Brock 1960).

The value of CPUE by line fishing as an indicator of stock density of *P. leopardus* has been questioned (Brown *et al.* 1992; Ferreira 1993; Williams and Russ 1994) and may depend on factors such as the general level of hunger in the population. In a 'fish down' experiment on *P. leopardus* on Boult Reef, which had been protected from fishing for three years, Beinssen (1989) surveyed the population and tagged 375 *P. leopardus* before the reef was reopened to fishing. Although 25% of the population of *P. leopardus* was removed in the first two weeks of fishing, after four days the CPUE did not reflect the abundance of the remaining population of *P. leopardus* on the reef. Beinssen (1989) attributes this to *P. leopardus* 'going off the bite', where they cease feeding for several weeks. Studies on digestion rates of *P. leopardus* and their feeding patterns do not support this conclusion because *P. leopardus* digest most of their prey in 24 hours and actively seek prey when hungry (Chapters 4 and 7). One possibility for the drop in catchability of *P. leopardus* was that the loss of bait from lines or through burleying the water provided enough food to satiate the hunger of the populations when line fishing occurred. Another reason could be the learning capacity of *P. leopardus*. After 4-5 days of intensive fishing, populations of *P. leopardus* witness the capture of their neighbours, and perhaps learn not to strike at bait.

The mean size of line-caught *P. leopardus* was significantly larger than that of the speared catch at only one of four reefs. Generally, line-caught *P. leopardus* from deep waters are larger than those speared in shallow waters. In this study, line fishers fished from small boats (4-5 m in length) and they were able to access shallow reefs. Fishing boats that are too large to enter shallow waters and don't carry dinghies would fish a deeper and possibly larger population of *P. leopardus.*

In conclusion, fishing pressure does not affect the feeding behaviour of *P. leopardus*. Dietary-overlap of *P. leopardus* in the two fishing zones was high relative to natural spatial and temporal variations in the diet of *P. leopardus* on the GBR. Within the Northern Section, the diet of *P. leopardus* was more similar when reefs were grouped by location than when reefs were grouped by fishing zones. Pomacentrids were the dominant family in the diet of *P. leopardus* and were eaten by all sizes of the piscivore. At summer rates of predation, one *P. leopardus* would consume between 54 and 75 pomacentrids annually and one species, *A. polyacanthus,* would account for approximately 20% of these pomacentrids. Adult *P. leopardus* were predators of *Plectropomus* recruits and rates of predation were extremely high. Populations of *P. leopardus* occurred in densities which could reduce the density of recruits on a reef during summer (7% daily). Finally, the natural diet of *P. leopardus* varied according to the fishing methods used to collect the samples. The results of dietary studies that use line fished samples of *P. leopardus* should be treated with caution.

Table 7.1 The number of *P. leopardus, P. laevis* and *P. areolatus* caught by line and spear from the two fished reefs and two unfished reefs. The proportions of the three species of *Plectropomus* in the catch varied between unfished reefs (Fisher's Exact test$_{[2]}$ = 6.141, p-value = 0.039) but not between fished reefs (Fisher's Exact test$_{[2]}$ = 1.562, p-value = 0.461). The percentage of line-caught fish in the total catch of *P. leopardus* was higher in the fished zone (15.2%) than in the unfished zone (9.5%, Fisher's Exact test$_{[1]}$ = 4.742, p= 0.035).

ZONE	REEFS	TOTAL	*P. leopardus*		*P. laevis*		*P. areolatus*	
			line	spear	line	spear	line	spear
FISHING	Nathan	203	33	158	1	9		2
	Potter	184	23	155		5		1
NO FISHING	Wardle	174	10	143		16		5
	Noreaster	173	19	131	1	22		
TOTAL		734	672		54		8	

Table 7.2 The abundance (in number and percentage) of prey belonging to families in the diet of *P. leopardus* caught by the two fishing methods. The diet of *P. leopardus* caught by line differed significantly from the speared catch (Fisher's Exact test$_{[21]}$ = 34.25, p-value = 0.034).

PREY FAMILIES	LINE number	LINE %	SPEAR number	SPEAR %	TOTAL
Pomacentridae	2	9.5	45	27.3	47
Labridae	1	4.8	36	21.8	37
Clupeidae	11	52.5	20	12.1	31
Caesionidae	1	4.8	11	6.6	12
Synodontidae	2	9.5	8	4.8	10
Scaridae			8	4.8	8
Blenniidae			7	4.2	7
Acanthuridae	1	4.8	5	3.0	6
Apogonidae			6	3.6	6
Serranidae	1	4.8	4	2.4	4
Engraulidae			3	1.8	3
Fistulariidae	2	9.5	1	0.6	3
Gobiidae			2	1.2	2
Balistidae			1	0.6	1
Creedidae			1	0.6	1
Lutjanidae			1	0.6	1
Monacanthidae			1	0.6	1
Nemipteridae			1	0.6	1
Platycephalidae			1	0.6	1
Plesiopidae			1	0.6	1
Scorpaenidae			1	0.6	1
Siganidae			1	0.6	1
Total	21		165		186
Number of *P. leopardus*	85		587		672

Table 7.3 The number of prey fish, crustaceans and cephalopods (excluding bait) found in a total of 672 *P. leopardus* collected from Nathan, Wardle, Potter and Noreaster Reef. The proportions of prey fish, crustaceans and cephalopods in the diet of *P. leopardus* did not vary significantly among the four reefs (Fisher's Exact test$_{[6]}$ = 4.836, p-value = 0.564).

PREY GROUPS	**REEFS**				**TOTAL**
	Nathan	**Potter**	**Wardle**	**Noreaster**	
fish	121	126	118	103	468
crustaceans	2	2	6	3	13
cephalopods		3	2	3	8
coral	3	2	1		6
unidentified	2	1	2	1	6
total	128	134	129	110	501
number of *P. leopardus*	191	178	153	150	672

Table 7.4 The number of prey in each family in the diet of *P. leopardus* collected from Nathan, Wardle, Potter and Noreaster Reef. The families are grouped by category; 'Common', 'Occasional', 'Rare' and 'Sporadic'. The abundance of prey in families in the diet of *P. leopardus* varied significantly among reefs (Fisher's Exact test$_{[63]}$ = 75.24, p-value = 0.007), but there were no patterns when the reefs were grouped by fishing zones. Although the diet of *P. leopardus* was similar between unfished reefs (Fisher's Exact test$_{[15]}$ = 18.49, p-value = 0.908), it differed significantly between fished reefs (Fisher's Exact test$_{[16]}$ = 22.51 p-value = 0.056). Thus, reefs within fishing zones could not be pooled for a zonal comparison. Furthermore, the diet of *P. leopardus* did not differ between reefs when they were grouped by location (North: Fisher's Exact test$_{[20]}$ = 23.23, p-value = 0.135, South: Fisher's Exact test$_{[11]}$ = 19.81, p-value = 0.155).

PREY	**FISHING**		**NO FISHING**		**TOTAL**
FAMILIES	**NORTH**	**SOUTH**	**NORTH**	**SOUTH**	
Common	Nathan	Potter	Wardle	Noreaster	
Pomacentridae	12	9	9	17	**47**
Labridae	9	8	9	11	**37**
Caesionidae		9	1	2	**12**
Occasional					
Synodontidae	4	3	1	2	**10**
Scaridae	4	2		2	**8**
Blenniidae	1	1	5		**7**
Acanthuridae	2	3	1		**6**
Apogonidae	1	5			**6**
Serranidae	3	1		1	**4**
Rare					
Fistulariidae	1	1	1		**3**
Gobiidae	2				**2**
Balistidae			1		**1**
Creedidae			1		**1**
Lutjanidae		1			**1**
Monacanthidae	1				**1**
Nemipteridae	1				**1**
Platycephalidae			1		**1**
Plesiopidae			1		**1**
Scorpaenidae	1				**1**
Siganidae			1		**1**
Sporadic					
Clupeidae	11	9	6	5	**31**
Engraulidae	2		1		**3**
total individuals	55	52	39	40	186
number of families	15	12	14	7	
number of *P. leopardus*	191	178	153	150	672

Table 7.5 The total digested weights (in g) of prey in each family in the diet of *P. leopardus* collected from Nathan, Wardle, Potter and Noreaster Reef. The families are grouped by category; 'Common', 'Occasional', 'Rare' and 'Sporadic'.

PREY	FISHING		NO FISHING		TOTAL
FAMILIES	NORTH	SOUTH	NORTH	SOUTH	
Common	Nathan	Potter	Wardle	Noreaster	
Pomacentridae	235.09	85.27	194.96	215.10	730.42
Labridae	159.70	58.58	140.54	148.46	796.28
Caesionidae		124.62	0.98	133.34	258.94
Occasional					
Synodontidae	23.42	58.33	5.61	12.03	99.39
Scaridae	230.00	127.76		79.75	437.51
Blenniidae	0.62	4.34	82.39		87.35
Acanthuridae	38.68	29.95	16.50		85.13
Apogonidae	0.98	5.74			6.72
Serranidae	37.43	10.83		9.77	58.03
Rare					
Fistulariidae	2.59	1.46	2.77		6.82
Gobiidae	2.24				2.24
Balistidae			2.32		2.32
Creedidae			1.00		1.00
Lutjanidae		0.16			0.16
Monacanthidae	0.12				0.12
Nemipteridae	82.55				82.55
Platycephalidae			0.68		0.68
Plesiopidae			13.24		13.24
Scorpaenidae	116.48				116.48
Siganidae			0.33		0.33
Sporadic					
Clupeidae	12.15	10.36	5.89	10.33	38.73
Engraulidae	1.45		4.77		6.22
TOTAL	943.50	517.40	471.98	608.78	
number of *P. leopardus*	191	178	153	150	672

Table 7.6 Values of the index of dietary overlap (Schoener *a*) for pairwise comparisons of the diet of *P. leopardus* between reefs within each of the two fishing zones. Values of Schoener *a* are calculated based on proportional values of the index of relative importance (IRI). The values are classified into three groups: <0.30 = low dietary overlap, <0.60 = medium dietary overlap and >0.60 = high dietary overlap.

ZONES	Schoener *a*	Dietary Overlap
FISHING	0.68	high
NO FISHING	0.68	high

Table 7.7 The index of relative importance (IRI) expressed as a percentage for each family of prey found in the stomachs of *P. leopardus* collected from Nathan, Wardle, Potter and Noreaster Reef. The families are grouped by category; 'Common', 'Occasional', 'Rare' and 'Sporadic'. The rank of each prey family in each reef is in bold.

PREY	**FISHING**				**NO FISHING**			
FAMILIES	**NORTH**		**SOUTH**		**NORTH**		**SOUTH**	
Common	Nathan		Potter		Wardle		Noreaster	
Pomacentridae	23.37	**1**	16.89	**2**	32.19	**1**	38.92	**1**
Labridae	16.64	**2**	13.35	**4**	26.43	**2**	25.94	**2**
Caesionidae			20.70	**1**	1.39	**5**	13.45	**3**
Occasional								
Scaridae	15.83	**3**	14.27	**3**			9.05	**4**
Acanthuridae	3.87	**9**	5.78	**7**	3.03	**5**		
Apogonidae	0.96	**13**	5.36	**8**				
Blenniidae	0.94	**14**	1.38	**10**	15.14	**3**		
Serranidae	4.71	**8**	2.01	**9**			2.05	**7**
Synodontidae	4.88	**7**	8.52	**6**	1.88	**7**	3.49	**6**
Rare								
Balistidae					1.53	**10**		
Creedidae					1.39	**11**		
Fistulariidae	1.05	**12**	1.10	**11**	1.58	**9**		
Gobiidae	1.94	**10**						
Lutjanidae			0.98	**12**				
Monacanthidae	0.92	**15**						
Nemipteridae	5.28	**6**						
Platycephalidae					1.35	**12**		
Plesiopidae					2.68	**6**		
Scorpaenidae	7.08	**5**						
Siganidae					1.32	**13**		
Sporadic								
Clupeidae	10.64	**4**	9.66	**5**	8.32	**4**	7.10	**5**
Engraulidae	1.90	**11**			1.79	**8**		
number of *P. leopardus*	191		178		153		150	

Table 7.8 The 22 families of prey classified into four broad habitats on the reef: demersal reef substrata, benthic reef substrata, midwater and soft sediment. Two habitats are strongly related to the reef substrata, demersal (with loose benthic association) and benthic (closely associated with benthos). The other two habitats are midwater and soft sediment. 'Common' families of prey are denoted by '*', 'Occasional' families of prey are denoted by '.', 'Rare' families of prey are not marked and 'Sporadic' families of prey are denoted by '!'.

DEMERSAL	BENTHIC	MIDWATER	SOFT SEDIMENT
.Acanthuridae	Balistidae	*Caesionidae	Creedidae
.Apogonidae	.Blenniidae	!Clupeidae	Nemipteridae
*Labridae	Gobiidae	!Engraulidae	Platycephalidae
*Pomacentridae	Monacanthidae	Fistulariidae	.Synodontidae
Plesiopidae	Scorpaenidae	Lutjanidae	
.Scaridae			
.Serranidae			
Siganidae			

Table 7.9 The number of prey in each of the four habitats on the four reefs (demersal reef substrata, benthic reef substrata, midwater and soft sediment). *P. leopardus* fed on prey from significantly different habitats among reefs (Fisher's Exact test$_{[9]}$ = 16.04, p-value = 0.047), but there was no difference in the habitats of the prey among fishing zones (Fisher's Exact test$_{[3]}$ = 3.341, p-value = 0.334).

HABITAT	FISHING		NO FISHING		TOTAL	
	NORTH	SOUTH	NORTH	SOUTH		%
	Nathan	Potter	Wardle	Noreast		
demersal reef	31	28	21	31	111	59.7
benthic reef	5	1	6	0	12	6.4
midwater	14	20	9	7	50	26.9
soft sediment	5	3	3	2	13	7.0
total	55	52	39	40	186	
number of *P. leopardus*	191	178	153	150	672	

Table 7.10 Values of the index of dietary overlap (Schoener *a*) for each pairwise comparison of the diet of *P. leopardus* at each fishing zone (reefs are pooled in the two zones at Innisfail) and at two locations of one fishing zone. Values of Schoener *a* are calculated based on the proportion of the index of relative importance (IRI) for each region. The values are classified into three groups: <0.30 = low diet overlap, <0.60 = medium diet overlap and >0.60 = high diet overlap.

FISHING ZONE	INNISFAIL	
LOCATIONS	FISHING	NO FISHING
BROADHURST REEF	0.61 High	0.46 Medium
INNISFAIL		0.65 High

Table 7.11 The number of species and genera of Pomacentridae in the diet of *P. leopardus*, when reefs were pooled for fishing zones (Nathan and Potter Reefs were open to fishing, and Wardle and Noreaster Reefs were closed to fishing). There was no detectable difference between fishing zones in the proportion of *P. leopardus* that consumed Pomacentridae (number eating pomacentrids/number eating prey, $t_{[2]}=-0.744$, $p>0.05$, $1-\beta<0.33$)

SPECIES	FISHING	NO FISHING	TOTAL
Acanthochromis polyacanthus	4	5	9
Abudefduf sexfasciatus		1	1
Chromis sp.	1	1	2
Dischistodus melanotus	1		1
Neopomacentrus azysron		1	1
Neoglyphidodon melas		1	1
Pomacentrus ambionensis		1	1
Pomacentrus chrysurus	1	1	2
Pomacentrus moluccensis	1		1
Pomacentrus nigromarginatus		1	1
Pomacentrus sp.	1		1
Stegastes fasciolatus	1		1
Pomacentridae sp.	11	13	24
Pomacentridae juvenile		1	1
total pomacentrids	21	26	47
number of trout that ate pomacentrids	21	26	47
number of trout that ate prey	204	188	392

Table 7.12 The mean and confidence limits (CL) of the density (number per 500 m^2) of *P. leopardus* on the four reefs from Table i, Ayling and Ayling (1992).

REEFS	*P. leopardus*					
	ADULTS (>35 cm TL)			RECRUITS		
	mean	95% CL		mean	95% CL	
		lower	upper		lower	upper
Wardle	1.57	0.5	2.64	0.10	0	0.372
Nathan	1.07	0	2.33	0.30	0	0.764
Noreaster	0.90	0.13	1.67	0.27	0	0.726
Potter	0.83	0	1.75	0.20	0	0.621
mean	1.09	0.16	2.10	0.22	0	0.62

Figure 7.1 The southern part of the Cairns Section of the Great Barrier Reef Marine Park showing Nathan and Potter Reefs (zoned GU 'B', all fishing allowed) and Wardle and Noreaster Reefs (zoned MNP 'B', closed to all fishing).

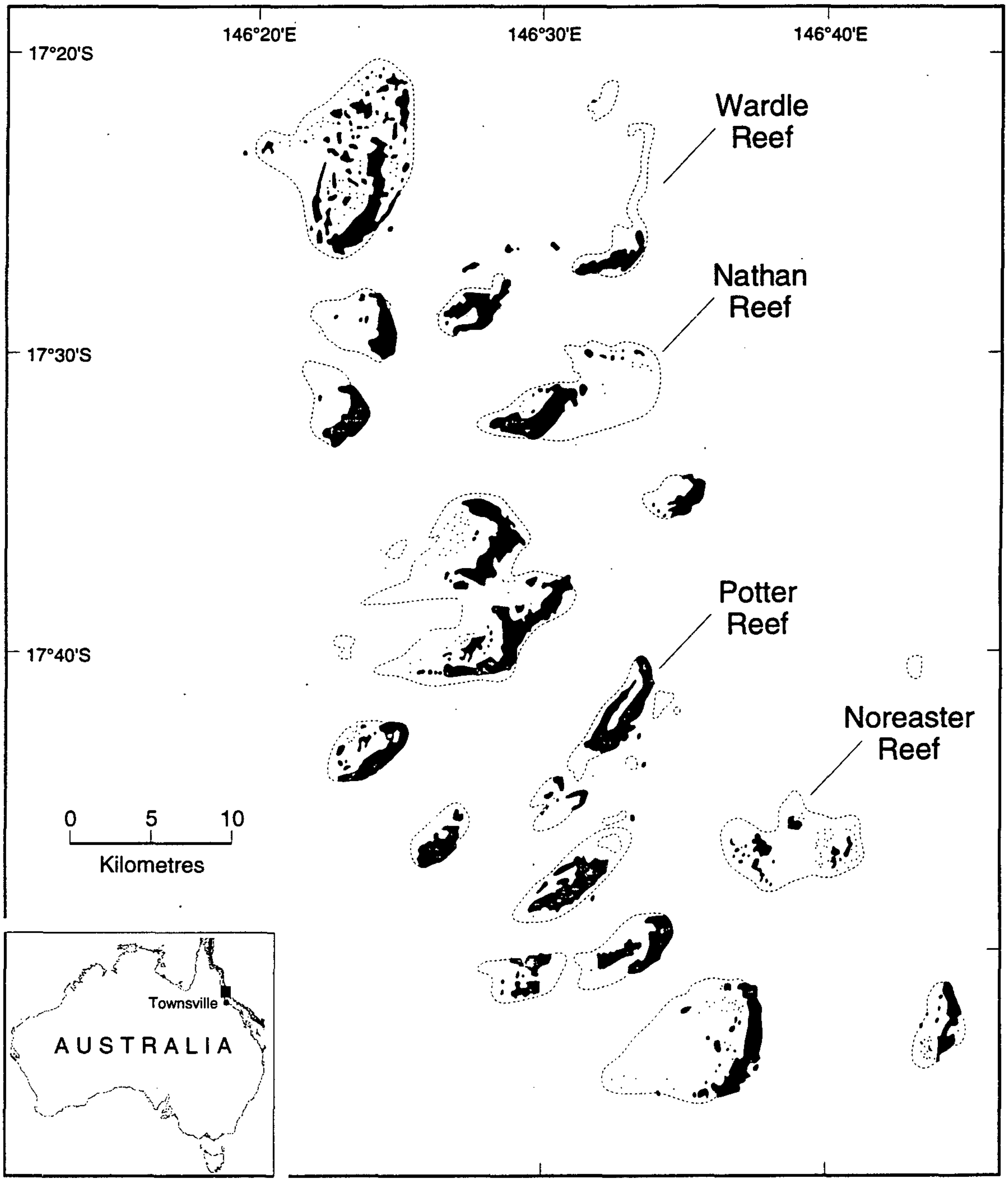


Figure 7.2 The length frequency distributions of *P. leopardus* collected by line and spear from the four reefs, Nathan (n=191), Wardle (n=153), Potter (n=178) and Noreaster (n=150) Reefs. The size of line-caught *P. leopardus* did not differ significantly from the speared catch at three of the four reefs (Wardle Rf Dmax = 0.127, Potter Rf Dmax = 0.271, Noreaster Rf Dmax = 0.270, K-S all p>0.05). At Nathan Reef, a higher proportion of large *P. leopardus* was caught by line than by spear (Dmax = 0.412, K-S p<0.01). The size-structure of the population of *P. leopardus* speared on the two unfished reefs, Wardle and Noreaster Reefs did not differ significantly (Dmax = 0.121, K-S p>0.05). The size structure of speared *P. leopardus* on the two fished reefs, Nathan and Potter Reef, differed significantly (Dmax = 0.109, K-S p<0.01).

