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Interactions between Piscivorous Coral Reef Fishes and their Prey

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Abstract

Predation appears to play an important role in the regulation of populations and communities of coral reef fish. Interactions between piscivorous coral reef fish and their prey have rarely been studied, however. The aim of this thesis was to examine how piscivorous coral reef fish respond to fluctuations in the abundance of their prey and to use this information to predict their impact on prey populations. In the first part of this thesis a broad suite of piscivorous species at Lizard Island on the Great Barrier Reef were studied, while in the second part I concentrated on the influence of prey abundance on the ecology of two common piscivores, the rock-cods, *Cephalopholis cyanostigma* and *C. boenak* (Serranidae).

The distribution, abundance and community structure of piscivorous fish at Lizard Island was examined initially. Central to this was the trial of a new baited census technique used to bring cryptic species into view. Traditional census methods (strip transects) were found to underestimate the abundance of cryptic piscivores by approximately 50%. In contrast, the baited technique accounted for approximately 90% of cryptic fish. Strip transects were found to be more appropriate for conspicuous, mobile species, however, as the baited method attracted mobile fish from an unknown area. By combining the baited method for cryptic species with the transect method for mobile species a relatively accurate picture of the piscivorous fish community at Lizard Island was obtained. Abundance of piscivores varied at both a large scale (between different zones of exposure kilometres apart) and a local scale (between sites hundreds of metres apart). This variation may have implications for the impact of piscivores on prey.

The abundance of piscivores and their prey was then monitored over an 18 month period in two different habitats, patch and contiguous reef. This allowed two hypotheses to be examined: (1) that piscivores would aggregate in areas of high prey abundance and (2) this aggregation would cause density-dependent mortality of prey. The abundance of both piscivores and prey was consistently higher on patch reefs than on contiguous reef. There were also strong positive relationships between prey and piscivore abundance within sites throughout the study. Mortality of prey was density-dependent over the 6 month period it was monitored. Mortality of prey was positively related to piscivore abundance but was also positively related to the ratio of prey to piscivores. This suggested piscivore abundance only partly explained patterns of prey mortality. Recruitment patterns did not explain the relationship between prey and piscivore abundance, suggesting post-settlement processes were responsible. Tagging of *Cephalopholis cyanostigma* and *C. boenak* was used to examine the contribution of movement. Movement between sites or habitats was rare for both species, however, suggesting it did not explain large-scale patterns of abundance. In contrast, at a local scale territory size was inversely proportional to prey density and a change in current direction caused a corresponding small-scale movement of both piscivores and prey. Hence, although the mechanisms could not be fully determined, the abundance of piscivores and their prey appeared to be strongly linked.

At the same sites and times as above the influence of prey abundance on the dietary composition, prey selection and feeding rates of *Cephalopholis cyanostigma* and *C. boenak* was examined. Gut contents were collected mainly from regurgitated samples, to allow the same populations to be monitored over time. Both species were found to be over 90% piscivorous with prey fish of the families Apogonidae, Pomacentridae and Clupeidae dominating the diet. The interacting effect of fluctuations in prey abundance and patterns of prey selection caused diet to vary both temporally and spatially. Mid-water schooling prey belonging to the family Clupeidae were selected for over other families. In the absence of these prey apogonids were selected for over more reef-associated pomacentrids. Feeding rates of both rock-cods were much higher in summer than winter and in summer they concentrated on small, recruit sized fish. There was little variation in feeding rates between patch and contiguous reef, however, despite apparent differences in prey abundance. The combination of high densities, high feeding rates and selection for certain sizes and types of prey suggested the two rock-cod species were having a considerable impact on populations and communities of their prey.