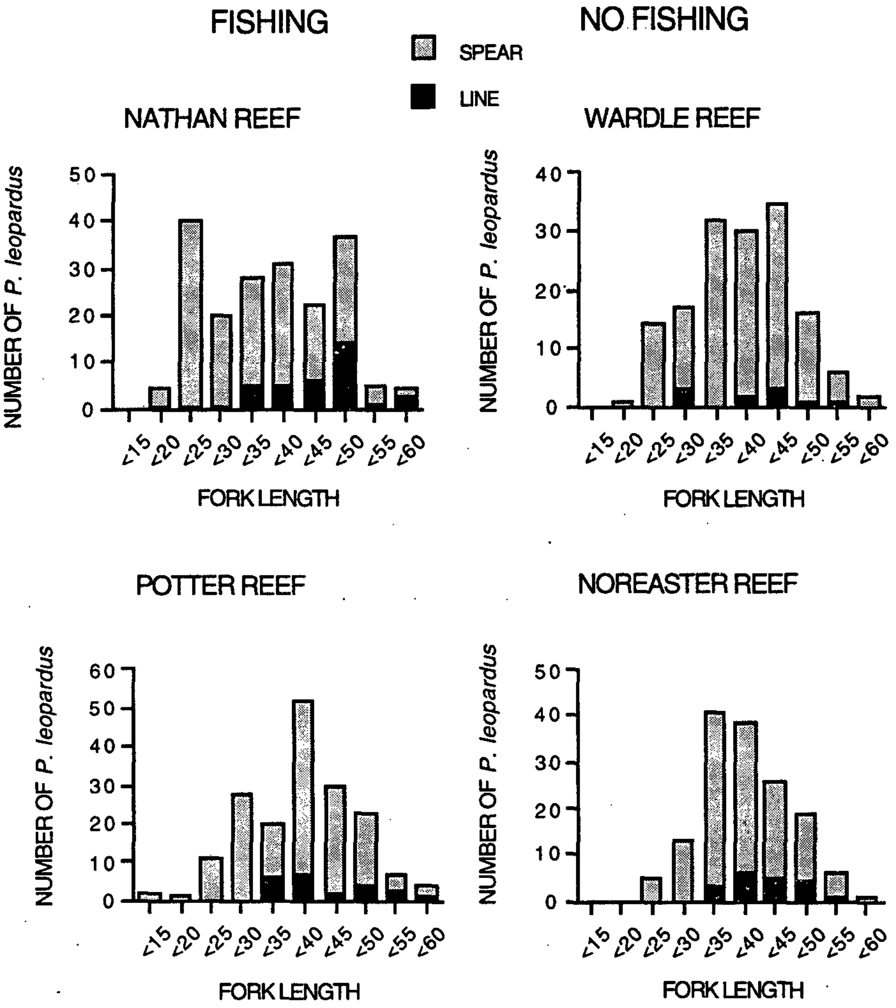


Figure 7.3 The percentage of *P. leopardus* caught by line compared to the percentage of empty stomachs in the speared catch on the four reefs. The positive correlation between these variables was significant (Pearson correlation coefficient = 0.969, Bartletts $X^2_{[1]} = 31.259$, $p<0.01$).

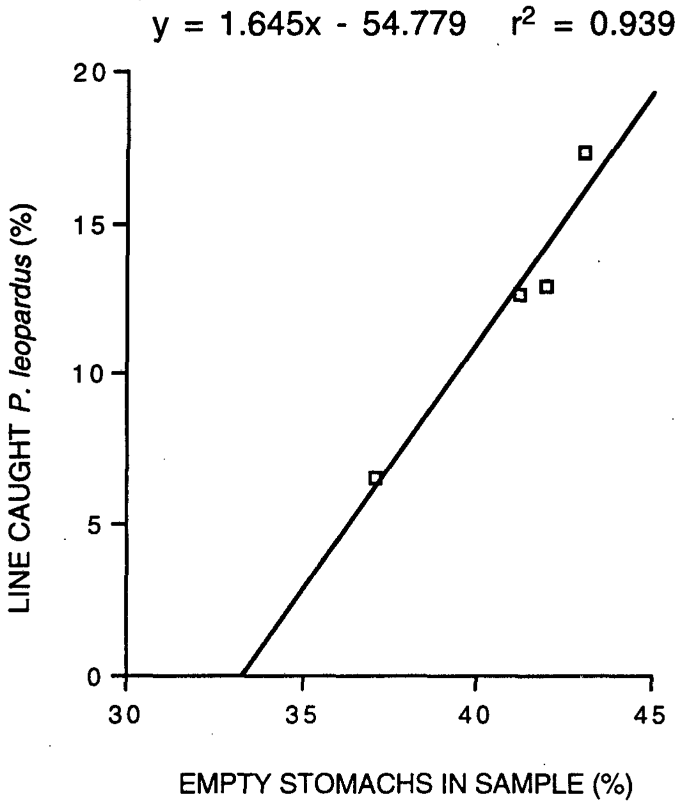


Figure 7.4 The age frequency distributions of the samples of *P. leopardus* collected by spear from the four reefs, Nathan, Wardle, Noreaster and Potter Reefs. This data is from Figure 4, Brown *et al.* (1992).

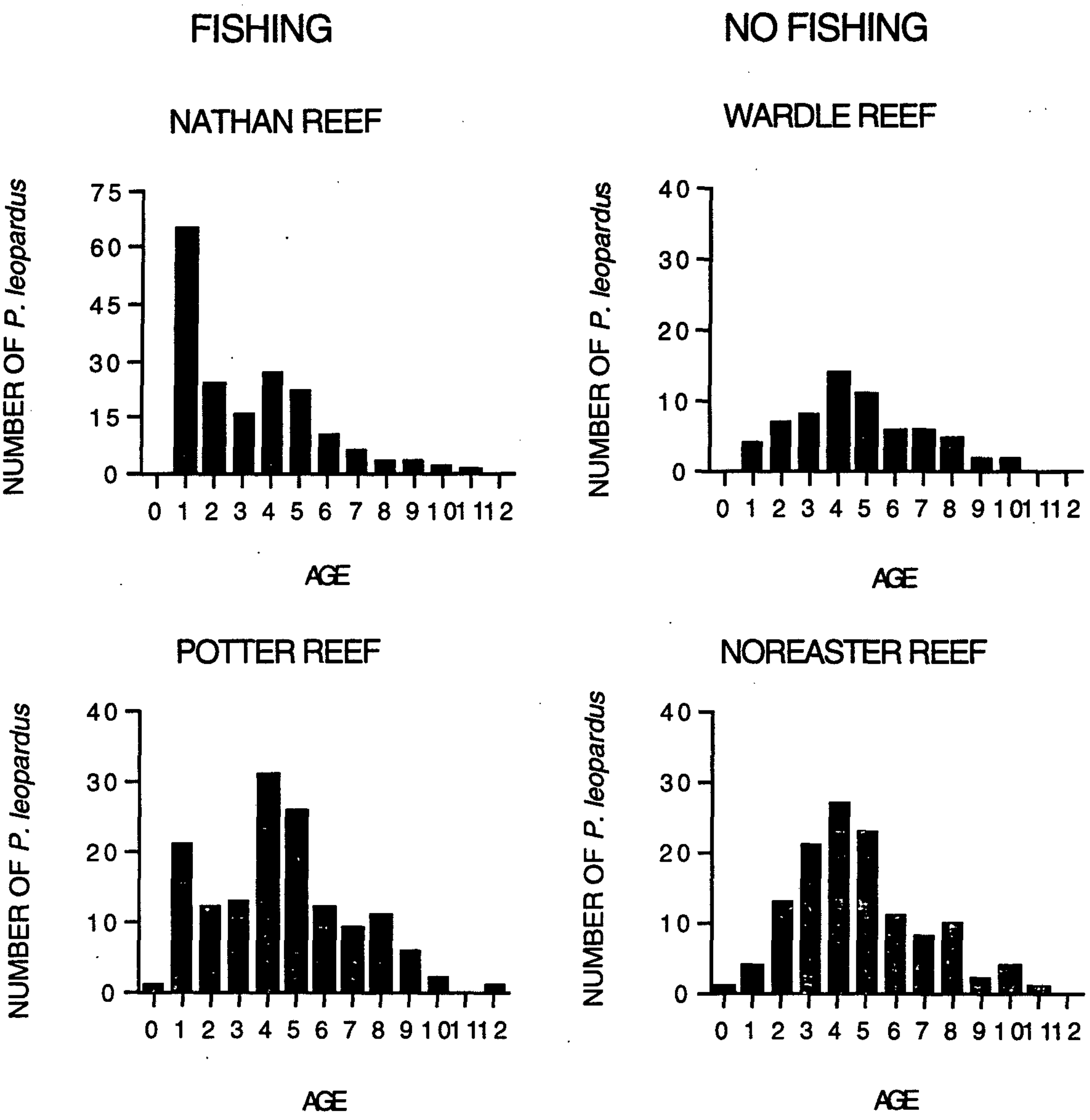


Figure 7.5 The percentage of one year old *P. leopardus* compared to the percentage of four year olds on each reef (using the speared catch only). The age data is from Brown *et al.* (1992). The percentage of one year olds was negatively correlated with the percentage of four year olds in the population of *P. leopardus* on reefs (Pearson correlation coefficient = 0.93, Bartletts $X^2_{[1]} = 3.632$, p=0.057).

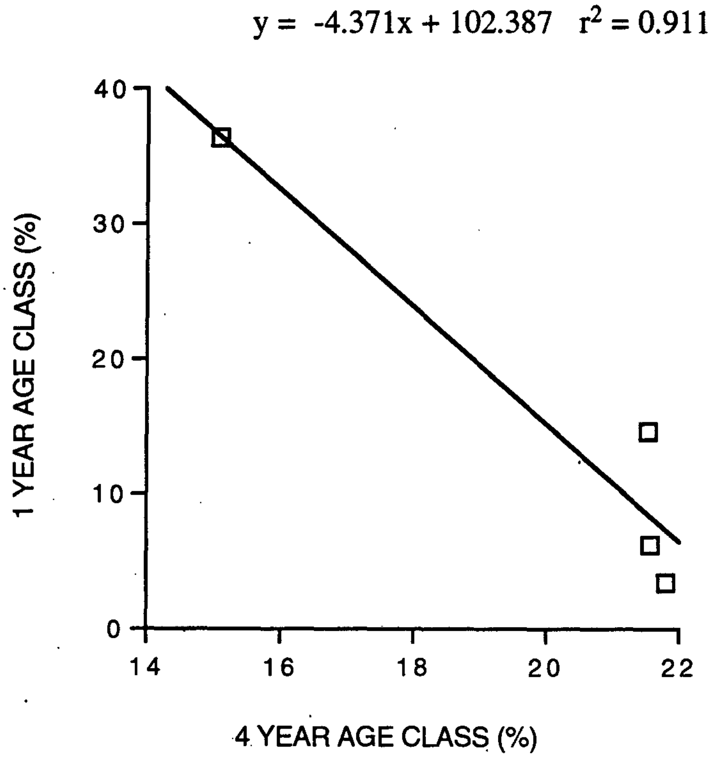
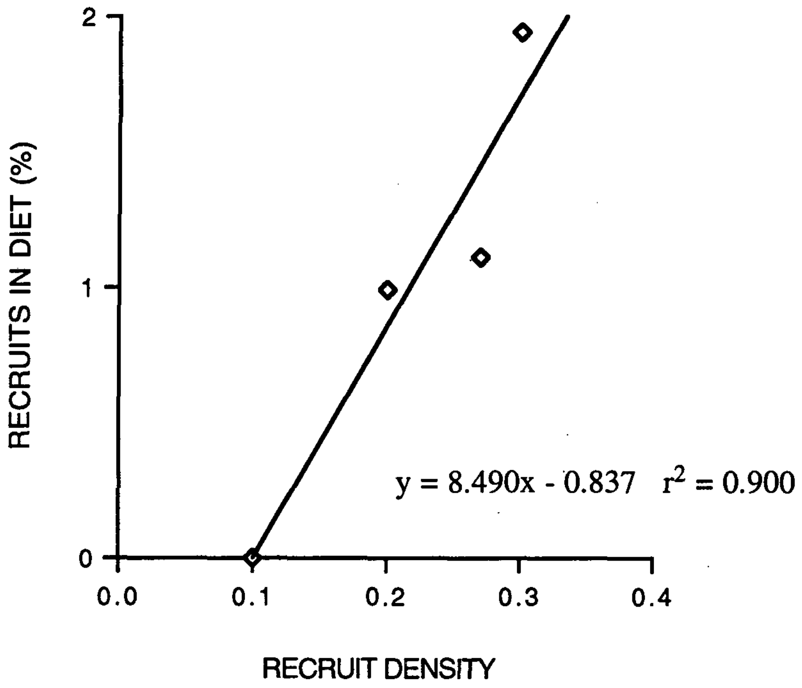


Figure 7.6 The percentage of recruit *Plectropomus* in the diet of *P. leopardus* compared to the densities of recruits on the four reefs. The density data is from Ayling and Ayling (1992). The two variables were positively correlated (Pearson correlation coefficient = 0.949, Bartletts $X^2_{[1]} = 3.459$, p=0.06).



CHAPTER 8

8.0 PREDATORY SUCCESS AND BEHAVIOUR OF INDIVIDUAL *P. leopardus* IN CAPTIVITY

8.1 INTRODUCTION

The view that predation is important on coral reefs has persisted for two reasons. First, piscivores form a large component of the fish community (Goldman and Talbot 1976; Willams and Hatcher 1983; Norris and Parrish 1988). Second, coral reef fishes, especially young and small fishes, have high rates of mortality which are considered to be a direct result of predation (see review by Hixon 1991). Despite this view, the feeding habits of most piscivores on coral reefs remain largely unknown. While a few studies have examined natural feeding rates of reef piscivores, field observations are very time consuming because successful predatory strikes are rare and difficult to confirm (Sweatman 1984; Diamant and Shpigel 1985). Predatory observations on larger piscivores, such as *P. leopardus*, are made more difficult by their very large home ranges (Goeden 1974; Samoilys 1987).

Population studies of coral reef fishes that examine survivorship provide some indirect evidence of predation and suggest that natural mortality of fishes varies spatially. Although the rate of adult mortality in species of coral reef fishes is assumed to be constant for many species (Doherty and Williams 1988), the few studies that have measured mortality found differences in mortality rates among sites, coral reef zones and cohorts within and among species (Eckert 1985,1987; Aldenhoven 1986; Mapstone 1988; Gladstone 1991). Tenfold differences in mortality rates occurred in both adult and juvenile *Centropyge bicolor* of each sex in two areas of differing habitat (Aldenhoven 1986). Eckert (1985) found major differences in survival between lagoon and reef-slope populations of *Thalasomma lunare.*

Factors affecting survivorship in coral reef fishes have focused on juvenile fishes on small, natural or artificial, patch reefs (Shulman 1984, 1985; Hixon and Beets 1989, 1993). In these studies mortality was presumed to have occurred when the fish disappeared. As emigration of fishes is difficult to measure (Robertson 1988) and predation is only one source of mortality, the link between disappearance of fish from patch reefs and predation can be tenuous.

Habitat appears to play dual roles in the survivorship of coral reef fishes because it provides both physical shelter from predation for prey and places of concealment for predators. The role of shelter in predator-prey interactions on coral reefs has been examined in studies of juvenile fishes settling onto artificial patch reefs. The number of refuges available have been shown to limit recruitment or early survivorship of juvenile fish (Shulman 1984). Shulman (1984) suggested that the availability of refuges indirectly limited fish populations by affecting predation rates (i.e. greater number of refuges resulted in greater recruitment and survivorship). This relationship is dependent on the size of the refuge because reef fishes use hole sizes similar to their body sizes (Randall 1963; Robertson and Sheldon 1979; Shulman 1984). Large holes provide shelter sites for large predatory fish, and the abundance of small fishes declined on patch reefs with large holes which were utilized by piscivores (Hixon and Beets 1989). These studies have demonstrated that the role of shelter in predator-prey interactions on coral reefs is very complex. Information on the behaviour of the predators and prey is required to interpret results of experiments on predation correctly.

The location of hides (defined here as shelter and/or ambush sites for predators) may affect spatial patterns of prey populations and communities. As the frequency of encounters with piscivores is considered to affect patterns of juvenile survivorship (Shulman 1985; Sweatman and Robertson 1994), sites near hides may have lower survivorship of prey fish. The threat of predation launched from hides is evident in the behaviour of prey on coral reefs. An increase in abundance of edible algae in front of overhangs suggests that herbivorous fish reduce their feeding in areas where predators are more likely to occur (Hay 1985).

Observations of predation on coral reefs suggest that it is advantageous for piscivores to have places of concealment. Predation by piscivorous fish is successful when the prey makes one of two mistakes, either:

1. it fails to see the predator before it strikes; or
2. it wanders too far away from shelter to return quickly (Sweatman 1984).

Prey fish will not see a predator if they do not look in the direction of the predator or if the predator is concealed.

In observations of predatory behaviour of *P. leopardus*, Samoilys (1987) described two main methods of hunting: ambush and prowl. In the first of these methods, ambush, *P. leopardus* makes use of the habitat remaining close to the substrata and either remaining stationary or stalking prey. *Plectropomus leopardus* hide under coral crevices, overhangs and in holes. Observations of this behaviour vary between studies. Goeden (1978) observed that *P. leopardus* spent between 20-50% of their time under cover depending on the habitats and the age of fish, and Samoilys (1987) observed that *P. leopardus* spent up to 34% of their time under cover. Goeden (1974) observed that *P. leopardus* (<31 cm SL) frequently took prey as a result of sighting them from under cover. Observations of tagged *P. leopardus* have shown that individuals prefer particular sites (Samoilys 1987). Regardless of whether or not *P. leopardus* feed from these preferred sites, mortality in prey fishes residing near *P. leopardus* sites can be expected to be higher if encounters with prey leads to opportunistic predation. Prey fishes residing near *P. leopardus* sites will have higher encounter rates with predators than prey residing elsewhere.

As groups or individually, *P. leopardus* are capable of intense rates of predation on one prey species. Dietary and behavioural studies have shown that one or more *P. leopardus* can feed on one prey species in a localized area within a short time frame (Goeden 1974; Samoilys 1987; St John unpubl.; Squire pers. comm.). Although *P. leopardus* are difficult to observe feeding as they strike, on average, once every hour (Samoilys 1987), divers have observed *P. leopardus* feeding repeatedly on schooling fishes (Goeden 1974; Samoilys 1987; Squire per comm). On several occasions one *P. leopardus* in captivity and in the field ate several similar-sized adult pomacentrid species within an hour (St John unpubl.). Also, several *P. leopardus* collected from the same area within an hour were found to be feeding on one species of schooling caesionid (St.John unpubl.).

When feeding, *P. leopardus* often change the colour of their skin. *Plectropomus leopardus* can alter their colour markings radically from plain markings with no differentiated pattern through to a strongly defined pattern (Goeden 1974; Samoilys 1987). Goeden (1974) distinguished two different phases of colouration (high and low) in *P. leopardus* and termed this mottle or mottling behaviour. In the field, the mottle pattern in *P. leopardus* has been observed in the following situations:

1. prior to a feeding attack: (high phase, Goeden 1974), ambush mode or during a feeding chase (Samoilys 1987);
2. close proximity to desirable prey (low phase, Goeden 1974);
3. prior to or during cleaning (Samoilys 1987; low phase, Goeden 1974);
4. intraspecific interactions (Samoilys 1987); and
5. hiding under coral overhangs.

Goeden (1974) reasoned that *P. leopardus* camouflaged (mottled) themselves during rest under a coral overhang, whereas Samoilys (1987) surmised it to be a fright-response elicited from the observer. Another reason may be that the *P. leopardus* were ambushing prey. Although it is difficult to differentiate mottling behaviour related to feeding from other mottling behaviour in the field, in a tank situation, mottling behaviour is always related to feeding if there are only prey species present. Thus, mottling colouration of *P. leopardus* was considered to indicate an intent to feed in the experiment reported here, despite observations by Goeden (1974) of 'unpremeditated' attacks by *P. leopardus* without the mottling behaviour.

Feeding experiments in tanks provide many advantages over field observations. The immediate feeding history of the predator is known, number and size of prey can be measured, and thus predation can be quantified without necessarily being seen. Aquaria can provide a simplified environment where the effects of single factors on predation can be measured using replicated experiments. Also, the habitat can be manipulated, standardised and replicated in tanks. Unlike field studies, where the subject fish may be difficult to find, behaviour of the predator can be observed at any time and replicated. Realistic experiments require knowledge of the diet of the predator and the habit of both the predator and prey, as it is important that the predator feeds as naturally as possible. As aquaria are artificial environments, extrapolating the results of aquarium studies to the field requires caution.

Plectropomus leopardus are suited to tank studies because:

1. they can be kept successfully in large tanks for extended periods of time and will feed on live bait;
2. they feed only during daylight hours (Goeden 1974) and have no diurnal or tidal feeding patterns (Samoilys 1987);
3. they feed on site attached pomacentrids which use coral for shelter from predators (see Chapter 4);
4. they are solitary feeders which hide in crevices and in holes; and
5. I have detailed information on the size and species composition of the prey eaten by this species from dietary studies.

The aim of this study was to observe feeding behaviour and rates of predation by captive *P. leopardus* on a small demersal pomacentrid.

The three main objectives were:

1. to examine the importance of hide use for feeding in *P. leopardus*; and
2. to compare the feeding behaviour of individual predators in similar environments; and
3. to compare the strike rates of captive *P. leopardus* on pomacentrids to those reported in the literature for other piscivorous coral reef fish.

8.2 METHODS

The predation experiment was run in the summer (January to March) and winter (August to September) of 1992 at Orpheus Island Research Station (described in Chapter 2.4).

8.2.1 Experimental preparations

Coral shelter and hides: Shelters for the prey in the experiment were made by wiring one or two pieces of dead branching coral (*Acropora* sp.) onto a mesh base (Fig. 8.1). Four shelters with similar dimensions were made. As the coral shelters were not identical, they were rotated among experimental tanks. The range of the maximum dimensions of the shelters was 40.5-50 cm long, 34-50 cm wide and 21-37 cm high. The mass of the shelters was not measured by water displacement because the coral was porous.

Hides for *P. leopardus* were identical in every tank (Fig. 8.1). Hides consisted of two parallel cement bricks set the width of a brick apart (39 cm long, 55 cm wide and 20 cm high). The positions of the two hides in the tank were changed for every experiment.

Tanks: The four experimental tanks were circular, 4.5 m in diameter and 1-1.5 m in depth (Fig. 8.1). The inside colour of the tank was light blue. Water temperature in each tank varied during each experiment depending on daily temperatures, shade and wind. The temperature of the water in tanks ranged 27-36 °C (usually maximum of 31-33 °C) in summer and 21-28 ° C in winter. Clean seawater entered the tank through a pipe near the floor while a vertical pipe drained surface water (Fig. 8.1). The plumbing in the tank was designed to create a weak circular current and to replace the water in the tank completely every 12 hours. The current was strongest in front of the inlet pipe and occasionally it attracted either the predator or a few prey to swim in the current. Thus, the coral shelter was positioned sufficiently far from the inlet to deter the prey from discovering the current and leaving the coral shelter. The inlet and the drain pipes were the only non-experimental structures in the tank and provided extra shelter for the prey. Although generally prey stayed close to their coral shelter, occasionally one or two individuals ventured over to the drain.

Places of observation: I observed the fish from an elevated position within three metres of the tank. At all observation places I was not visible to the *P. leopardus* because I was either hidden behind shade cloth or inside a building. I entered and vacated the observation place without disturbing the fish.

8.2.2 Experimental design and protocol

The design of the experiment differed between summer and winter. During the summer the experiment had three treatments. Three trials, one of each treatment, were run with each of eight individual predators. In winter, the captive *P. leopardus* were unsuccessful predators (i.e. did not capture any prey during the trials) so the experiment was reduced to one treatment. Two trials of the one treatment were run with each of the four predators to compare summer and winter feeding.

Treatments: The treatments were named by their distance between the treatment hide and the coral shelter. Distances between shelter and hides were measured from the nearest outside edge of the shelter to the edge of the nearest entrance of the hide.

The three treatments were:

Control: two far hides that were >2 m from coral shelter

Medium: one far hide and one medium hide that was 1 m from shelter
Near: one far hide and one near hide that was 0.3 m from the shelter

Predators: One *P. leopardus* was moved into an experimental tank and allowed as many days as needed to adjust to the tank environment. As *P. leopardus* fed normally when not stressed, individuals were considered to be ready for the predation experiment after they had fed on more than one occasion. *Plectropomus leopardus* were starved 24 hours prior to the start of each experiment. If the predator had not fed during the experiment it was fed after the experiment terminated. The size of *P. leopardus* used in the experiment ranged from 32 to 39 cm SL in summer and from 33 to 47 cm SL in winter.

Prey: *Acanthochromis polyacanthus* (F. Pomacentridae) were used as prey in the experiment because they are the most common pomacentrid species eaten by *P. leopardus* (Chapter 4). Ten *A. polyacanthus* were used in every experiment. The size of *A. polyacanthus* ranged from 5.7 to 9.5 cm SL (8.13-38.8 g). *Acanthochromis polyacanthus* were individually marked to determine which prey were eaten by the predator. Each *A. polyacanthus* was anaesthetised using quinaldine in ethanol, weighed (+/- 0.01 g), measured (TL and SL +/- 1 mm) and tattooed using alcian blue dye in 19-22 gauge needles on hypodermic syringes. Groupings of prey differed in every experiment but individual prey fish not consumed were reused. To avoid problems of rejection of one or two newcomers entering an established pomacentrid hierarchy, new groups were made by adding five different prey to an existing group of five. Before the experiment began, the coral shelter was isolated from the tank by a net on a cylindrical frame (diameter 85-100 cm, Fig. 8.1). Sand was used to seal the net at the floor of the tank so that prey could not escape. Ten prey were then added to the shelter to familiarise themselves with the coral and each other for 24 hours prior to the beginning of the experiment. Prey were fed during this time with mashed pilchard. The net was removed at the start of the experiment and replaced at the end. After the experiment was terminated and the net was replaced around the prey fish, I removed the coral shelter then caught and identified every remaining pomacentrid.

The experimental protocol

The experiment began at one of three times of day (morning 9 am, noon 12am or late evening 7pm) and ran for 24 hours. The starting time of the experiment was independent of the periods of observation. Fish were observed four times a day throughout the experiment for 15 minutes. The four observation periods were within 7-8:00, 10-11:00, 13-14:00 and 16-17:00 hours. The behaviour of the *P. leopardus* was recorded at 15 second intervals throughout the 15 minute observation period and all predatory behaviours observed during the 15 minute period were recorded. Samoilys (1987) used 15 minute observation periods on *P. leopardus* in the field. She justified this on the basis of two ethological methods, repertory fraction and sample coverage (Samoilys 1987).

Observations

Four aspects of the behaviour of the *P. leopardus* (Activity, Position, Visibility and Orientation) were recorded during the observations (see definitions below). Position in the tank and orientation were recorded when the *P. leopardus* was stationary or gliding. When swimming, the position of the *P. leopardus* in the tank (shelter or other half) was recorded.

Definitions of observations

Activity

- Swimming - muscular movement visible and the body curves to propel the fish forward
- Gliding - slow drifting movement with no visible movement of the body, movement may be forward or backward
- Stationary - not moving

Position

- hides or shelter -within 0.3 m of a hide or shelter

- open - > .3 m away from any structure in the tank

Visibility

- visible to the prey - when the *P. leopardus* was in front of or above the hides or in the open
- invisible to prey - when the *P. leopardus* was inside or behind the hides

Orientation (in relation to the prey)

- watching or able to see prey -when the head of the *P. leopardus* was oriented towards the shelter and they could see the shelter with one or both eyes. It was difficult to ascertain when the *P. leopardus* was looking through the hide at the prey. For the purposes of this study, the terms watching and able to see are synonymous as the observer could not determine whether the *P. leopardus* was watching the prey (the *P. leopardus* was too far away to observe eye movement).
- not watching or not able to see prey - facing away from the prey

Definitions of:

predatory behaviours by predator

- attack - extremely rapid movement directed at prey (Samoilys 1987) with mouth opened to engulf prey (strike)
- pursuit - rapid movement towards prey but no strike
- chase - fast swim after one prey
- follow - slow swim after one prey

defensive behaviour by prey

- tail-chase - aggressive chase by one prey toward the predator when it is swimming away from the group of prey

8.2.3 Justification of methods used

Hides and Shelter

To determine the best shelter and hide design for the experiment I tried different sizes and numbers of both hides and shelter. It was imperative that the prey remained in or mostly near the shelter and did not swim across to the hides. I used *Acropora* sp. coral for the shelter because it is part of the natural habitat of the prey. Shelter for the prey only needed to be similar rather than identical to each other.

The requirements of hides were different from those of prey shelters. Every hide had to be identical because I was examining choice of position of hide. Hides needed to provide cover for the *P. leopardus* and to be visible to the observer, who needed to detect the *P. leopardus* inside. Hides needed to be directional to determine whether or not the *P. leopardus* was watching the prey. For these reasons I made hides from identical cement bricks.

Choice of prey species

As a certain size range of *A. polyacanthus* use coral for shelter in their natural habitat, prey of this size used the coral shelter in the tank. Other species such as *Abudefduf sexfasciatus* swam around the tank and did not use the coral shelter. The number of *A. polyacanthus* used in the experiment was within the range of natural densities found on reefs (Kavanagh pers. comm.).

Duration of experiment

Twenty four hours was selected for the predation experiment for the following reasons:

1. in the trial experiments run for 36-48 hours, no more fish were eaten after 24 hours;
2. 24 hours included all diurnal phases, thus covering the different feeding strategies of morning and evening (Samoilys 1987); and
3. prey in the stomach of *P. leopardus* was mostly digested after 24 hours (chapter 3). As predators were starved for 24 hours prior to the experiment,

they should have been ready to feed during the experiment.

8.3 RESULTS

8.3.1 Predatory experiment

Predatory ability

Five of the eight *P. leopardus* were successful predators, (i.e. they caught one or more prey during all three trials) in summer, and these predators were used in the analysis. One prey fish received a non-fatal injury in another trial.

There was no detectable difference in the predation success of *P. leopardus* among hides of different distances (Table 8.1a). Furthermore, the chronological order of the trials did not influence predation success of *P. leopardus* (Table 8.1b). Variation in predatory success among individual fish was high in both of these tests (p<0.10 for 'fish' in both treatments 8.1a & b).

The high variability of predatory ability among all individuals was evident when the eight fish were classified into five categories of predator-type based on the number of prey consumed (≥2, 1 or 0) and the consistency of their ability in all three treatments (consistent or inconsistent, Table 8.2). Every one of the five categories was represented by at least one individual (Table 8.2).

The predation experiment was unsuccessful in winter: during the experiment, only one prey was eaten by four *P. leopardus* used in eight trials (two trials each). Furthermore, the captured prey was sick, which made it easy prey since groups of *A. polyacanthus* chased sick individuals away from their coral shelter. Another prey was eaten after an experiment was terminated (i.e. the hoop was replaced with one fish left outside, which was easily caught by the hungry *P. leopardus*). Compared to summer, predatory behaviours by captive *P. leopardus* were less frequent in winter. The mean number of predatory behaviours observed in summer (2.79 per hour, SE = 0.14) was double those observed in winter (1.37 per hour, SE = 0.70). Also, mottling behaviour occurred in nearly one third of observations in summer (26.0%)

and in less than one tenth of observations in winter (8.7%).

Reasons for the failure of the experiment in winter may be related to higher levels of stress in winter due to capture methods, fungal infections which were prevalent in the colder water, or both. Winter results were not used in any analyses and seasons were not compared.

Prey

The prey used in the experiment did not affect the results. As some prey were reused in the experiment up to six times, the possibility that previous participation in predation experiments may have lowered their capture rate was tested. When prey were categorized by the number of times they were used in the experiments, there was no difference between survivorship ($K\text{-}W_{[5]} = 3.353$, Monte Carlo p-value = 0.69). Thus, survivorship of the prey during experiments was not related to the experience of the prey. *Plectropomus leopardus* did not select prey by size or rank. The size structure of the prey eaten did not differ from the population size structure of *A. polyacanthus* used in the experiment ($K\text{-}S_{[18]}$ test=0.081, p=0.31, Fig. 8.2). When the prey in each trial were ranked by size and the predators were grouped into three size classes (<35, 35-37.9 and 38-40 cm SL), there was no difference in the size rank of prey eaten by the three groups of predators ($K\text{-}W_{[6]} = 8.350$, Monte Carlo p-value = 0.19).

8.3.2 Behaviour of *P. leopardus* in the experiment

Did *P. leopardus* attempt to catch prey?

All *P. leopardus* appeared to attempt to catch prey. Predatory behaviour (attack, pursuit, chase and follow) was observed in 62.5% of the experiments while predation occurred in half (50%, Table 8.3). Occurrences of predatory behaviour ranged from 0 to 14 times.h^{-1} with an average of 2.75 (SE=0.14). Only three attacks were observed (total observation period =24 h, mean 0.125 strikes.h^{-1}). While successful predators must have expended effort to catch prey, the *P. leopardus* that were not successful predators were considered to have attempted predation for two reasons. Firstly, all predators displayed mottling behaviour which indicated an intent to feed. Mottling behaviour occurred during 26% (SE=3.8) of all observations. Furthermore, on several occasions, the mottling pattern on stationary predators in the open became more defined when prey approached. Secondly, every *P. leopardus* ate after the experiment, which indicated that they were hungry after 48 hours of starvation, and therefore were motivated to feed.

Was predation independent of predatory effort?

Using mottling and predatory behaviour as indicators of predatory effort, there appeared to be no relationship between effort and predatory success in *P. leopardus*. Predatory behaviours (attack, pursuit, chase and follow) were observed at an average rate of 2.75 behaviours.h^{-1}. Predatory behaviours were observed in successful predators in similar proportions to unsuccessful predators (Fisher Exact test =0.230, p=0.32, Table 8.3), but the test of whether successful predators mottled more than unsuccessful predators was inconclusive ($t_{[22]}=1.034$, $p>0.05$, $\beta=0.09$).

Did *P. leopardus* use the hides?

On average, predators used hides 46% of the time in the predation experiments. When under, behind or beside the hides the predators were assumed to be unseen by the prey, and predators remained unseen 80% of the time they were associated with hides. *Plectropomus leopardus* often watched the prey from behind the hide. When watching the prey, *P. leopardus* seemingly used the hides to disguise their silhouette, particularly their head, from the prey. On three occasions a predator ambushed prey from a stationary position from within a hide. In addition, mottled *P. leopardus* swam through the hides slowly. Despite this use of hides for predatory behaviour, successful predators used hides less than unsuccessful predators (Fig. 8.3).

Did the placement of the hides alter behaviour of predators?

Use of hides by *P. leopardus* varied among treatments and fish (Table 8.4a). In the control treatment, which had two far hides, *P. leopardus* used hides more than in the other treatments where one of the hides was closer (Fig. 8.4). Visibility of the predator to the prey in the hides may or may not have varied. There was no detectable difference in the visibility of the predators in the hides among treatments but the results were inconclusive (ANOVA, Hides $F_{[2,53]}=1.41$, $p=0.25$, $\beta=0.31$).

The frequency of predatory behaviours (attack, pursuit, chase and follow) was similar among treatments (K-W= 3.836, df=2, Monte Carlo p-value =0.151) Furthermore, there was no detectable difference in the percentage of mottling by *P. leopardus* among treatments (Table 8.4b). Predators ambushed prey only from the two closer hides (Near and Medium).

Do predators watch their prey?

Watching prey did not appear to be associated with predation or predatory behaviour. Firstly, there was no detectable increase in mottling behaviour when *P. leopardus* were able to see the prey (paired t-test, $t_{[31]}=-0.158$, $p>0.05$). Secondly, not watching prey was a common occurrence in several predatory sequences (e.g. Chase Back in Table 8.5). Thirdly, prey behaviour changed markedly when *P. leopardus* was watching . When the predator was in the near hide, prey clustered around the shelter if the predator was watching, but moved away from the shelter if the predator was not watching.

General predatory sequences

Plectropomus leopardus repeated behavioural sequences during experiments, and eight predatory sequences, with slight variations, were identified during the experiment (Table 8.5). One very common action pattern was used in several of the predatory sequences and was named 'Chase Back' (see Table 8.5). Predatory sequences used by individual fish did not appear to be related to the success of the predator (Table 8.6). No one predatory sequence was used by every successful predator even though the most common predatory sequence, Pass by Shelter, was used by seven of the eight *P. leopardus* (Table 8.6). Nor was there any difference in the number of different predatory sequences used by successful or unsuccessful predators ($t_{[6]}$=-1.225, p=0.27, n too small for power test). In fact one of the unsuccessful predators used the highest number of predatory sequences (six out of eight, Table 8.6).

Individual differences and changes in behaviour of predators

The patterns of behaviour for two groups of predators, consistently successful (n=2) and consistently unsuccessful (n=2), were examined (Fig. 8.5). In both groups, behaviour of individuals varied within treatments and between treatments (Table 8.7).

8.3.3 Rates of predation by piscivores on coral reefs

Rates of three of the four predatory behaviours (attack, chase and pursuit) in captive *P. leopardus* appeared to be similar to those in the field (attack, chase and dart, Samoilys 1987). Rates of predation were higher in captive *P. leopardus* (2.8 hour^{-1}) than in wild *P. leopardus* (1.2 hour^{-1}).

Strike rates of captive *P. leopardus* were similar to other serranids in the field (Table 8.8). Strike rates of all serranids were $\leq$1 hour.$^{-1}$ whereas strike rates of a smaller species of pseudochromid and a synodontid were >1 hour^{-1}.

8.4 DISCUSSION

The main result of the experiment was establishing the variation in rates of predation among individuals. Predators varied in both their level and consistency of predatory success (i.e. some predators were consistently or inconsistently successful whereas others were always unsuccessful). Observations of *P. leopardus* showed no obvious reasons for the high success of one predator and the lack of success in another as predatory effort (i.e. the amount of predatory behaviour) was similar among both groups. Predators used similar repertoires of predatory sequences, and there was no one predatory strategy used by every successful predator but not used by unsuccessful predators. Individual differences in behaviour were not limited to predatory behaviour and success.