The life history characteristics and population structure of *Cephalopholis cyanostigma* and *C. boenak* on patch and contiguous reef were also examined over a 2 year period. Knowledge of these patterns can provide indirect evidence of different processes limiting populations and the mechanisms that determine these effects. Tetracycline injection of tagged fish allowed for validation of annual increments in the otoliths of both species. Estimates of growth rate could therefore be obtained from both size-at-age data and recaptured tagged fish. Both species were relatively long-lived (32 years for *C. cyanostigma* and 16 years for *C. boenak*) and slow growing. Size-at-age curves of both species were almost identical on the two reef types, although growth of tagged *C. boenak* was slightly higher on patch reefs. Growth of tagged *C. cyanostigma* was significantly higher in summer than spring but this may have been due to either water temperature or prey abundance. Age and size-at-maturity also showed no difference between patch and contiguous reef. Age and size structures were similar on the two reef types for *C. cyanostigma* but there were more small / young *C. boenak* on patch reefs. *C. boenak* may undergo an ontogenetic shift from patch to contiguous reef. Based on longevity, mortality of both species was also similar on the two reef types. Sex ratios of *C. boenak* indicated they were monogamous on patch reefs but polygamous on contiguous reef. This may have been due to increased predation pressure on patch reefs. Overall, despite apparent differences in prey abundance there were few differences in the life history and population structure of the rock-cods on patch and contiguous reef. Differences in prey abundance appeared to be compensated for by territory size and the abundance of competitors and predators of the rock-cods themselves.

The behavioural and developmental responses of *Cephalopholis boenak* to variation in prey abundance were further examined in a field experiment. Two hypotheses were tested: (1) that *C. boenak* would move from areas of low to high prey density and (2) that feeding and growth rates of *C. boenak* would be higher in areas of high prey density. Small patch reefs, which were equivalent in terms of habitat type, isolation and competitor and predator density, were used in the experiment. Over the 6 months of the experiment 31% of tagged *C. boenak* moved between patch reefs, all from reefs of low to high prey density. Feeding rates were also higher on patch reefs of higher prey to piscivore ratio. Due to few recaptures of tagged fish on reefs of low prey density, growth rates could not be compared within the experiment. Both feeding and growth rates on the experimental reefs, however, were much higher than on natural patch reefs over the same period. These patterns corresponded with much higher prey densities on experimental reefs. Hence these results suggest that growth of *C. boenak* was food-limited on natural patch reefs studied and that *C. boenak* responds both behaviourally and developmentally to variation in prey abundance.

In summary, this study provided considerable evidence that piscivorous coral reef fish are limited by the availability of prey and are therefore likely to be in competition for this resource. This food-limitation appeared to cause numerical, behavioural and developmental responses of piscivores to variation in prey abundance. These responses may also have a stabilising effect on prey populations and communities. Predation by piscivorous fish is therefore likely to have been at least partly responsible for recent observations of density-dependent mortality of coral reef fish. This study has therefore supplied further support for the regulatory role of predation in coral reef fish communities.

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Chapter 1

General Introduction

Predation as a Structuring Process

Understanding how various factors influence population size and the structure of ecological communities is a central goal of ecologists. A wide range of biotic and abiotic factors such as predation, competition, parasitism, disease, climate and resource supply may cause changes in population size and community structure (Hunter & Price 1992). One of the most common approaches to investigating the control of community structure has been the analysis of trophic interactions (Hairston et al. 1960, Menge & Sutherland 1976, 1987, Fretwell 1977, 1987, McQueen et al. 1989, Menge 1992). The top-down view, first introduced by Hairston et al. (1960), suggests that predators at the top of food chains are prey-limited, while herbivores (prey) are predator-limited and plants are resource-limited. In contrast, the bottom-up view suggests that community structure is primarily driven by the supply of nutrients (eg. Hall et al. 1970; White 1978). As a consequence organisms at each trophic level are thought to be food-limited, for example, plants are limited by the supply of nutrients, herbivores by the supply of plants and predators by the abundance of herbivores. These two models were originally seen as alternatives, although emphasis has now shifted to examine how top-down and bottom-up forces interact and under what conditions one force dominates over the other (Hunter & Price 1992, Menge 1992, Power 1992).