All major categories of behaviour of *P. leopardus* varied among individuals in the experiment: the behaviour of some individuals varied throughout the day in one treatment but were similar throughout the day in another. Although individual differences in behaviour and ecology have traditionally been ignored (Magurran 1986), the importance of individual-based approaches to ecology has recently been recognised (De Angeleas and Goss 1992). The results of this study raise questions about how predatory behaviour varies among individuals in populations of *P. leopardus*. Are populations of *P. leopardus* composed of only generalist feeders that have wide ranging abilities to feed? Alternatively, do populations of *P. leopardus* comprise groups that specialise on different prey species? If so, do individuals with differing specialisations consume a similar biomass of prey? If the latter was true, the variation in the experiment would be the result of a population of *P. leopardus* with individuals that specialise on the particular prey used in the experiment (consistently highly successful), those that specialise on very different prey (consistently unsuccessful predators) and generalists which feed less efficiently on a wide range of prey (inconsistently successful). The evidence for specialist or generalist feeding in *P. leopardus* will be discussed for two reasons. Firstly, the high variability of predatory success in *P. leopardus* masks the results of the experimental feeding study, and so individual feeding needs to be understood before effects of habitat on feeding can be investigated adequately. Secondly, specialist or generalist feeding has very different consequences for populations of *P. leopardus*.

'Predator versatility', which is the variability in the choice of food, and method of capture and handling prey varies among individuals in populations (Curio 1976). Individuals may have one of two foraging strategies and populations may consist of both types of individuals (Curio 1976). Individuals may specialise in a few tactics or prey types or may alternatively be generalists which adopt most, if not all tactics available to the species. For example, populations of the bluegill sunfish *Lepomis macrochirus* can be divided into specialists which forage on either plankton or benthos and generalists which feed in both habitats (Werner *et al.* 1983). The generalist strategy is more appropriate when the food supply is unpredictable (Dill 1983). Observations of *P. leopardus* on the southern GBR suggest that they have two main methods of feeding, ambush and prowl, that are directed at different types of prey (Samoilys 1987). These are described as follows.

<u>Ambush</u> (Goeden 1974; Samoilys 1987) -The feeding attack is initiated from a stationary position very close to the substratum. *Plectropomus leopardus* were usually displaying the intense mottle colouration and were very cryptic. Typically, they would move a short distance then stop and display the mottle pattern, and the procedure would be repeated.

<u>Prowl</u> (Samoilys 1987) - the attack initiated by a slowly moving *P. leopardus* well above the substrata.

Field observations suggest that the feeding behaviour of *P. leopardus* changes when they feed on schooling fishes (Choat 1968; Goeden 1974; Samoilys 1987; Kingsford 1992). More specifically, *P. leopardus* use ambush methods to hunt prey closely associated with the substrata (e.g. pomacentrids that live amongst the coral) and prowl methods to hunt schooling midwater fishes (including planktivorous pomacentrids that school high in the water column, Samoilys 1987). Dietary studies of *P. leopardus* on the midshelf reefs of the central GBR show that these predators feed on both demersal (e.g. Pomacentridae) and schooling (e.g. Caesionidae) prey (Chapter 5). Pomacentrids comprise a higher proportion of the diet (27% by number, 28% by weight) than caesionids (6% by number, 20% by weight, see Chapter 5) but some planktivorous pomacentrids are considered as schooling prey (Samoilys 1987).

These observations of predator behaviour in the field and the variability of predatory ability observed in the experiment suggest that populations of *P.*

leopardus may consist of at least two groups of specialist feeders. As some predators could not catch any pomacentrid prey fishes in the experiment, these individuals may have specialised more on schooling prey (e.g. caesionids) and have little or no experience in capturing demersal pomacentrids. Feeding specialisations are positively reinforced because skill at finding and capturing prey increases with experience (Magurran 1986). The specialist strategy is more appropriate when the food supply is abundant, as on coral reefs (Ringler 1983). Evidence for specialist feeding in populations of *P. leopardus* in the field would be difficult to obtain because it would involve watching repeated predation by individuals. Adult *P. leopardus* feed rarely and intermittently (Chapter 3), mostly on one prey at a time (Chapter 4). Specialist feeding could have been shown in the experiment if the unsuccessful predators of pomacentrids were more successful at capturing different types of prey (e.g. caesionids or schooling pomacentrids) and vice-versa. But this was impossible since the tank was too small to simulate a coral reef habitat for realistic predation experiments on small schooling fishes. Captive *P. leopardus*, however, were adept at capturing small schooling fishes (2 out of 11 *Valamugil sp*, were eaten immediately they were placed in a tank with one predator and a school of 8 *Gerres* sp. was reduced to 3 within 12 hours when two predators were present).

Although individual variation in predatory behaviour of one species of serranid, *Cephalopholis boenack*, was found in a study of predation on the GBR (Martin 1994), individual variation within other species of serranids generally has not been examined. Three species of serranids from the genus *Cephalopholis* vary in their preference for prey (Shpigel and Fishelson 1989). *C. argus* and *C. miniata* were specialists feeding mostly on selected fishes whereas *C. hemistiktos* was a generalist. The generalist ate throughout the day whereas the specialists fed when prey were abundant. All species, however, readily switched to other prey when their preferred food was absent (Shpigel and Fishelson 1989).

It seems unlikely, however, that rigid specialisation in feeding by predators would occur on coral reefs since these predators have abundant and diverse prey. Four pieces of information provide circumstantial evidence to suggest that populations of *P. leopardus* are not comprised of specialists on different prey fishes.

Firstly, serranids have several well developed feeding behaviours and are capable of learning (see Chapter 6) which suggests that they would be able to learn a wide variety of predatory tactics. The main feeding behaviours of serranids are three types of ambush behaviours: ambush from the bottom or from the water column, which is similar to prowl in *P. leopardus* (Hobson 1974; Harmelin-Vivien and Bouchon 1976, in Shpigel and Fishelson 1989) and 'cave ambush' where the predator waits at a cave entrance and strikes after the prey has entered (Diamant and Shpigel 1985). Although there are anecdotal accounts of *P. leopardus* ambushing prey from outside a dark cave (Squire pers. comm.), *P. leopardus* have not been observed using the 'cave ambush' method of feeding. In addition to these ambush feeding behaviours, serranids engage, to some extent, in interspecific feeding associations (Diamant and Shpigel 1985). *Plectropomus leopardus* have been observed feeding in interspecific associations with scarids (Goeden 1974; Samoilys 1987), labrids, haemulids and lutjanids (Samoilys 1987).

Secondly, generalists are considered to have a variety of foraging tactics. Despite being restricted to a subset of behaviours associated with searching and feeding on one prey type only, every individual *P. leopardus* used a wide repertoire of predatory behaviours and sequences in the experiment. Also, *P. leopardus* appeared to be opportunistic in the experiment because individuals used several predatory sequences in an attempt to eat one particular species of prey, even when their attempts were consistently unsuccessful. Whereas, a specialist feeder may not have attempted predation on potential prey that were not its specialty.

Thirdly, switching prey is predominantly a feeding strategy of generalists and common in serranids (Shpigel and Fishelson 1989). Switching to small schooling prey suggests that the huge reduction in size of prey is balanced by the ease of their capture. Group hunting by *P. leopardus* on schooling fishes has been observed on the southern GBR (Goeden 1974; Samoilys 1987; Kingsford 1992; pers. obs.) and rates of attack appeared to increase when *P. leopardus* fed on schools (Goeden 1974). Furthermore, dietary studies of *P. leopardus* have shown that, particularly when large, they eat large numbers of small schooling fishes at one time (up to 18 of these prey have been found in their stomachs, Chapter 4). But success rate of these attacks cannot be inferred from the high number of strikes observed. The synodontid, *Synodus variegatus*, increased strike rates from 1.7 to 10.6 strikes hour^{-1} when feeding on schooling fishes, but the percentage of successful strikes dropped from 11% to 7% (Sweatman in prep). This phenomenon was noted by Radakov (1958 cited in Goeden 1974) who showed that cod spent up to five times longer to catch a schooling fish than a solitary one. Strike rates in serranids vary according to the circumstances of the predator. Strike rates in *Cephalopholis* spp. increased from 0.1 strikes hour^{-1} when feeding alone to 2.5 strikes hour^{-1} when feeding in association with other species (Diamant and Shpigel 1985). Furthermore, strikes by these associating fish were more successful (80%) than strikes made by solitary feeders (20%, Diamant and Shpigel 1985).

The last but most important piece of evidence for generalist feeding in *P. leopardus* where individuals vary widely in their success, is the variation in growth, fecundity and territory size of populations reported in other studies of *P. leopardus* (Ferreira 1993; Davies 1995; Zeller unpubl.). In a trapping study at Lizard Is. lagoon, northern GBR, growth rates of 16 *P. leopardus* (mean 40 cm FL) varied four-fold, ranging from 0.15 - 0.4 cm month^{-1} (Davies 1995). High variability in growth was found in another study of age and growth at Lizard Is., as six year old *P. leopardus* ranged in size from 32 to 58 cm FL (Ferreira 1993). Variations in growth rates influence fecundity in coral reef fishes (Jones 1991) because fecundity is related to size more than age (see review by Robertson 1991) and female fecundity increases with body size (Gladstone and Westoby 1988). *Plectropomus leopardus* are protogynous hermaphrodites where sex reversal is related to size and age, but the underlying mechanisms behind the onset of reversal are not well understood (Ferreira 1993). Thus growth affects fecundity in *P. leopardus* in two ways. First, *P. leopardus* with faster growth will reach sexual maturity earlier. Ferreira (1993) found that sexual maturity of male and female *P. leopardus* spanned a wide range of sizes and ages. Second, faster growth could play two important roles in increasing fecundity of individuals. Faster growth in females will increase their fecundity by increasing their body size. If faster growth leads to an earlier onset of sex reversal, then individuals with fast growth will be more fecund as males, which have increased reproductive output, than as their female contemporaries (Warner 1991). At a population level, however, female reproductive output has the greatest impact. Reasons for the onset of sex reversal in *P. leopardus* need to be verified experimentally because sex reversal is induced socially and behaviourally in many coral reef fish (Shapiro 1991; Warner 1991)

Thus the results of this experiment and other observations in the field suggest strongly that populations of *P. leopardus* are made up of individuals which are generalist feeders on a broad range of prey fishes but with varying degrees of success. Thus populations of *P. leopardus* are made up of individuals that have several sets of diet-growth-fecundity patterns, which may affect the net contribution to future generations (Ringler 1983).

The results of the predation experiment were inconclusive due to high variability among individuals and the low number of fish replicates, but the placement of hides appeared to play some role in predation. Unsuccessful predators used hides more than successful predators, and hide use was highest in the control treatment. Thus hides nearer to prey promoted predatory success without being used. The overall successful strategy employed by *P. leopardus* for these prey was the prowl type of predation (i.e. swim/glide in open). *Plectropomus leopardus* use hides for shelter but were stimulated to leave the hide when they detected prey. When the hides were furthest from the prey (i.e. control treatment), they did not facilitate predation because there were few opportunities for prey capture as prey rarely ventured the distance from the shelter to the far hides. Thus, the control treatment changed the predatory methods employed and did not appear to alter the amount of time *P. leopardus* spent trying to capture the prey. The main predatory behaviour that was associated with the hides was the 'ambush' or 'sit and wait' behaviour. *Plectropomus leopardus* ambushed prey from both the near and medium hides rarely (0.125 h-1). *P. leopardus* did not ambush prey from the far hides.

There were no obvious patterns of predation on *A. polyacanthus* in the experiment. Measurable attributes of the prey, such as size, rank (by size) and experience in terms of exposure to the predator, did not affect survivorship of *A. polyacanthus.* As dietary studies have demonstrated a relationship between size of pomacentrid prey and predators (Chapter 4), three reasons may account for the lack of size related feeding patterns. Firstly, the size-range of the prey in the experiment may have been too limited to show size selection. This is unlikely as prey ranged two-fold in length and five fold in weight. Secondly, chances of predation were limited by small numbers of prey and thus *P. leopardus* could not miss any chance of predation regardless of prey size. Thirdly, size may be less important when the predator can consume more than one prey, which occurred in 36% of trials where predators were successful. The lack of difference in mortality rates between experienced *A. polyacanthus* and prey new to the experiment is not surprising. *Acanthochromis polyacanthus* may well be accustomed to *P. leopardus* as they were caught from the wild where these predators lived. Nevertheless social prey fishes can learn anti-predator responses without direct experience of predatory attacks (Tully and Huntingford 1987).

Detection of predators is very important on coral reefs because prey that are aware of predators are in no danger (Sweatman 1984). Coral reef fishes detect predators visually. The faces of predators have characteristic wide mouths and wide set eyes (Karplus and Algon 1981) and pomacentrids, such as *Dascyllus aruanus* (Coates 1980) and *Stegastes planifrons* (Helfman 1989) can distinguish predatory and nonpredatory species. When *P. leopardus* watched prey from the near and medium hides, the prey could see the face of the predator and exhibited predator-avoidance behaviour by clustering within the coral shelter. To ensure the prey showed no predator-avoidance, *P. leopardus* watched prey from a distance using the far hides to conceal themselves and disguise their face. Chemoreception is also important in fishes because some fishes use vision and chemoreception jointly to detect prey (Luczkovich 1988) and chemical cues emitted by conspecifics are used to alert prey to the presence of a predator (Smith 1992). Thus, *A. polyacanthus* may have been able to detect the presence of a predator in the tank by chemoreception. Their behaviour suggested otherwise. When the predator remained concealed for several minutes, the prey stopped their predator-avoidance behaviour and appeared to return to normal behaviour. As for other damselfishes on coral reefs, escape responses to predators waned quickly after the immediate danger had passed (Helfman 1989). Damselfishes, like most reef fishes, live amongst predators and live with the threat of predation due to the high abundance of piscivores on coral reefs.

In the tanks, concealment from the prey did not appear to be important in predatory success for *P. leopardus* even though prey change their behaviour in the presence of a predator. Concealment, which mostly involved the ambush behaviour, did not alter the behaviour of the prey but was not a very successful predatory behaviour. To remain visible to the prey, but not threatening, predators feigned disinterest in prey, and the behaviour of the prey did not alter. This response of the prey is not unusual as some prey respond to different behavioural characteristics of the predator (Morse 1980). Thus, 'indifference to the prey' was a common tactic in *P. leopardus* and occurred in three of the eight predatory sequences identified in the experiment. Also, predatory sequences of *P. leopardus* involved both watching and not watching prey because the prey behaved differently when being watched by *P. leopardus* than when not.

Familiarization with the prey type over time did not improve the success of predators in the experiment. This suggests that successful predatory behaviour in *P. leopardus* is either learned over a longer time frame, or could not be learned alone. As serranids are capable of learning new behaviours and feeding associations in groupers are common (Diamant and Shpigel 1985), *P. leopardus* may learn predatory strategies from conspecifics. Two possible methods of learning are passively watching and actively following (see Chapter 6). Following behaviour, whereby one *P. leopardus* follows and mimics another slightly larger one, has been observed in *P. leopardus* (see Chapter 6). Doubling the number of predators may increase their ability to capture prey. In an independent trial similar to those in the experiment, two previously unsuccessful predators, that were exhibiting following behaviour during the trial, caught one prey fish in 24 hours. Interspecific following behaviour is well documented in fishes as a means to increase foraging success by the follower capturing escaping prey (Strand 1988).

During the main experiment, *P. leopardus* concentrated on predation about 30% of the time even though predatory strikes were rare. Rates of predatory behaviour in captive *P. leopardus* were similar to those observed in the field on the Southern GBR (Samoilys 1987). In the field, rates of feeding were slightly lower but probably not significantly so. Captive *P. leopardus* could be expected to have higher rates of feeding since, unlike wild *P. leopardus,* they did not have the opportunity to engage in other inter- and intra-specific non-predatory behaviours (e.g. cleaning, territorial interactions). Feeding rates of *P. leopardus* did not vary diurnally or tidally in the field (Samoilys 1987).

Strike rates of serranids are much lower than other piscivorous species examined on coral reefs and may be related to size of the predator. In general, *P. leopardus* are 3-10 times the mass of the other piscivores examined. Abundant new recruits in summer may alter strike rates of predators. Strike rates of *Cephalopholis boenack* feeding on recruits on the GBR (Martin 1994) were nine times higher than *Cephalopholis* spp. feeding in the Red Sea (Diamant and Shpigel 1985). Martin's (1994) study may have been biased as strike rates were counted when the piscivores were near coral heads (and in the field of view of the camera) and other behaviours away from the coral heads were not included.

Experiments with *P. leopardus* in large tanks have limitations. One of the main problems of this predation experiment was that the habitat was not as complex as coral reef habitat. Prey only had one predator to contend with, and the lack of habitat prevented *P. leopardus* from making unexpected encounters with the prey as it would in the field. This is in contrast to the general conclusion that predation decreases linearly as complexity of habitat increases (Crowder and Cooper 1979; Nelson and Bonsdorff 1990) due to changes in behaviour of the prey (Nelson and Bonsdorff 1990) or predators (Savino and Stein 1982), but all of these studies were done on reed beds or seagrass habitats with prey that school in open water. Another potential problem in artificial experiments is that foraging behaviours may appear under artificial circumstances that rarely if ever are observed in nature (Morse 1980). This did not appear to be the case in this experiment because many of the behaviours were similar amongst predators and the prey were in conditions close to natural. Despite the many limitations of predation experiments involving large piscivores in tanks, extensive field observations of individual *P. leopardus* may never have revealed the extent of variability in the success of individuals on one species of prey. Nor can dietary overlap be used to measure individual variation in predatory ability since the majority of *P. leopardus* eat one prey at a time and feed intermittently (Chapter 3).

In conclusion, the results of the predation experiment and observations of the use of hides in the experiment suggest that location of the hides relative to prey is important for their use in predation but their role is complex. Individual differences in *P. leopardus* need to be understood before the role of hides in feeding can be elucidated. The results of this study combined with results of other studies on *P. leopardus* provide circumstantial evidence that *P. leopardus* is a generalist feeder, with individuals showing varying degrees of predatory success.

Table 8.1 Two factor ANOVA (unreplicated block design) of three variables in the experiment. The factors were individual fish and a. hides (far, medium and near) or b. chronological order of treatments (first, second third), all factors were fixed.

a. number of prey eaten, 1- β=0.20

b. chronological order of the treatments

a. number of prey eaten					b. chronological order				
Source	**df**	**MS**	**F**	***P***	**Source**	**df**	**MS**	**F**	***P***
Hides	2	1.067	1.306	0.323	Order	2	1.267	1.652	0.251
Fish	4	2.767	3.388	0.067	Fish	4	2.767	3.609	0.058
Error	8	0.817			Error	8	0.767		

Table 8.2. Patterns of predatory success of individuals in the experiment. Predatory consistency refers to the success of each individual throughout all three treatments. Predatory success refers to the number of prey caught in the treatments.

PREDATORY CONSISTENCY	PREDATORY ABILITY		
	HIGHLY SUCCESSFUL (≥2 prey)	SUCCESSFUL (1 prey)	UNSUCCESSFUL (0 prey)
EVERY TREATMENT	fish #7	fish # 5	fish #4, 6 & 8
ONE OR TWO TREATMENTS	fish #1	fish #2 & 3	N/A

Table 8.3 Predatory behaviour observed in successful and unsuccessful predators in the experiment during summer (n=24 trials).

FISH EATEN	PREDATORY BEHAVIOUR		TOTAL (%)
	Yes	No	
Yes	8	4	12 (50%)
No	7	5	12 (50%)
total (%)	15 (62.5%)	9 (37.5%)	

Table 8.4 Two factor ANOVA in unreplicated block design of two variables in the experiment. The factors are hides (far, medium and near) and individual fish. Both factors are fixed.
a. the use of hides by *P. leopardus* in the experiment,
b. the percentage of mottling by trout in the experiment, $1-\beta = 0.09$

		a. use of hides			**b. % of mottling**		
Source	**df**	**MS**	**F**	***P***	**MS**	**F**	***P***
Hides	2	661.7	6.167	0.01	113.88	0.337	0.720
Fish	7	3221	30.02	0.01	441.79	1.307	0.316
Error	14	107.3			338.06		

Table 8.5. Predatory behaviours observed in the tanks during the experiments. Chase Back =predator facing away from prey, turns quickly to chase prey back to shelter. Tail-chase is an aggressive chase toward the predator by the prey when the predator is swimming away from the group of prey. (pred. =predator)

NAME OF PREDATORY SEQUENCE	DESCRIPTION	VARIATIONS	ASSOCIATED PREY BEHAVIOUR
1 Intrusive Watching	pred. stays close to coral shelter, watching, waiting for prey to make mistake	may harass prey, may circle shelter	prey stays close to coral
2 Passive Watching	pred. watches prey from a distance	mottles if prey approaches	prey swim away from shelter
3 Pass by Shelter	pred. swims slowly past shelter, Chase Back (often while cruising i.e. swimming a set path around the tank which may include swimming through one or two hides)	stops and waits for prey to tail swipe before Chase Back	prey tail-chase
4 Luring in Open	pred. faces away from prey, mottles, Chase Back		prey tail-chase often
5 Circles in Open	pred. slowly circles in open either near the shelter or farther away	may include Luring in Open, may swim through shelter	
6 Waiting in Hides	pred. waits in hides for prey to move closer	able or not able to see prey, mottled or not, Chase Back	prey swim further from shelter, sometimes look in hides
7 Swim Between Hides	pred. swims between two hides	from far to medium hide (trying to sneak up on prey unawares)	
8 Ambush from Hides	pred. waits in hide until prey comes close, then attempts to capture	pursuit from medium hide or attack from near hide	prey move away from coral

Table 8.6. Predatory behaviours (listed in Table 8.5) of the eight *P. leopardus* during the experiments. The total number of trials was 24.
Symbols:

- • used during successful and unsuccessful predation trials,
- + used during successful predation trials only,
- o used during unsuccessful predation trials only.

PREDATORY BEHAVIOUR	PREDATORS								TOTAL
	SUCCESSFUL					UNSUCCESSFUL			
	fish 7	fish 1	fish 5	fish 3	fish 2	fish 4	fish 6	fish 8	
1. Pass by Shelter	+	o	+	o		o	o	o	7
2. Circles in Open	+	o			•		o	o	5
3. Waiting in Hides			+	•		o	o	o	5
4. Swim between Hides			+	+	o	o		o	5
5. Luring in Open	+	o	+		•				4
6. Intrusive Watching	+				•		o	o	4
7. Passive Watching		•			•		o		3
8. Ambush from Hides	+					o		o	3
Total behaviours	5	4	4	3	5	4	5	6	
Total number of prey eaten	8	4	3	2	1	0	0	0	18
The number of trials the predator was successful	3	2	3	2	1	0	0	0	11

Table 8.7. Patterns of change in behaviour of two fish that were successful during every treatment and of two which were not. NO and YES refer to whether the behaviour of the fish changed significantly within a treatment (i.e. among the four times of day). Behaviour was measured by the location and movement of the predator. Except in the SWIM category, the predator was gliding or stationary. In OPEN, the predator was >0.3m from all structures in the tank. All other categories (SHELTER, NEAR, MEDIUM, FAR and FAR CONTROL) refer to the location of the predator (within 0.3m). See Fig. 8.5 for a graphic representation. Values in parentheses are Kruskal-Wallace (K-W) test statistics and significance: ns is non significant at $\alpha=0.05$).

HIDE TREATMENT	PREDATORS			
	SUCCESSFUL		UNSUCCESSFUL	
	fish 5	fish 7	fish 4	fish 6
NEAR	NO (5.14, ns)	YES (21.73, p<0.01)	NO (3.95 ns)	YES (10.55, p<0.01)
MEDIUM	YES (37.98, p<0.01)	NO (0.39, ns)	NO (3.83, ns)	YES (37.98, p<0.01)
FAR	NO (7.32, ns)	YES (14.14, p<0.01)	YES (34.26, p<0.01)	YES (68.76, p<0.01)

Table 8.8. Strike rates of piscivores on coral reefs from various studies

PISCIVOROUS SPECIES	STRIKE RATE (hour^{-1})	STUDY
Plectropomus leopardus	0.125	present study
Cephalopholis spp.	0.1	Diamant and Shpigel (1985)
Cephalopholis boenak	0.9	Martin (1994)
Pseudochromis fuscus	1.37	Martin (1994)
Synodus variegatus	1.7	Sweatman (1984)

Figure 8.1 The experimental tank set up as a "Medium hide" treatment prior to the start of the experiment. Note that the net cage is in place around the *Acropora* sp. sheltering 10 *A. polyacanthus* and that two hides are a Far (>2 m) and a Medium (1 m) distance from the shelter. The *P. leopardus* is closest to the Medium hide.

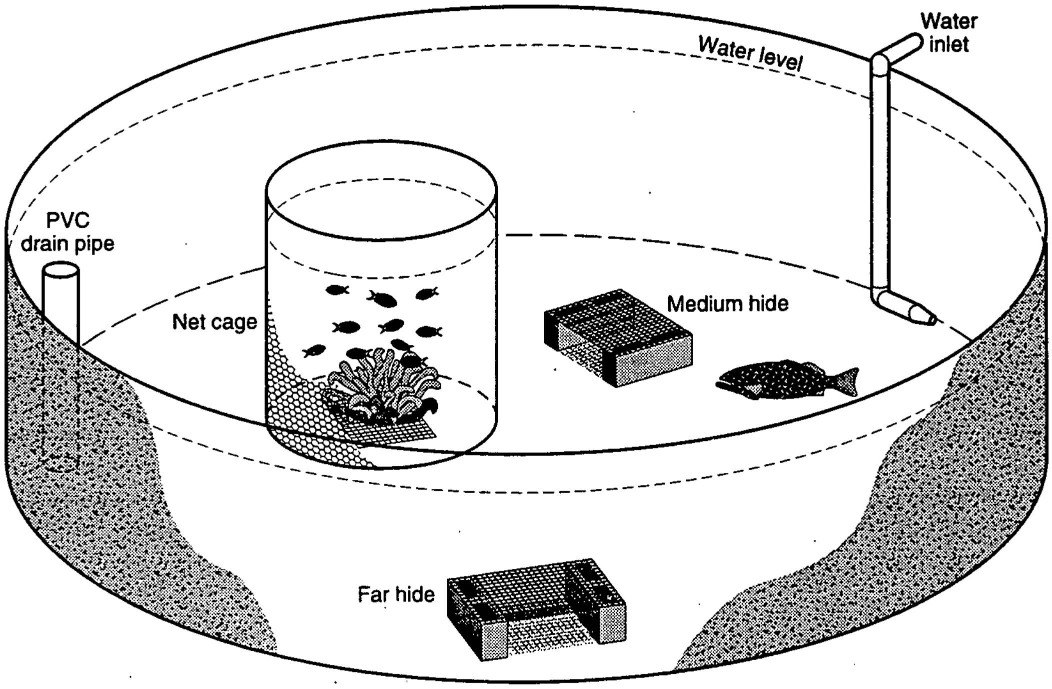


Figure 8.2 The size-structure of all prey used in the experiment (this includes every time an individual was used) and all prey that were eaten.

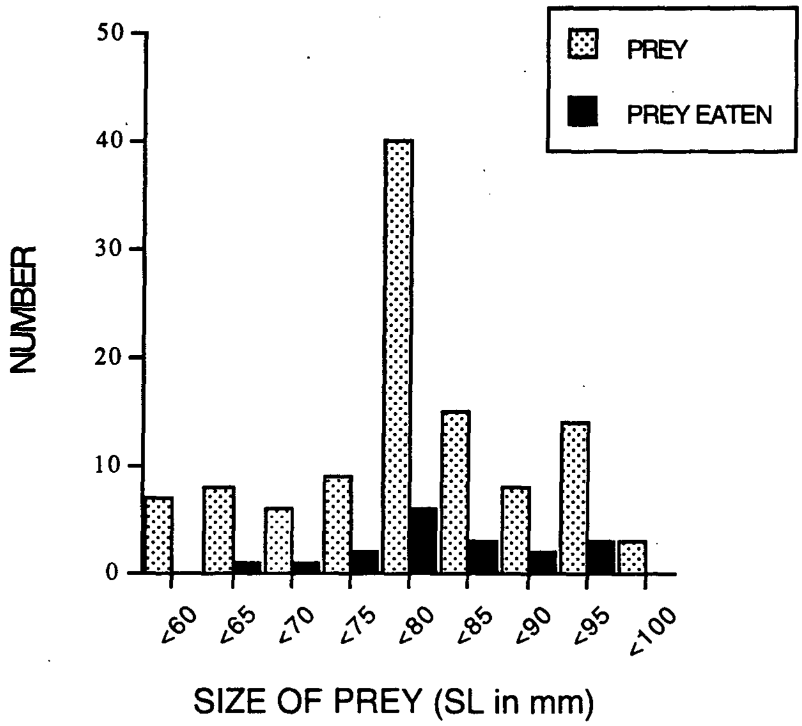


Figure 8.3 Use of hides (mean percentage and SE), including the far and the treatment hide, by successful and unsuccessful *P. leopardus* during the experiment. Successful predators used hides significantly less than unsuccessful predators ($t_{[22]}$=-2.246, $p<0.05$).

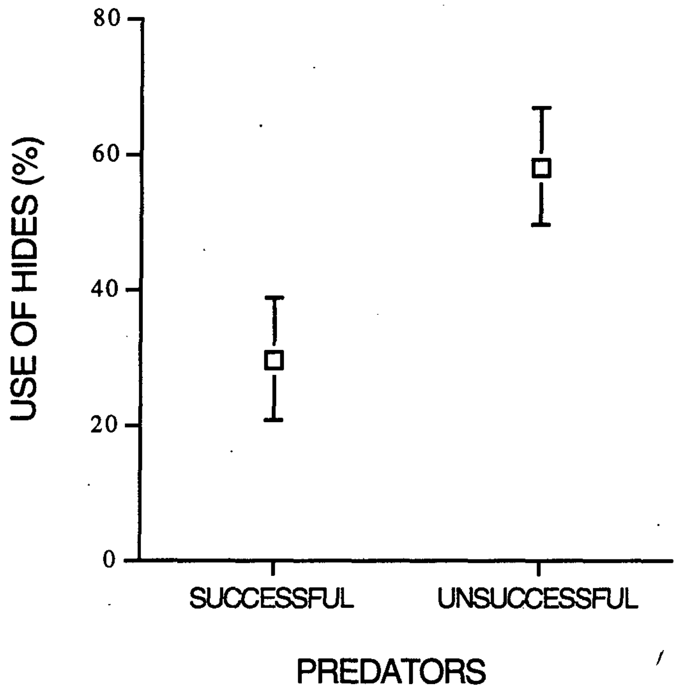


Figure 8.4 Use of hides (mean and SE percentage), including the far and the treatment hide, by *P. leopardus* during each of the three treatments. Use of hides by *P. leopardus* varied among treatments and fish (Table 8.4a).

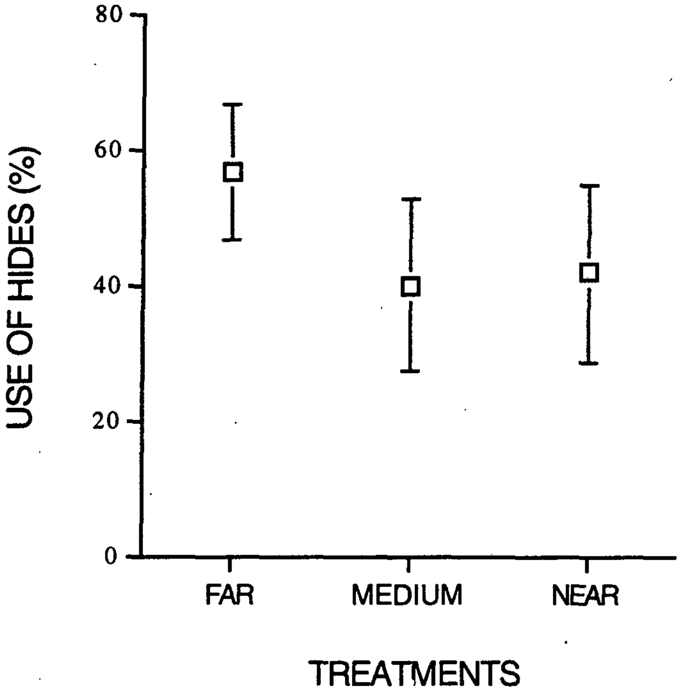
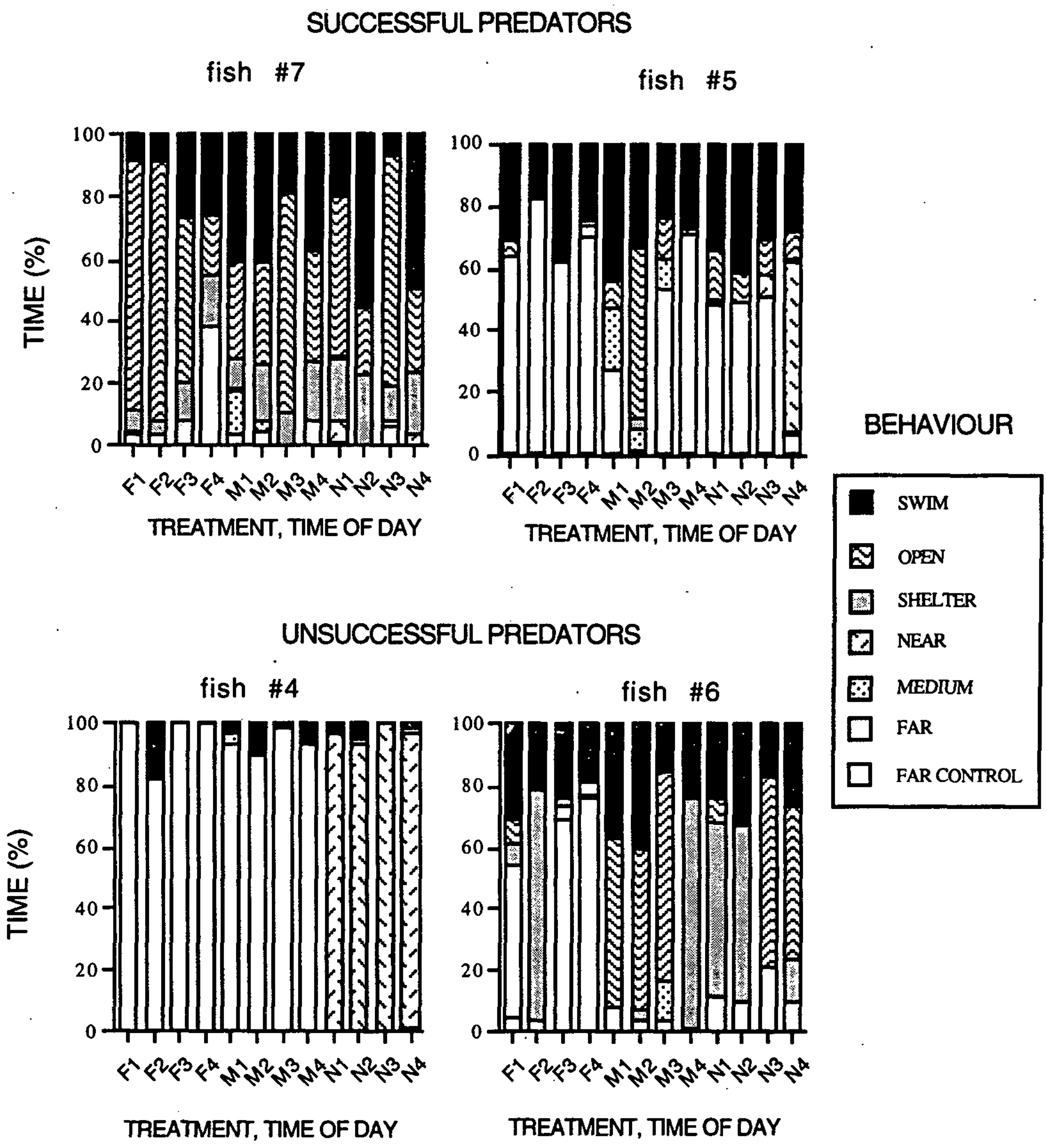


Figure 8.5 Behavioural patterns of four *P. leopardus* divided into the three trials (Control or Far, Medium and Near) and four times throughout the day (see 'TIMES' below). The four fish were either consistently successful predators (fish 5 and 7) or consistently unsuccessful predators (fish 4 and 6). The behaviours are as follows;

1. SWIM- swimming around the tank;
2. OPEN- stationary or gliding > .3 m away from any structure in the tank; In the following behaviours the predators are stationary or gliding within 0.3 m of the following experimental structure in the tank:
3. SHELTER-coral shelter;
4. NEAR-near hide;
5. MEDIUM- medium hide;
6. FAR-far hide; and
7. FAR CONTROL- far hide present in every treatment

TREATMENT is denoted by **F**-far, **M**-medium and **N**-near,

TIMES are **1** - 7-8:00 h, **2** - 10-11:00 h, **3** - 13 -14:00 h and **4** - 16 -17:00 h.



CHAPTER 9

9.0 GENERAL DISCUSSION

Predators influence the distribution and abundance of their prey directly by removing individuals from populations. The mere presence of predators in a community suggests that predation affects the abundance of their prey. Predation, unlike other processes such as competition, does not have variable or temporary effects on an individual (i.e. reduced growth, reduced fecundity); when successful, it is an irrevocable event.

The view that predation on coral reefs is important in structuring patterns of abundance of reef fish communities originated for two reasons. Firstly, piscivores form a large component of the fish community (Goldman and Talbot 1976; Williams and Hatcher 1983; Norris and Parrish 1988) and many small coral reef fishes are generalist carnivores with very opportunistic feeding habits (Hiatt and Strasburg 1960). Secondly, coral reef fishes are generally assumed to have high rates of natural mortality, especially of young and small fishes (see reviews by Doherty and Williams 1988; Hixon 1991). Despite this implied importance, predation and feeding ecology have not often been the focus of studies on coral reef fishes. In 1980, Sale commented on the paucity of information about predation on coral reefs and the impact of piscivorous fish on assemblages of reef fishes. Fifteen years later this situation still persists.

Several experiments on coral reefs have attempted to exclude or remove predators to test the impact of predation on assemblages of fishes (see review by Hixon 1991). These have been largely unsuccessful because of problems caused by experimental caging (Lassig 1982; Doherty and Sale 1985) or high variability (Caley 1993). Descriptive information about the predators and their prey is required to set up meaningful experiments that can test the biological impact of predation within the constraints of the natural variability of the system. This includes such basic information as the determination of which predators take which prey (Jones 1991), the proportion of fish in the diet of each species of piscivore and their feeding behaviour. Surprisingly, there is very little descriptive information on feeding of piscivores on coral reefs. A few studies have examined natural feeding rates of reef piscivores, but field observations are very time consuming since successful predatory strikes are rare (Goeden 1974; Sweatman 1984; Diamant and Shpigel 1985; Samoilys 1987). Most studies of diets of piscivorous fishes on coral reefs examined gut contents (Hiatt and Strasburg 1960; Randall 1967; Hobson 1974; Goldman and Talbot 1976; Harmelin-Vivien and Bouchon 1976; Sano *et al.* 1984; Parrish *et al.* 1985; Parrish 1987; Norris and Parrish 1988). When compared to other studies on gut contents of predatory fishes collected by trawls, the sample sizes of predators recorded in tropical reef dietary studies are usually low (n<50), with some exceptions (e.g. Choat 1968; Kingsford 1992). Dietary studies with small sample sizes can be of limited value due to low numbers of identified prey. Under such circumstances, the absence of particular prey in the diet does not mean that they are not consumed. This is particularly problematic in studies of piscivores on coral reefs, where prey fish communities are diverse and species are abundant (Sale 1977). Lastly, dietary studies are considered to under-represent juvenile and small prey fishes that are digested faster than larger prey items because of their small size (see reviews by Windell and Bowen 1978; Hyslop 1980).