Regardless of whether top-down or bottom-up forces predominate or whether they interact, predation plays an important role in trophic interactions. The most direct impact of predators is by the consumption of prey individuals. This may have a stabilising effect on prey populations (Hassell & May 1974, Murdoch & Oaten 1975), reduce prey populations to a size below the carrying capacity of the environment (Hairston et al. 1960, Menge & Sutherland 1976) or may lead to the local extinction of prey populations (Murdoch & Bence 1987). Consequently, the structure and species diversity of prey communities may also be effected (Paine 1966, Connell 1975, Menge & Sutherland 1976). Predators are also known to have a range of indirect affects on prey morphology, physiology, chemistry, life history and behaviour (Sih 1987). For example, high levels of predation pressure may effect habitat selection, feeding rates, growth and reproductive output of prey individuals (Milinski 1986, Sih 1987, Holbrook & Schmitt 1988).

One of the most common and powerful ways to investigate the role of predation has been through manipulation of predator densities (for review see (Sih et al. 1985)). This approach has been widely used in terrestrial (Joern 1992, Belovsky & Slade 1993), freshwater (Zaret 1980, Kerfoot & Sih 1987, Forrester 1994) and rocky intertidal (Paine 1966, Connell 1975, Menge 1976) environments. Although this technique has greatly enhanced our knowledge, a full understanding of the role of predation can only be achieved when the results of these experiments are combined with information on the predators responsible for the effects.

Predator Responses

Studying the ecology of predators not only augments the results of experiments in which predator abundance is manipulated, but is also an alternative method for assessing the role of predation. Given that traditional theory suggests predators are food-limited (Hairston et al. 1960, Menge and Sutherland 1976), predators are expected to respond to fluctuations in the density of their prey. Longer term responses include numerical (Solomon 1949) and developmental (Murdoch 1971) responses. For example, predator abundance may fluctuate as prey abundance changes or growth rates of predators may increase when higher numbers of prey are available. These responses may therefore have implications for the impact of piscivores on their prey and keep prey numbers below the carrying capacity of the environment (Hairston et al. 1960, Menge and Sutherland 1976).

Alternately or in addition, predator behaviour may respond to changes in prey abundance (Holling 1959, Hassell & May 1974). As predator life cycles are often much longer than those of prey, behavioural responses generally track fluctuations in prey density more closely and are expected to be more important in population regulation (Murdoch & Bence 1987). Behavioural responses include aggregative and functional responses. Aggregative responses refer to the common observation of predator aggregations in areas of high prey abundance (Goss-Custard 1970, Hassell & May 1974, Robles et al. 1995). This pattern is thought to be maintained by movement of predators as prey abundance fluctuates over time (Fretwell & Lucas 1970, Hassell & May 1974). Functional responses on the other hand, refer to the relationship between a predators consumption rate and the density of prey available (Holling 1959, Murdoch 1973). Functional responses generally involve a positive relationship between consumption rate and prey density, which eventually reach a plateau due to prey handling time setting an upper limit on consumption rates (Holling 1959).

The individual or combined effect of behavioural responses may have a stabilising effect on prey populations and communities (Hassell & May 1974, Murdoch & Oaten 1975). This is because predators are predicted to target high density patches of prey while low density patches receive proportionally less attention (Hassell & May 1974, Hassell 1982). Low density patches of prey therefore represent a partial refuge from predation. Theoretically, the resultant density-dependent mortality of prey should cause all patches to tend towards the same density (Fretwell & Lucas 1970, Hassell & May 1974, Murdoch & Oaten 1975). In reality, however, the situation may be more complex, due to interactions between the behavioural response of predators and other factors such as the abundance of other predators (Hassell 1978), habitat type (Lipcius & Hines 1986, Mattila 1992), and preferences for certain prey types (Downing 1981, Mattila & Bonsdorff 1998).

By combining information predator behaviour, abundance and distribution it should be possible to predict their impact on prey populations. In the same way information on prey abundance could also be used to predict the reciprocal effect of prey numbers on predator populations. These approaches have been applied to address fisheries management questions in freshwater lakes eg. (Cartwright et al. 1998, Mason et al. 1998) but have rarely been extended to other ecosystems.