On the Great Barrier Reef (GBR), spanning almost 2500 km of coastline, describing the diet of a common and widespread piscivorous coral reef fish is a considerable undertaking. Sampling large piscivores poses further problems. Firstly, it is difficult to obtain the sample sizes required for effective dietary study as there is no commercial spear fishery on the GBR and specimens caught by line contain fewer prey. Secondly, the collection of large samples of *P. leopardus* means a large biomass is removed from reefs, which is undesirable on protected reefs. Thirdly, a high proportion of samples of large fish have empty stomachs and therefore provide no information on diet (Randall and Brock 1960; Randall 1967; Choat 1968; Goeden 1978; Hussain and Abdullah 1977; Kingsford 1992). Fourthly, identification of digested prey items is difficult when a wide diversity of prey is consumed. Finally, information on rates of digestion and patterns of feeding are required to interpret the results of dietary analyses.

Classifications of four types of predators are defined. Generalists and specialist feeders are determined by the range and types of prey consumed. Whereas generalists feed on many type of prey, specialists consume very few. The classification of opportunistic and selective predators, however, is based on the abundance of prey available to the predator. Opportunistic predators take prey in abundances relative to those present, whereas selective predators take all, or some prey, in different proportions to their abundance (Jaksic 1989, see Chapter 1).

9.1 *P. leopardus* are predators on a wide variety of fish prey on the GBR

The GBR is the largest coral reef system in the world and *P. leopardus* is one of the most widespread and abundant piscivores on this reef system (Ayling and Ayling 1986). After attaining 20 cm SL (approximately the first year of life) *P. leopardus* are almost entirely piscivorous on adult fishes (99% of fish diet). *Plectropomus leopardus* are generalist piscivores as they eat a wide range of prey species: individuals of 37 families were identified in their stomachs. As *P. leopardus* are such large predators ($L_\infty = 60$ cm TL), most families of fishes on coral reefs would be available to them as prey, and even species that are large as adults must pass through smaller size classes when they may be eaten. Yet, within this highly speciated community of prey fishes, *P. leopardus* appear to be selective feeders, at both a family and a species level. Many families of fishes that are abundant on the GBR (e.g. Chaetodontidae, Holocentridae, Pomacanthidae and Siganidae) were rarely eaten while others (e.g. Haemulidae) were not identified in the diet at all. On the GBR, the most common family of prey in the diet of *P. leopardus*, Pomacentridae, has some 120 species in the family and is the most numerically abundant family of reef fishes (Randall *et al.* 1990). Approximately 25% of the 120 species were identified in the stomachs of *P. leopardus*. Some of these prey species were eaten in much higher proportions than expected when compared to their general abundance on reefs (e.g. *Acanthochromis polyacanthus*), whereas other species were eaten in much lower proportions (e.g. *Pomacentrus amboinensis, Pomacentrus molluccensis* and *Neopomacentrus azysron*, on midshelf reefs, Williams 1982). The selectivity of predation by *P. leopardus* on the species of prey in other families could not be examined in all of the other families, as the numbers of species in the diet were very low. In this study, however, I did not set out to test selectivity in feeding by *P. leopardus* because I did not estimate the abundances of prey at locations where these predators were collected.

Plectropomus leopardus is one of the most highly piscivorous serranids. In a review of dietary information for 78 species of temperate and tropical serranids (Parrish 1987), *P. leopardus* was one of five species that were more than 90% piscivorous (in studies where predator samples were n >30). Other genera of serranids may also be highly piscivorous. For example, in the Red Sea, *Cephalopholis argus* was the most piscivorous serranid (95% fish in diet) out of three species of this genus studied (Shpigel and Fishelson 1989). But this genus does not grow as large as *Plectropomus* spp. As *P. leopardus* is large and highly piscivorous, it is likely to be one of the most important predators of adult coral reef fishes on the GBR.

9.2 Potential impact of *P. leopardus* on coral reef fish communities

Mortality in coral reef fishes is highest in young (Sale and Ferrell 1988; Shulman and Ogden 1987) and small fishes (Mapstone 1988). Several studies have shown that survivorship of juvenile prey is negatively related to increases in predator abundance (Shulman 1985; Thresher 1983a; Doherty and Sale 1985; Hixon and Beets 1993). Although predation is the most likely cause of this pattern, none of these studies provide direct evidence for this relationship. Furthermore, large predatory fish are often considered to be important predators of juvenile reef fish (Williams 1979; Forrester 1990; Kingsford 1992; Hixon 1991; Hixon and Beets 1993). But the large piscivore in this study, *P. leopardus,* rarely consumed very young fishes of other genera. Therefore, there is no evidence to suggest that this large piscivore plays a direct role in modifying the abundances within assemblages of juvenile coral reef fishes.

Plectropomus leopardus may affect communities of coral reef fishes indirectly.

Their predation may cause a 'cascading' effect to other trophic levels (review by Mills *et al.* 1987). Prey in nearly one quarter of the families (by numerical abundance) consumed by all sizes of *P. leopardus* included potential (and voracious) predators of young coral reef fishes (Labridae, Synodontidae (Sweatman 1984), Apogonidae, Serranidae (Martin 1994), Tripterigiidae, Scorpaenidae and Lutjanidae). Thus, predation by *P. leopardus* may affect levels of predation on assemblages of young coral reef fishes indirectly by reducing the numbers of piscivores that prey on these assemblages.

Fishes on coral reefs may be long-lived (10-20 years, Samuel *et al.* 1987; Fowler 1989; 1990; Lou 1992), and *P. leopardus* live to at least 14 years (Ferreira and Russ 1994). Over such a time span even slow rates of predation by a moderately selective predator, such as *P. leopardus,* will affect the numbers of adult coral reef fishes. At One Tree Reef, the annual natural mortality of adult *Thalassoma* (F. Labridae), which are common prey of *P. leopardus,* was 20.6% (calculated by Hixon 1991 from Eckert 1987). If a large proportion of this mortality was caused by predation, then predation will affect the abundances of adults of these species. Furthermore, the relationship between assemblages of juvenile fishes and subsequent assemblages of adult fishes on coral reefs has not been quantified. If the species richness and abundance of communities of juvenile fishes do not correlate with those of adults (as in some species of labrids, Eckert 1987), then selective predation by large piscivores may contribute to this difference. To date predation experiments have focused on assemblages of juveniles and small reef fishes on small artificial or natural patch reefs (see review by Hixon 1991); the effect of predation on these assemblages cannot be assumed to be similar to predation on communities of adult coral reef fish on larger or contiguous reefs because of differences in the assemblages of piscivores and their rates of predation. Large scale studies of the effects of predation on adult coral reef fishes need to be made over a much longer time scale than previously considered (around 10 years). This study provides information on the major prey species to be targeted for an experiment examining predation by *P. leopardus*.

9.3 Relevance to management of fisheries

Coral reef fisheries tend to remove large piscivorous fishes from the community (Bohnsack 1982; Russ 1985, 1991; Huntsman and Waters 1987; Koslow *et al.* 1988). The effect of the removal of these fishes on coral reefs is in dispute (see review by Russ 1991). Some authors have argued that the removal of large piscivorous fishes leads to an increase in overall abundance or change in relative abundance of prey often termed ‘prey release’ (Beddington and May 1982; Goeden 1982; Beddington 1984; Grigg *et al.* 1984; Koslow *et al.* 1988). Russ (1991), however, argued that the evidence for ‘prey release’ on coral reefs is limited and equivocal for two reasons. First, coral reef fish communities have a large range of opportunistic predators that are capable of rapid functional response (i.e. switching). Second, both predator and prey populations are open. More specifically, Goeden (1982) considered that the removal of *P. leopardus* by fishing resulted in changes in the relative abundances of other large predatory species including several that are not part of the usual hook and line catch (but see comments by Russ 1991). Direct effects of fishing on the prey communities, however, cannot be measured without detailed information on the prey of the particular species being fished. This study provides such information for *P. leopardus*. In the past, spurious relationships between *P. leopardus* and their supposed prey have been proposed without this information (Goeden 1982; Ayling and Ayling 1992).

This study suggests that fishing plays two major roles in structuring populations of *P. leopardus.* Fishing causes increased mortality rates of adults and perhaps reduced mortality rates of juveniles. Adult *P. leopardus* were predators of *Plectropomus* recruits and populations of *P. leopardus* occurred in densities which could reduce the density of recruits on a reef during summer. Predation rates on recruits and juvenile *Plectropomus* spp. by *P. leopardus* were calculated to be extremely high and appeared to be density dependent (Chapter 7). Reduced predation by *P. leopardus* has been suggested to be the cause of the higher densities of *P. leopardus* recruits on fished reefs compared to reefs protected from fishing for seven years (2.5 times higher on fished back reefs, n=26, Ayling *et al.* 1991).

This study makes several conclusions useful to management of stocks of *P. leopardus* and to future studies on their diet. Specimens for dietary studies of *P. leopardus* should be collected by spear when possible. Specimens caught by the commercial fishery on the GBR should be used with caution, as their stomach contents provide a different picture of diet and feeding rate. These *P. leopardus* have a low proportion of stomachs with natural prey and pelagic prey are over-represented in the diet. When examining the effect of fishing on the fished species, any changes in feeding need to be examined in the context of natural (i.e. temporal and spatial) variations in their diet. On the GBR there were no detectable effects of fishing on feeding and diet of *P. leopardus*. This outcome is not surprising because most of the major changes in the diet of *P. leopardus* occur before the piscivores enter the fishery. Size-selective fishing of *P. leopardus* would not cause different impacts of the predators on the prey communities because the diet of *P. leopardus* within the fishery does not vary in composition and size of fish prey. This is not completely the case for smaller adults (< 35 cm SL). The diet of small *P. leopardus* (< 35 cm SL) varied considerably among size classes and thus removal of *P. leopardus* below legal size (< 38 cm FL) would have varying impacts on prey communities.

Feeding patterns of *P. leopardus* were not homogenous along the GBR. Target families of prey varied latitudinally. Thus, results of detailed dietary studies of populations at one reef cannot be applied with confidence to the rest of the GBR. Drastic reductions in abundance of fishable *P. leopardus* could interfere with the predatory behaviour and success of future generations, if predatory behaviour is learned by copying in *P. leopardus* (see Chapter 6), but there is no evidence to suggest that the probability of this occurring is high. An understanding of the role of conspecifics in the behaviour and predatory success of *P. leopardus* is necessary to determine the effect of fishing on the feeding biology of this piscivore.

Food availability does not appear to be limiting for the coral trout populations on the GBR. Depletion of one species of prey from a reef or region would be unlikely to affect the trout fishery. The coral trout fishery is not dependent on one prey group in terms of behavioural group or taxonomy because of the high diversity of prey consumed. Prey in the four most common families of *P. leopardus* included species with wide ranging habits that lived in various habitats on the reef. Two of these families, Pomacentridae and Labridae, are highly diverse and abundant on the GBR.

The removal of *P. leopardus* can be viewed in terms of potential changes to the impact of this predator on the prey community. The annual consumption of prey can be calculated from dietary information in this study. Competitive release, however, where removal of one predator allows another to take its place, may occur (Shpigel and Fishelson 1991).

The results of this study suggest that line fishing plays only a minor role in reducing predation on prey indirectly by feeding predators. Approximately

1.5% of the daily diet of *P. leopardus* may be substituted by bait on reefs (17-39 km^2 in size) on days when recreational fishing occurs. When reefs are fished commercially, this figure may be greater because larger quantities of bait and burley are used. Line fishing does not appear to alter the feeding behaviour of *P. leopardus.* The catch rates of *P. leopardus* by baited line on fished and unfished reefs did not vary. Instead, the catch of line-fished *P. leopardus* was significantly correlated to hunger. Coral trout consumed more food in winter in preparation for reproduction in early spring. Thus, in winter, *P. leopardus* may be more susceptible to line fishing because their levels of hunger are higher and thus their selectivity of food is lower. Also, captive *P. leopardus* were more successful at predation on a common prey species in summer than in winter, but the reasons for this result are unclear (Chapter 8). Seasonal variations in feeding by *P. leopardus* are correlated to seasonal variations in their commercial catch. Catches of *P. leopardus* by commercial line fishing are highest during August to November (Trainor 1991), particularly in October and November (Bandaranaike and Hampton 1979). Low catches are recorded in January through to March, but rather than representing differences in CPUE, these low catches are most probably due to reduction of fishing effort in the cyclone season when many commercial boats are refitted (Brown pers. comm.). Other behavioural factors, however, influence catchability of *P. leopardus.* Spawning aggregations of coral trout occur in October and November and spawning sites are excellent fishing grounds, increasing catchability substantially (L Squire pers. comm.).

In conclusion, the results of this study emphasise the need for the effects of fishing on coral reefs to be considered on a species by species basis. Coral reefs are very complex, and feeding by large piscivores in general cannot be assumed to be purely opportunistic and non-selective. Indeed feeding by *P. leopardus* is somewhat selective by taxon and size. Thus, without detailed information on the diet and feeding behaviour of the fished species, correlations between abundances of predators and supposed prey may be spurious.

9.4 Future directions for research

This study paves the way for future experiments on predator-prey interactions of *P. leopardus* and the effect of the removal of *P. leopardus* from reefs. Firstly, the study outlines the major prey species to be targeted in such an experiment. The prey species and their variability in the diet will depend on the location of the experiment on the GBR. Secondly, annual estimates of prey consumption can be used to determine the biological impact of the removal of predators (in terms of the estimated effect on prey). In this way statistical power can be matched to an expected biological impact on the prey before the experiment proceeds.

Modelling is an important tool in fisheries science as it is used to predict yield capabilities for the fishery. Trophic models have recently become popular methods to examine natural and man-made ecosystems in temperate (Bering Sea: Laevastu and Larkins 1981) and tropical seas (Polovina 1984, see review by Christensen and Pauly 1993). The usefulness of trophic models to fisheries management has also been questioned recently (Hilborn and Walters 1992). On coral reefs, a large amount of trophic information is required for the application of these models. This study provides reliable dietary information for a major species in the fishery on the GBR.

Finally, due to the popularity of *P. leopardus* as a food fish and its depletion on reefs that have been heavily fished, seeding of populations of *P. leopardus* onto reefs has already been considered. If successful, such reseeding of reefs with depauperate populations of *P. leopardus* will undoubtably become very popular, especially in densely populated countries which have subsistence fisheries (e.g. Philippines). In Japan, the replacement of natural populations of *P. leopardus* with hatchery reared juveniles has been attempted. In the first attempt, one reef was reseeded with four thousand juvenile *P. leopardus,* but mortality was extremely high and the recolonization was unsuccessful (S. Masuma pers. comm.). Knowledge of the feeding habits and the composition of prey of different size classes of *P. leopardus* could be used to assess potential reefs for reseeding trials. The suitability of the reef can be examined by measuring abundances of potential prey for the particular size of *P. leopardus,* and information about prey abundance may in turn determine the appropriate size for their release.

9.5 Conclusions

The importance of large predators and predation on coral reefs cannot be understood until extensive descriptive information on the diet of the predators is available. Coupled with information on abundances of predators and prey, this information can be used to determine an appropriate biological significance to test the impact of large predators over appropriate time scales. In the literature to date, many of the experiments designed to test the impact of predation have proceeded without knowledge of the predators involved, or their diet and feeding rates. The absence of such information makes effective design of experiments and interpretations of results very difficult.

On the GBR, a lack of knowledge about the predators has hampered our understanding of the influence of predation on coral reefs (Jones 1991). This lack of descriptive information about predators on coral reefs is probably mostly an historical accident. Due to the advent of diving, coral reef fish ecology became popular around the time descriptive studies went out of vogue in favour of experimental work. Determining the importance of predation in structuring communities of coral reef fishes is a major challenge yet to be met by coral reef fish ecologists. Descriptive studies of diet and feeding have an important contribution to make to this field.

10.0 BIBLIOGRAPHY

Alcala, A. C., & Russ, G. R. (1990). A direct test of the effect of protective management on abundance and yield of tropical marine resources. *J. Cons., Cans. Int. Explor. Mer.*, **46**, 40-47.

Aldenhoven, J. M. (1986). Local variation in mortality rates and life-expectancy estimates of the coral reef fish Centropyge bicolor (Pisces: Pomacanthidae). *Mar. Biol.*, **92**, 237-244.

Allen, G. H., & Aron, W. (1958). Food of salamonid fishes of western north Pacific Ocean. *Spec. scient. Rep. U. S. Fish Wildl. Serv. Fisheries*, **237**, 1-11.

Allen, G. R. (1975). "Damselfishes of the South Seas." Neptune City, New Jersey: TFH Publications. 240 pp.

Austin, H., & Austin, S. (1971). The feeding habits of some juvenile marine fishes from the mangroves in Western Puerto Rico. *Carib. J. Sci.*, **11**(3-4), 171-178.

Ayling, A. M., & Ayling, A. L. (1986). "A biological survey of selected reefs in the Capricorn section of the Great Barrier Reef Maine Park." Unpubl. report to GBRMPA.

Ayling, A. M., & Ayling, A. L. (1992). "Effects of fishing pilot study: visual surveys on Cairns section closed reefs that will be opened under the new zoning plan." Unpubl. report to GBRMPA. 48 pp.

Ayling, A. M., Ayling, A. L., & Mapstone, B. D. (1991). Possible effects from protection by fishing pressure on recruitment rates of the coral trout (Plectropomus leopardus: Serranidae). In Proceedings of the 1991 Recruitment Workshop of the Australian Society for Fish Biology.

Baker, J. R. (1958). "Principles of biological microtechnique." London: Methuen.

Bandaranaike, S., & Hampton, J. (1979). "Commercial fisheries of the north Queensland region." In An account of the previous knowledge and use of the Great Barrier Reef from Lizard Island to Bowen. Report to GBRMPA and the GBRMPA Committee, pp. 75-86.

Beddington, J. R. (1984). The responses of multispecies systems to perturbations. In R. M. May (eds.), "Exploitation of marine communities", 209-225. Berlin: Springer-Verlag.

Beddington, J. R., & May, R. M. (1982). The harvesting of interacting species in a natural ecosystem. *Sci. Am.*, **247**, 42-49.

Beinssen, K. (1989). "Results of the Boult Reef replenishment area study." Unpubl. report to GBRMPA.

Blaber, S. J. M., Milton, D. A., Rawlinson, N. J. F., Tiroba, G., & Nichols, P. V. (1990). Diets of lagoon fishes of the Solomon Islands: Predators of tuna fishes and trophic effects of baitfishing on the subsistence fishery. *Fish. Res.*, **8**, 263-286.

Blamey, R. K., & Hundloe, T. J. (1991). "Characteristics of recreational boat fishing in the Great Barrier Reef region." Unpubl. report to GBRMPA.

Bohnsack, J. A. (1982). Effects of piscivorous predator removal on coral reef fish community structure. In G. M. Caillet & C. A. Simenstad (eds.), Gutshop '81: Fish food habit studies., pp. 258-267. Seattle, Washington: Wash. Sea Grant Publ.

Bohnsack, J. A. (1990). "The potential of marine fishery reserves for reef fish management." The US South Atlantic NOAA Technical Memorandum NMFS-SEFC 261, 40 PP.

Booth, D. J. (1995). Juvenile groups in a coral-reef damselfish: density-dependent effects on individual fitness and population demography. *Ecology*, **76**(1), 91-106.

Bowman, R. E. (1986). Effect of regurgitation on stomach contents of marine fishes. In C. A. Simenstad & G. M. Caillet (eds.), Contemporary studies on fish feeding: the proceedings of gutshop 1984, , The Netherlands: Junk Publ.

Brown, I. W. (1991). "Estimation of changes in instantaneous mortality rates in fish populations following a regional zoning policy change from protected (MNP-B) to open (General Use B): Phase I." Unpubl. project proposal to GBRMPA.

Brown, I. W. (1994). "Growth, reproduction and recruitment of Great Barrier Reef food fish stocks." Fisheries Research and Development Corporation Project No. 90/18.154 pp. Southern Fisheries Centre Queensland Department of Primary Industries.

Brown, I. W., Squire, L., & Mikula, L. (1992). "Effect of zoning changes on the fish populations of unexplotted reefs. Stage I: pre-opening assessment." Draft interim report to the Great Barrier Reef Marine Park Authority. 27 pp.

Caddy, J. F., & Sharp, G. D. (1980). "An ecological framework for marine fishery investigations." FAO Fisheries Technical Paper No 283.

Caley, M. J. (1991) "Mechanisms of coexistence in communities of coral-reef fishes." Dissertation, The University of Sydney, Sydney.

Caley, M. J. (1993). Predation, recruitment and the dynamics of communities of coral-reef fishes. *Mar. Biol.*, **117**, 33-43.

Chave, E. H. (1978). General ecology of six species of Hawaiian cardinal fishes. *Pac. Sci.*, **32**, 245-270.

Choat, J. H. (1968). Feeding habits of and distribution of Plectropomus maculatus (Serranidae) at Heron Island. *Proc. R. Soc. Qd*, **80**(2), 13-18.

Choat, J. H. (1982). Fish feeding and the structure of benthic communities in temperate waters. *Ann. Rev. Ecol. Syst.*, **13**, 423-449.

Choat, J. H. (1991). The biology of herbivorous fishes on coral reefs. In P. F. Sale (ed.), "The ecology of fishes on coral reefs", 120-155. San Diego: Academic Press.

Christensen, V., & Pauly, D. (Ed.) (1993). "Trophic models of aquatic ecosystems.". ICLARM. Manila 390 pp.

Coates, D. (1980). The discrimination of and reaction towards predatory and non-predatory species of fish by humbug damselfish, Dascyllus aruanus (Pisces, Pomacentridae). *Z. Tierpsychol.*, **52**, 347-354.

Cohen, D. M. (1970). How many recent fishes are there? *Proc. California Acad. Sci.*, **38**, 341-346.

Cohen, J. (1988). "Statistical power analysis for the behavioural sciences." (2nd ed.). Hillsdale, N.J.: Lawrence Erlbaum Associates.

Connell, J. H. (1972). Community interactions on marine rocky intertidal shores. *Ann. Rev. Ecol. Syst.*, **3**, 169-192.

Connell, J. H. (1975). Some mechanisms producting structure in natural communities: a model and evidence from field experiments. In M. L. Cody & J. M. Diamond (eds.), "Ecology and evolution of communities", 460-490. Cambridge, Massachusetts: Belknap-Harvard University Press.

Connell, S. D., & Kingsford, M. J. (1992). Interactions between piscivores and their prey. In Proc. 7th Int. Coral Reef Sym., 2, pp. 952. Guam: University of Guam, Marine Lab.

Craik, G. J. S. (1981). Underwater survey of coral trout Plectropomus leopardus (Serranidae) populations in the Capricornia Section of the Great Barrier Reef Marine Park. In Proc. 2nd Int. Cor. Reef Symp., 1, pp. 54-58. Manilla.

Crowder, L. B., & Cooper, W. E. (1979). Structural complexity and fish-prey interactions in ponds: a point of view. In D. L. Johnson & R. A. Stein (eds.), "Response of fish to habitat structure in standing water", 2-10. : North Central Division American Fisheries Society.

Curio, E. (1976). "The ethnology of predation.". Berlin: Springer-Verlag.

Davies, C. (1995) "Patterns of movement of three species of coral reef fish on the Great Barrier Reef." Dissertation, James Cook University of North Queensland.

Day, R. W., & Quinn, G. P. (1989). Comparisons of treatments after an Analysis of Variance in ecology. *Ecol. Monogr.*, **59**, 433-463.

Dayton, P. K. (1984). Processes structuring some marine communities: are they general? In D. R. Strong, D. Simberloff, L. G. Abele, & A. B. Thistle (eds.), "Ecological communities: conceptual issues and the evidence", 181-197. Princeton, New Jersey: Princeton University Press.

DeAngelis, D. L., & Gross, L. J. (1992). Individual-Based Models and Approaches in Ecology. In Proceedings of a Symposium/ Workshop, 1990, , pp. 529. Knoxville Tennessee: Chapman & Hall.

Desselle, W. J., Poirrier, M. A., Rogers, J. S., & Cashner, R. C. (1978). A discriminate function analysis of Sunfish (Lepomis) food habits and feeding niche segregation in the Lake Pontchartrain, Louisiana Estuary. *Trans. Am. Fish Soc.*, **107**(5), 713-719.

Diamant, A., & Shpigel, M. (1985). Interspecific feeding associations of groupers (Teleostei: Serranidae) with octopuses and moray eels in the Gulf of Eilat (Aqaba). *Env. Biol. Fishes*, **13**(2), 153-159.

Dill, L. M. (1983). Adaptive flexibility in the foraging behavior of fishes. *Can. J. Fish. Aquat. Sci.*, **40**, 398-408.

Doherty, P., & Fowler, T. (1994). An empirical test of recruitment limitation in a coral reef fish. *Science*, **263**, 935-939.

Doherty, P. J. (1991). Spatial and temporal patterns in recruitment. In P. F. Sale (ed.), "The ecology of fishes on coral reefs", 261-293. San Diego: Academic Press.

Doherty, P. J., Fowler, A. J., Samoilys, M. A., & Harris, D. A. (1994). Monitoring the replenishment of coral trout (Pisces: Serranidae) populations. *Bull. Mar. Sci.*, **54**(1), 343-355.

Doherty, P. J., & Sale, P. F. (1985). Predation on juvenile coral reef fishes: an exclusion experiment. *Coral Reefs*, **4**, 225-234.

Doherty, P. J., & Williams, D. M. (1988). The replenishment of coral reef fish populations. *Oceanogr. Mar. Biol. Ann. Rev.*, **26**, 487-551.

Eckert, G. J. (1985) "Population studies of labrid fishes on the Southern Great Barrier Reef." Dissertation, University of Sydney, Sydney, Australia.

Eckert, G. J. (1987). Estimates of adult and juvenile mortality for labrid fishes at One Tree Reef, Great Barrier Reef. *Mar. Biol.*, **95**, 167-171.

Elliot, J. M. (1991). Rates of gastric evacuation in piscivorous brown trout Salmo trutta. *Freshwater Biol.*, **25**, 297-305.

Elliott, J. M., & Persson, L. (1978). The estimation of daily rates of food consumption for fish. *J. Ani. Ecol.*, **47**, 977-991.

Fairweather, P. G. (1990). Is predation capable of interacting with other community processes on rocky reefs? *Aust. J. Ecol.*, **15**, 453-464.

Ferreira, B. P. (1993) "Age, growth, reproduction and population biology of Plectropomus spp (Epinephelinae: Serranidae) on the Great Barrier Reef, Australia." Dissertation, James Cook University of North Queensland.

Ferreira, B. P., & Russ, G. R. (1994). Age validation and estimation of growth rate of the coral trout, Plectropomus leopardus, (Lacepede 1802) from Lizard Island, Northern Great Barrier Reef. *Fish. Bull*, **92**, 46-57.

Ferreira, B. P., & Russ, G. R. (1995). Population structure of the coral trout Plectropomus leopardus on fished and unfished reefs off Townsville, Central Great Barrier Reef, Australia. *Fish. Bull.*, **93**, 629-642.

Forrester, G. E. (1990). Factors influencing the juvenile demography of a coral reef fish. *Ecology*, **71**(5), 1666-1681.

Fortunatova, K. R., & Popova, O. A. (1972). "The food and food interrelationships of predatory fish in the Volga delta.". Moscow: Nauka Press.

Fowler, A. J. (1989). Description, interpretation and use of the microstructure of otoliths from juvenile butterflyfishes (Family Chaetodontidae). *Mar. Biol.*, **102**, 167-181.

Fowler, A. J. (1990). Validation of annual growth increments in the otoliths of a small, tropical coral reef fish. *Mar. Ecol. Prog. Ser.*, **64**, 25-38.

Gillen, A. L., Stein, R. A., & Carline, R. F. (1981). Predation by pellet-reared tiger muskellunge on bluegills and minnows in experimental systems. *Trans. Am. Fish. Soc.*, **110**, 199-211.

Gladstone, W. (1988). Correlates and possible costs of reproductive success in males of a haremic coral reef fish. In Proc. 6th Coral Reef Symp., 2, pp. 693-398. Australia.

Gladstone, W. (1991). Early reproduction and reduction in survivorship and lifetime reproductive success in a coral reef fish. *Env. Biol. Fishes*,

Gladstone, W., & Westoby, M. (1988). Growth and reproduction in Canthigaster valentini (Pisces, Tetradontidae): a comparison of a toxic reef fish with other reef fishes. *Env. Biol. Fish.*, **21**, 207-221.

Godfriaux, B. L. (1969). Food of a predatory demersal fish in Hauraki Gulf 1: Food and feeding habits of snapper. *N. Z. Jl mar. Freshwater Res.*, **3**, 518-44.

Goeden, G. B. (1974) "Aspects of the biology and ecology of the coral trout, Plectropomus leopardus (Lacepede) (Serranidae) at Heron Island, Great Barrier Reef." Dissertation, Univ. of Queensland.

Goeden, G. B. (1978). A monograph of the coral trout Plectropomus leopardus. *Res. Bull. Qld. Fish. Ser.*

Goeden, G. B. (1982). Intensive fishing and a 'keystone' predator species: ingredients for community instability. *Biol. Conserv.*, **22**, 273-281.

Goldman, B., & Talbot, F. H. (1976). Aspects of the ecology of coral reef fishes. In A. O. Jones & R. Endean (eds.), "Biology and geology of coral reef", 125-154. New York, USA: Academic Press.

Gordoa, A., & Macpherson, E. (1990). Food selection by a sit-and-wait predator, the monkfish, Lophius upsicephalus, off Namibia (South West Africa). *Env. Biol. Fishes*, **27**, 71-76.

Grigg, R. W., Polovina, J. J., & Atkinson, M. J. (1984). Model of a coral reef ecosystem. III. Resource limitation, community regulation, fisheries yield and resource management. *Coral Reefs*, **3**, 23-27.

Gulland, J. A. (1982). Why do fish numbers vary? *J. Theor. Biol.*, **97**, 69-75.

Haight, W. R., Parrish, J. D., & Hayes, T. A. (1993). Feeding ecology of deepwater lutjanid snappers at Penguin Bank, Hawaii. *Trans. Am. Fish. Soc.*, **122**, 328-347.

Hambright, K. D. (1991). Experimental analysis of prey selection by largemouth bass: role of predator mouth width and prey body depth. *Trans. Amer. Fish. Soc.*, **120**, 500-508.

Harmelin-Vivien, M. L., & Bouchon, C. (1976). Feeding behavior of some carnivorous fishes (Serranidae and Scorpaenidae) from Tulear (Madagascar). *Mar. Biol.*, **37**, 329-340.

Hay, D. E. (1981). Effects of capture and fixation on gut contents and body size of pacific herring larvae. *Rapp. P.-v. Reun. Cons. int. Explor. Mer.*, **178**, 395-400.

Hay, M. (1985). Spatial patterns of herbivore impact and their importance in maintaining algal species richness. In Proc. 5th Int. Coral Reef Congr., 4, pp. 29-34. Tahiti.

Helfman, G. S. (1989). Threat-sensitive predator avoidance in damselfish-trumpetfish interactions. *Behav. Ecol. Sociobiol.*, **24**, 47-58.

Hiatt, R. W., & Strasburg, D. W. (1960). Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. *Ecol. Monogr.*, **30**, 65-127.

Hilborn, R., & Walters, C. J. (1992). "Quantitative fisheries stock assessment.". New York and London: Chapman and Hall. 570 pp.

Hixon, M. A. (1991). Predation as a process structuring coral-reef fish communities. In P. F. Sale (ed), "The ecology of fishes on coral reefs", 475-508. San Diego: Academic Press.

Hixon, M. A., & Beets, J. P. (1989). Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs. *Bull. mar. Sci.*, **44**(2), 666-680.

Hixon, M. A., & Beets, J. P. (1993). Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecol. Monogr.*, **63**(1), 77-101.

Hobson, E. S. (1965). Diurnal-nocturnal activity of some inshore fishes in the Gulf of California. *Copeia*, 291-302.

Hobson, E. S. (1972). Activity of Hawaiian reef fishes during the evening and morning transitions between daylight and darkness. *Fish Bull. U.S.*, **70**, 715-740.

Hobson, E. S. (1974). Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. *Fish. Bull.*, **72**, 915-1031.

Hood, P. B., Godcharles, M. F., & Barco, R. S. (1994). Age, growth, reproduction, and the feeding ecology of black sea bass, Centropristis striata (Pisces: Serranidae), in the eastern Gulf of Mexico. *Bull. Mar. Sci.*, **54**(1), 24-37.

Hoogland, D., Morris, D., & Tinbergen, N. (1956). The spines of stickle backs (Gasterosteus and Pygosteus) as a means of defense against predators (Perca and Esox). *Behavior*, **10**, 205-236.

Hoyle, J. A., & Keast, A. (1987). The effect of prey morphology and size on handling time in a piscivore, the largemouth bass (Micropterus salmoides). *Can. J. Zool.*, **65**, 1972-1977.

Huntsman, G. R., & Waters, J. R. (1987). Development of management plans for reef fishes - Gulf of Mexico and U.S. South Atlantic. In J. J. Polovina & S. Ralston (eds.), "Tropical snappers and groupers: biology and fisheries management", 533-560. Boulder, Colorado: Westview Press Inc.

Hussain, N. A., & Abdullah, M. A. S. (1977). The length-weight relationship, spawning season and food habits of six commercial fishes in Kuwaiti waters. *Indian J. Fish.*, **24**, 181-194.

Hyslop, E. J. (1980). Stomach content analysis - a review of methods and their application. *J. Fish Biology*, **17**, 411-429.

Jaksic, F. M. (1989). Opportunism vs selectivity among carnivorous predators that eat mammalian prey: a statistical test of hypotheses. *Oikos*, **56**(3), 427-430.

Jones, G. P. (1986). Food availability affects growth in a coral reef fish. *Oecologia (Berl.)*, **70**, 136-139.

Jones, G. P. (1991). Post-recruitment processes in the ecology of coral reef fish populations: a multifactorial perspective. In P. F. Sale (ed.), "The ecology of fishes on coral reefs.", 294-328. San Diego: Academic Press.

Jones, R. S. (1982). Ecosystems, food chains and fish yields. *ICLARM Conf. Proc.*, **9**, 195-239.

Kapoor, B. G., Smith, H., & Verighina, I. A. (1975). The alimentary canal and digestion in teleosts. *Adv. mar. Biol*, **13**, 109-239.

Karplus, I., & Algom, D. (1981). Visual cues for predator face recognition by reef fishes. *Z. Tierpsychol.*, **55**, 343-364.

Kingsford, M. J. (1992). Spatial and temporal variation in predation on reef fishes by coral trout (Plectropomus leopardus, Serranidae). *Coral Reefs*, **11**, 193-198.

Koslow, J. A. (1991). The influence of fishing on reef fish of the western Carribean and Bahamas. *MS*,

Koslow, J. A., Hanley, F., & Wicklund, R. (1988). Effects of fishing on reef fish communities at Pedro Bank and Port Royal Cays, Jamaica. *Mar. Ecol. Progr. Ser.*, **43**, 210-212.

Kruse, G. H., & Dalley, E. L. (1990). Length changes in capelin, Mallotus villosus (Muller), larvae due to preservation in formalin and anhydrous alcohol. *J. Fish. Biol.*, **36**, 619-621.

Laevastu, T., & Larkins, H. A. (1981). "Marine fisheries ecosystem: its quantitative evaluation and management.". England: Farnham Surrey. 162 pp.

Langton, R. W. (1982). Diet overlap between Atlantic Cod, Gadus morhua, silver hake, Merluccius bilinearis, and fifteen other northwest Atlantic finfish. *Fish. Bull.*, **80**(4), 745-759.

Lassig, B. R. (1982) "Determinants of the structure of small-scale coral patch reef fish assemblages." Dissertation, Macquarie University.

Leis, J. M. (1987). Review of the early life history of tropical groupers (Serranidae) and snappers (Lutjanidae). In J. J. Polovina & S. Ralston (eds.), "Tropical snappers and groupers: biology and fisheries management", 189-237. Boulder, Colorado: Westview Press Inc.

Lou, D. C. (1992). Validation of annual Growth bands in the otolith of tropical parrotfishes (Scarus schelegeli Bleeker). *J. Fish Biol.*, **41**, 775-790.

Luczkovich, J. J. (1988). The role of prey detection in the selection of prey by pinfish Lagodon rhomboides (Linnaeus). *J. Exp. Mar. Biol. Ecol.*, **123**, 15-30.

Macdonald, J. S., & Green, R. H. (1983). Redundancy of variables used to describe importance of prey species in fish diets. *Can. J. Fish Aquat. Sci.*, **40**, 635-637.

Magnuson, J. J. (1969). Digestion and food consumption by skipjack tuna (Katsuwonus pelamis). *Trans. Am. Fish. Soc.*, **98**(3), 379-392.

Magurran, A. E. (1986). Individual differences in fish behaviour. In T. J. Pitcher (ed.), "The behaviour of teleost fishes", 338-365. : Croom Helm.

Main, K. L. (1985). The influence of prey identity and size on selection of prey by two marine fishes. *J. Exp. Mar. Biol. Ecol.*, **88**, 145-152.

Manly, B. F. J. (1991). "Randomization and Monte Carlo methods in Biology.". : Chapman and Hall.

Mapstone, B. D. (1988) "The determination of patterns in the abundance of Pomacentrus moluccensis Bleeker on the southern Great Barrier Reef." Dissertation, University of Sydney, Sydney.

Marcotte, B. M., & Browman, H. I. (1986). Foraging behaviour in fishes: perspectives on variance. In C. A. Simenstad & G. M. Caillet (eds.), Contemporary Studies on Fish Feeding: the Proceedings of Gutshop 1984, The Netherlands: Junk Publishers.

Martin, J. (1994) "Predation on juvenile coral-reef fish at Lizard Island, Northern Great Barrier Reef: an ecological and behavioural study." Honours Dissertation, James Cook University of North Queensland.

Masuda, H., Amaoka, K., Araga, C., Uyeno, T., & Yoshino, T. (1984). "The fishes of the Japanese archipelago.". Tokyo: Tokai Univ. Press. 437 pp. + 370 plates.

Mathur, D., & Robins, T. W. (1971). Food habits and feeding chronology of young white crappie, Pomoxis annularis Rafinesque, in Conowingo Reserve. *Trans. Am. Fish. Soc.*, **2**, 307-311.

Meekan, M. G. (1988). Settlement and mortality patterns of juvenile reef fishes at Lizard Island Northern Great Barrier Reef. In Proc. 6th Int. Coral Reef Symp., 2, pp. 779-784. .

Mehta, C., & Patel, N. (1992). StatXact. In . Cambridge: CYTEL Software Corporation.

Menzel, D. W. (1960). Utilization of food by a Bermuda reef fish, Epinephelus guttatus. *J. Cons. int. Explor. Mer*, **25**, 216-222.

Mills, E. L., Forney, I. J., & Wagner, K. J. (1987). Fish predation and its cascading effect on the Oneida food chain. In W. C. Kerfoot & A. Sih (eds.), "Predation: direct and indirect impacts on aquatic communities", 118-131. Hanover, New Hampshire: University Press of New England.