Predation in Coral Reef Fish Communities

The importance of predation as a process structuring coral reef fish communities received little attention until recently (Hixon 1991). Some early workers (eg. Talbot et al. 1978) gave consideration to the role of predation in community regulation, however, attention was diverted to the competition (Smith & Tyler 1972, Smith 1978) and recruitment-limitation hypotheses (Doherty 1981, Victor 1983, 1986, Doherty & Fowler 1994). Consensus now appears to have been reached on a more pluralistic approach which sees recruitment, competition and predation as processes which may interact to form patterns of adult abundance (Jones 1991, Caley et al. 1996, Beukers & Jones 1997, Connell 1998b, Steele et al. 1998). However, research into how these different processes interact and whether or not predation has a general role in community regulation is still at an early stage.

The inclusion of predation in models of population and community regulation has seen an explosion of studies into the role of predation in coral reef fish communities (Doherty & Sale 1985, Caley 1993, Hixon & Beets 1993, Carr & Hixon 1995, Connell 1996, 1997, 1998c, Beets 1997, Beukers & Jones 1997, Eggleston et al. 1997, Hixon & Carr 1997, Steele et al. 1998). All of these workers manipulated predator densities as a means to examining the effect of predation on prey communities. Along with reduced prey abundance in the presence of predators they observed a range of other effects including reduced species diversity (Caley 1993; Beets 1997; Eggleston 1997) variation in mortality between species (Doherty and Sale 1985; Carr and Hixon 1995; Steele et al. 1998), mediation of mortality by habitat structure (Hixon and Beets 1993; Beukers and Jones 1997; Eggleston 1997) and effects of prey density on mortality rates (Hixon and Carr 1997, Connell 1998b). All of these studies, however, would have benefited from additional information on the predators responsible for the observed effects. Most studies on coral reef fish have focussed on planktivorous and herbivorous species (Doherty & Williams 1988, Jones 1991). In contrast, piscivorous species have received relatively little attention (Jones 1991).

The impact of piscivorous coral reef fishes on prey will depend upon their abundance, distribution, movement, diet and consumption rates. Of these, the distribution and abundance of piscivorous coral reef fish has probably been best documented. Piscivorous fish are known to make up large proportions of the biomass of coral reef fish communities (Goldman & Talbot 1976, Parrish et al. 1986), and may show considerable spatial variation in abundance (Williams & Hatcher 1983, Newman et al. 1997, Connell & Kingsford 1998). One potential problem with the description of these patterns, however, is that many piscivorous reef fish are cryptic by nature (Randall et al. 1990), making them difficult to census accurately with standard visual techniques (Brock 1954, Brock 1982). The use of destructive censuses (eg. Williams & Hatcher 1983) may solve this problem somewhat, although this method causes considerable disturbance to the community in question. The development of accurate, non destructive census techniques is therefore needed to assess the contribution of cryptic species to patterns of abundance of piscivorous coral reef fishes.

Little is known of the processes controlling the distribution and abundance of piscivorous fish. If, as traditional theory suggests, piscivores are limited by the availability of food (Menge and Sutherland 1976), they may be expected to aggregate in areas of high prey abundance. Piscivores do appear to concentrate in areas of high structural complexity as these provide shelter sites (Hobson 1965, Huntsman & Waters 1987, Connell & Kingsford 1998) and this distribution may also be linked to the high density of prey fish which inhabit similar areas (Bell & Galzin 1984, Roberts & Ormond 1987). Of the few researchers who have investigated the relationship between prey and piscivore density, however, 2 found a positive relationship (Kock 1982, Beukers 1996) while 3 found a negative relationship (Thresher 1983, Hixon & Beets 1989, 1993). Hence further work is needed to establish if there any general principles regarding the effect of prey abundance on the abundance of piscivorous coral reef fish.

Piscivorous reef fish rarely recruit in high numbers (Shpigel & Fishelson 1991a, Beets & Hixon 1994, Lewis 1997) and new recruits are often cryptic (Eggleston 1995). As a result, only one study (Meekan 1988) has monitored the mortality of a newly recruited piscivorous reef fish. Therefore, little is known of the contribution of recruitment and early life history to patterns of adult abundance.