Moody, R. C., Helland, J. M., & Stein, R. A. (1983). Escape tactics used by bluegills and fathead minnows to avoid predation by tiger muskellunge. *Env. Biol. Fish.*, **8**(1), 61-65.

Morse, D. H. (1980). "Behavioral mechanisms in ecology." Cambridge: Harvard University Press. 383 pp.

Mummert, J. R., & Drenner, R. W. (1986). Effect of fish size on the filtering efficiency and selective particle ingestion of a filter-feeding clupeid. *Trans. Am. Fish. Soc.*, **115**, 522-528.

Murdoch, W. W., Avery, S., & Smyth, M. E. B. (1975). Switching in predatory fish. *Ecology*, **56**, 1094-1105.

Myers, R. F. (1991). "Micronesian Reef Fishes: a practical guide to the identification of the inshore marine fishes of the tropical and central Pacific." (2nd ed.). Barrigada, Guam: Coral Graphics. 298 pp.

Nelson, W. G., & Bonsdorff, E. (1990). Fish predation and habitat complexity: are complexity thresholds real? *J. Exp. Mar. Biol. Ecol.*, **141**, 183-194.

Norris, J. E., & Parrish, J. D. (1988). Predator-prey relationships among fishes in pristine coral reef communities. In Proc. 6th. Int. Coral Reef Symp., 2, pp. 107-113. Townsville.

Oda, D. K., & Parrish, J. D. (1981). Ecology of commercial snappers and groupers introduced to Hawaiian reefs. In Proc. 4th Int. Coral Reef Symp., 1, pp. 59-67 Manila.

Paine, R. T. (1966). Food web complexity and species diversity. *Am. Nat.*, **100**, 65-75.

Paine, R. T. (1977). Controlled manipulations in the marine intertidal zone and their contributions to ecological theory. *Spec. Publ. Acad. Nat. Sci. Philadelphia*, **12**, 245-270.

Palomares, M. L., & Pauly, D. (1989). A multiple regression model for predicting the food consumption of marine fish populations. *Aust. J. Mar. Freshwater Res.*, **40**, 259-273.

Parker, R. R. (1963). Effects of formalin on length and weight of fishes. *J. Fish. Res. Bd. Canada*, **20**(6), 1441-1455.

Parrish, J. D. (1987). The trophic biology of snappers and groupers. In J.J.Polovina & S. Ralston (eds.), "Tropical snappers and groupers: biology and fisheries management", 405-463. Boulder, Colorado: Westview Press Inc.

Parrish, J. D., Callahan, M. W., & Norris, J. E. (1985). Fish trophic relationships that structure reef communities. In Proc. Int. Coral Reef Congr., 5th, 4, pp. 73-78. .

Parrish, J. D., Norris, J. E., Callahan, M. W., Callahan, J. K., Magarifugi, E. J., & Schroeder, R. E. (1986). "Piscivory in a coral reef community." Dordrecht: Junk. 285-297

Pauly, D. (1979). "Theory and management of tropical multispecies stocks: a review with emphasis on the South East Asian demersal fisheries.". Manila, Philippines: ICLARM Studies and Reviews 1. 35pp

Peterson, C. H. (1979). Predation, competitive exclusion, and diversity in the soft-sediment communities of estuaries and lagoons. In R. J. Livingstone (eds.), "Ecological processes in coastal and marine systems", 233-264. New York: Plenum Press.

Polovina, J. J. (1984). Model of a coral reef ecosystem. Part I. The ECOPATH model and its application to French Frigate Shoals. *Coral Reefs*, **3**, 1-11.

Ponton, D., & Muller, R. (1990). Size of prey ingested by whitefish, Coregonus sp., larvae. Are Coregonus larvae gape-limited predators? *J. Fish Biol.*, **36**, 67-72.

Popova, O. A. (1967). The "predator-prey" relationship among fish. In "The biological basis of freshwater fish production", . Oxford and Edinburgh: Blackwell Scient. Publ.

Ralston, S. (1987). Mortality rates of snappers and groupers. In J. J. Polovina & S. Ralston (eds.), "Tropical snappers and groupers: biology and fisheries management", 375-404. Boulder, Dolorado: Westview Press Inc.

Randall, J. E. (1963). An analysis of the fish populations of artificial and natural reefs in the Virgin Islands. *Caribb. J. Sci.*, **3**, 31-47.

Randall, J. E. (1965). Food habits of the Nassau grouper (Epinephelus striatus). *6th meeting Assoc. Island Mar. Labs. Caribb.*, **6**, 13-16.

Randall, J. E. (1967). Food habits of reef fishes of the West Indies. *Stud. Trop. Oceanogr.*, **5**, 665-847.

Randall, J. E., & Brock, V. E. (1960). Observations on the ecology of epinephiline and lutjanid fishes of the Society Islands, with emphasis on food habits. *Trans. Am. Fish. Soc.*, **89**, 9-16.

Randall, J. E. (1987). A preliminary synopsis of the groupers (Perciformes: Serranidae: Epinephelinae) of the Indo-Pacific region. In J. J. Polovina & S. Ralston (eds.), "Tropical snappers and groupers: biology and fisheries management", 89-187. Boulder, Colorado: Westview Press Inc.

Randall, J. E., & Hoese, D. F. (1986). Revision of the groupers of the Indo-Pacific genus Plectropomus (Perciformes; Serranidae). *Indo-Pacific Fishes*, **13**, 31pp.

Randall, J. E., Allen, G. R., & Steene, R. C. (1990). "Complete diver's and fisherman's guide to fishes of the Great Barrier Reef and Coral Sea.". Bathurst: Crawford House Press. 507 pp.

Rawlinson, N. (1989). Fishing competitions as a means of data collection. *Fishbyte*, **7**(2), 22.

Reimchen, T. E. (1990). Size-structured mortality in a threespine stickleback (Gasterosteus aculeatus) - cutthroat trout (Oncorhynchus clarki) community. *Can. J. Fish Aquat. Sci.*, **47**, 1194-1205.

Reshetnikov, Y. S., Claro, R., & Silva, A. (1972). The pattern of feeding and the rate of digestion in some tropical predatory fish. *J. Ichthyol.*, **12**, 818-824.

Ringler, N. H. (1983). Variation in foraging tactics of fishes. In L. G. David, D. Noakes, G. Lindgust, G. S. Helgmum, & J. G. Ward (eds.), "Predators and prey in fishes", 159 pp. Netherlands: The Hague.

Robertson, D. R. (1988). Abundances of surgeonfishes on patch reefs in Caribbean Panama: due to settlement, or post-settlement events? *Mar. Biol.*, **97**, 495-501.

Robertson, D. R. (1991). The role of adult biology in the timing of spawning of tropical reef fishes. In P. F. Sale (ed.), "The ecology of fishes on coral reefs.", 356-386. San Diego: Academic Press.

Robertson, D. R., & Sheldon, J. M. (1979). Competitive interactions and the availability of sleeping sites for a diurnal coral reef fish. *J. exp. mar. Biol. Ecol.*, **40**, 285-298.

Rose, G. A., & Leggett, W. C. (1990). The importance of scale to predator-prey spatial correlations: an example of Atlantic fishes. *Ecology*, **71**(1), 33-43.

Russ, G. R. (1985). Effects of protective management on coral reef fishes in the central Philippines. In Proc. 5th Int. Coral Reef Congr., 4, pp. 219-224. .

Russ, G. R. (1991). Coral reef fisheries: effects and yield. In P. F. Sale (ed.), "The ecology of fishes on coral reefs", 601-636. San Diego: Academic Press.

Sainsbury, K. J. (1986). Estimation of food consumption from field observations of fish feeding cycles. *J. Fish Biol.*, **29**, 23-36.

Sainsbury, K. J., & Jones, G. B. (MS). Daily food consumption of Nemipterus furcosus (Pisces: Nemipteridae) from the North West Shelf of Australia.

Sale, P. F. (1977). Maintenance of high diversity in coral reef fish communities. *Am. Nat.*, **111**(978), 337-359.

Sale, P. F. (1980). The ecology of fishes on coral reefs. *Oceanogr. Mar. Biol.*

Ann. Rev. **18**, 367-421.

Sale, P. F., & Ferrell, D. J. (1988). Early survivorship of juvenile coral reef fishes. *Coral Reefs*, **7**, 117-124.

Sale, P. F. (1991). "The Ecology of Fishes on Coral Reefs." (ed). San Diego: Academic Press. pp. 754

Salini, J. P., Blaber, S. J. M., & Brewer, D. T. (1990). Diets of piscivorous fishes in a tropical Australian estuary, with special reference to predation on penaeid prawns. *Mar. Biol.*, **105**, 363-374.

Samoilys, M. A. (1987) "Aspects of behaviour, movements and population density of Plectropomus leopardus (Lacepede) (Pisces: Serranidae) at Heron Island Reef, Southern Great Barrier Reef, Australia." Dissertation, Univ. of Queensland.

Samuel, M., Mathews, C. P., & Bazeer, A. S. (1987). Age and validation of age from otoliths for warm water fishes from the Arabian Gulf. In R. C. Summerfelt & G. E. Hall (eds.), "The age and growth of fish", 253-266. Ames: Iowa State University Press.

Sano, M., Shimizu, M., & Nose, Y. (1984). Food habits of the teleostean reef fishes in Okinawa Island, southern Japan. *Jpn. Univ. Mus., Univ. Tokyo Bull.*, **25**, 1-128.

Santos, D. J., & Jobling, M. (1991). Factors affecting gastric evacuation in cod, Gadus morhua L., fed single-meals of natural prey. *J. Fish Biol.*, **38**, 697-713.

Savino, J. F., & Stein, R. A. (1982). Predator-prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. *Trans. Am. Fish. Soc.*, **111**, 255-266.

Schael, D. M., Rudstam, L. G., & Post, J. R. (1991). Gape limitaion and prey selection in larval yellow perch (Perca flavescens), freshwater drum (Aplodinotus grunniens), and black grappie (Pomoxis nigromaculatus). *Can. J. Fish. Aquat. Sci.*, **48**, 1919-1925.

Schoener, T. W. (1970). Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology*, **51**(3), 408-418.

Shand, J. (1994) "Changes in the visual system of teleost fishes during growth and settlement: and ecological perspective." Dissertation, James Cook University of North Queensland.

Shapiro, D. Y. (1991). Intraspecific variability in social systems of coral reef fishes. In P. F. Sale (ed.), "The ecology of fishes on coral reefs", 331-355. San Diego: Academic Press.

Shpigel, M., & Fishelson, L. (1989). Habitat partitioning between species of the genus Cephalopholis (Pisces, Serranidae) across the fringing reef of the Gulf of Aqaba (Red Sea). *Mar. Ecol. Prog. Ser.*, **58**, 17-22.

Shpigel, M., & Fishelson, L. (1991). Experimental removal of piscivorous groupers of the genus Cephalopholis (Serranidae) from coral habitats in the Gulf of Aqaba (Red Sea). *Env. Biol. Fish.*, **31**, 131-138.

Shulman, M. J. (1984). Resource limitation and recruitment patterns in a coral reef fish assemblage. *J. exp. mar. Biol. Ecol.*, **74**, 85-109.

Shulman, M. J. (1985). Recruitment of coral reef fishes: effects of distribution of predators and shelter. *Ecology*, **66**(3), 1056-1066.

Shulman, M. J., & Ogden, J. C. (1987). What controls tropical reef fish populations: recruitment or benthic mortality? An example in the Caribbean reef fish Haemulon flavolineatum. *Mar. Ecol. Progr. Ser.*, **39**, 233-242.

Shulman, M. J., Ogden, J. C., Ebersole, J. P., McFarland, W. N., Miller, S. L., & Wolf, N. G. (1983). Priority effects in the recruitment of juvenile coral reef fishes. *Ecology*, **64**, 1508-1513.

Sih, A., Crowley, P., McPeek, M., Petranka, J., & Strohmeier, K. (1985). Predation, competition, and prey communities: a review of field experiments. *Ann. Rev. Ecol. Syst.*, **16**, 269-311.

Smale, M. J. (1987). Food partitioning by coastal predatory teleosts in south-eastern Cape waters of South Africa. *Est. Coastal Shelf Sci.*, **24**, 241-251.

Smith, C. L. (1978). Coral reef fish communities: a compromise view. *Env. Biol. Fish.*, **3**, 109-128.

Smith, M. M., & Heemstra, P. C. (1986). "Smiths' sea fishes.". Berlin: Springer-Verlag. 1047 pp.

Smith, R. J. F. (1992). Alarm signals in fishes. *Rev. Fish Biol. Fish.*, **2**, 33-63.

Smith, R. L., Salini, J. P., & Blaber, S. J. M. (1991). Food intake and growth in the Moses perch, Lutjanus russelli (Bleeker), with reference to predation on penaeid prawns. *J. Fish Biol.*, **38**, 897-903.

Sokal, R. R., & J., R. F. (1981). "Biometry." (2nd ed.). San Francisco: W.H. Freeman. 859 pp.

Steven, A. (1988). "An analysis of fishing activities on possible predators of the crown of thorns starfish (Acanthaster planci) on the Great Barrier Reef." Unpubl. report to GBRMPA (Project 329: 1986-88), 131 pp.

Strand, S. (1988). Following behaviour: Interspecific foraging associations among Gulf of California reef fishes. *Copeia*, **2**, 351-357.

Sweatman, H., & Robertson, D. R. (1994). Grazing halos and predation on juvenile Caribbean surgeonfishes. *Mar. Ecol. Prog. Ser.*, **111**, 1-6.

Sweatman, H. P. A. (1984). A field study of the predatory behaviour and feeding rate of a piscivorous coral reef fish, the lizardfish Synodus englemani. *Copeia*, **84**, 187-193.

Sweatman, H. P. A. (1985). The influence of adults of some coral reef fishes on larval recruitment. *Ecol. Monogr.*, **55**(4), 469-485.

Talbot, F. H., Russell, B. C., & Anderson, G. R. V. (1978). Coral reef fish communities: Unstable, high-diversity systems? *Ecol. Monogr.*, **48**, 425-440.

Thompson, R., & Munro, J. L. (1983). The biology, ecology and bionomics of the hinds and groupers, Serranidae. *ICLARM Stud. Rev.*, **7**, 59-81.

Thresher, R. E. (1983a). Environmental correlates of the distribution of planktivorous fishes in the One Tree Reef Lagoon. *Mar. Ecol. Progr. Ser.*, **10**, 137-145.

Thresher, R. E. (1983b). Habitat effects on reproductive success in a coral reef fish, Acanthochromis polyacanthus (Pomacentridae). *Ecology*, **64**, 1184-1199.

Thresher, R. E. (1984). "Reproduction in reef fishes.". Neptune City, New Jersey: TFH Publications Pty Ltd. 399 pp.

Trainor, N. (1991). Commercial line fishing. *The Queensland Fisherman*, March, 17-24.

Tseitlin, V. B. (1980). Duration of gastric digestion in fishes. *Mar. Ecol. Prog. Ser.*, **2**, 277-280.

Tulley, J. J., & Huntingford, F. A. (1987). Age, experience and the development of adaptive variation in anti-predator responses in three-spined sticklebacks (Gasterosteus aculeatus). *Ethnology*, **75**, 285-290.

Underwood, A. J. (1981). Techniques of analysis of variance in experimental marine biology and ecology. *Oceanogr. Mar. Biol. Ann. Rev.*, **19**, 513-605.

Ursin, E. (1973). On the prey size preferences of cod and dab. *Meddr. Danm. Fisk.-og Havunders*, **7**, 85-98.

Victor, B. C. (1991). Settlement strategies and biogeography of reef fishes. In P. F. Sale (eds.), "The ecology of fishes on coral reefs.", 231-260. San Diego: Academic Press.

Wainwright, P. C. (1988). Morphology and ecology: functional basis of feeding constraints in Caribbean Labrid fishes. *Ecology*, **69**(3), 635-645.

Wallace, R. K. (1981). An assessment of diet overlap indexes. *Trans. Am. Fish. Soc.*, **110**, 72-76.

Walters, C., & Sainsbury, K. (1990). "Design of a large scale experiment for measuring effects of fishing on the Great Barrier Reef." Unpubl. report to GBRMPA, 47 pp.

Warner, R. R. (1991). The use of phenotypic plasticity in coral reef fishes as tests of theory in evolutionary ecology. In P. F. Sale (ed.), "The ecology of fishes on coral reefs", 387-400. San Diego: Academic Press.

Webb, P. W. (1986). Effect of body form and response threshold on the vulnerability of four species of teleost prey attacked by largemouth bass (Micropterus salmoides). *Can. J. Fish. Aquat. Sci.*, **43**, 763-771.

Werner, E. E. (1974). The fish size, prey size, handling time relation in several sunfishes and some implications. *J. Fish. Res. Board Can.*, **31**, 1531-1536.

Werner, E. E. (1977). Species packing and niche complementarity in three sunfishes. *Am. Nat.*, **111**, 553-578.

Werner, E. E., & Gilliam, J. F. (1984). The ontogenetic niche and species interactions in size-structured populations. *Ann. Rev. Ecol. Sys.*, **15**, 393-425.

Werner, E. E., Gilliam, J. F., Hall, D. J., & Mittelbach, G. G. (1983). An experimental test of the effect of predation risk on habitat use in fish. *Ecology*, **64**, 1540-1548.

Williams, D. M. (1979) "Factors influencing the distribution and abundance of pomacentrids (Pisces: Pomacentridae) on small patch reefs in the One Tree Reef Lagoon (Great Barrier Reef)." Dissertation, Univ. of Sydney.

Williams, D. M. (1982). Patterns in the distribution of fish communities across the Central Great Barrier Reef. *Coral Reefs*, **1**, 35-43.

Williams, D. M. (1983). Longitudinal and latitudinal variation in the structure of reef fish communities. In J. T. Baker, R. M. Carter, P. W. Sammarco, & K. P. Stark (eds.), Proceedings Inaugural Great Barrier Reef Conference, , Townsville, Australia: James Cook Univ. Press.

Williams, D. M. (1991). Patterns and processes in the distribution of coral reef fishes. In P. F. Sale (ed.), "The ecology of fishes on coral reefs", 437-474. San Diego: Academic Press.

Williams, D. M., & Hatcher, A. I. (1983). Structure of fish communities on outer slopes of inshore, mid-shelf and outer shelf reefs of the Great Barrier Reef. *Mar. Ecol. Progr. Ser.*, **10**, 239-250.

Williams, D. M., & Russ, G. R. (1994). "Review of data on fishes of commercial and recreational fishing interest on the Great Barrier Reef." Research Publication No.33. Great Barrier Reef Marine Park Authority. 103 pp.

Wilson, W. H. (1991). Competition and predation in marine soft-sediment communities. *Ann. Rev. Ecol. Syst.*, **21**, 221-241.

Windell, J. T., & Bowen, S. H. (1978). Methods for study of fish diets based on analysis of stomach contents. In T. Bagenal (ed.), "Methods for assessment of fish production in fresh waters", 219-226. Oxford: Blackwell Scientific Publications.

Winemiller, K. O. (1989). Ontogenetic diet shifts and resource partitioning among piscivorous fishes in the Venezuelam ilanos. *Env. Biol. Fishes*, **26**, 177-199.

Winer, B. J. (1971). "Statistical Principles in Experimental Design.". Tokyo, Japan: McGraw-Hill Kogakusha.

Winsor, L. (1994). Tissue processing. In A. E. Woods & R. C. Ellis (eds.), "Laboratory histopathology - a complete reference", 42 pp. London: Churchill-Livingstone.

Wyatt, J. R. (1983). The biology, ecology and bionomics of the squirrelfishes, Holocentridae. *ICLARM Stud. Rev.*, **7**, 50-58.

Zaret, T. M. (1980). "Predation and Freshwater Communities." New Haven: Yale University Press,.