The role of movement in the organisation of reef fish communities has been emphasised recently (Lewis 1997, Ault & Johnson 1998), and it is possible piscivorous fish may move in response to fluctuations in prey abundance. Indeed aggregative responses of predators have been suggested as a potential mechanism explaining recent observations of density-dependent mortality of coral reef fish (Forrester 1995, Beukers & Jones 1997, Hixon & Carr 1997). Ontogenetic movement has been documented for several species (Eggleston 1995, Light & Jones 1997) and recently ultrasonic telemetry on one species of serranid, *Plectropomus leopardus*, has provided much useful information on movement of adult fish (Zeller 1997a, 1998, Zeller & Russ 1998). However, these patterns of movement have not been related to variables such as prey abundance.

The diet of piscivorous fish received considerable attention early in the study of coral reefs (eg. Hiatt & Strasburg 1960, Randall & Brock 1960, Randall 1967) but again was largely neglected until recently (eg. Shpigel & Fishelson 1989, Kingsford 1992, St John 1995, Connell 1998a). Many of the early studies focused on a large number of potentially piscivorous species, which although very useful for identifying piscivores, meant sample sizes were generally quite low for individual species. Gut contents of piscivorous coral reef fish are often empty or contain few items. In addition prey are often highly digested, making them difficult to identify. As a result large sample sizes are required to make detailed descriptions of the diet of coral reef piscivores. Two recent studies (Kingsford 1992; St John 1995) have provided a comprehensive examination of the diet of one species, *Plectropomus leopardus*. Unfortunately, the removal of large numbers of the study species makes it difficult to conduct a long term monitoring program.

Coral reef piscivores are considered to be general, opportunistic predators which consume the most common prey available (Harmelin-Vivien & Bouchon 1976, Parrish 1987). Only one study, however, has monitored piscivore diet and prey composition at the same time and place (Shpigel & Fishelson 1989). They reported that the rock-cods they studied consumed the most common prey in their territories, although results were only reported in general terms. The response of coral reef piscivores to fluctuations in prey abundance is unknown. This may be particularly important for the regulation of reef fish populations as there are often dramatic increases in prey populations during recruitment periods (Doherty 1991). Whether or not these large pulses are maintained through to the adult populations may depend largely on how predators respond. Mortality of newly recruited reef fish is often very high (Doherty & Sale 1985, Eckert 1987, Meekan 1988), however, the contribution of predation to this pattern is not clear (Hixon 1991).

Recent validation of annual increments in the otoliths of coral reef fish (Fowler 1990, 1995, Ferreira & Russ 1994, Choat & Axe 1996, Choat et al. 1996) provides several response variables for examining the effect of prey abundance on the growth of coral reef fish. Such information may allow us to determine if coral reef piscivores are prey-limited and shed further light on their role in trophic interactions. Using such an approach (Hart & Russ 1996) found that mean size and size-at-age of a herbivorous reef fish, *Acanthurus nigrofuscus*, was higher on reefs affected by crown-of-thorns starfish, presumably due to increased food supply. Although age estimates have now been validated for several piscivorous species of coral reef fish (Manooch 1987, Ferreira & Russ 1992, Sadovy et al. 1992, Ferreira & Russ 1994) the effect of prey abundance on their life history has not been investigated. Effects on growth rate, in particular, may translate into reduced mortality and increased reproductive output over the life time of an individual (Jones 1991).

The study of piscivorous reef fish is important, not only for assessing their role in community regulation, but also for their effective management. Piscivorous species are disproportionately targeted by both commercial and recreational fishers (Russ 1991) which often causes dramatic reduction of their stocks (Russ & Alcala 1989, 1996). If piscivores are prey-limited then management of their prey populations may be crucial for sustaining commercially viable stocks. Likewise, if prey populations are predator-limited then overfishing should theoretically result in increases in prey abundance and diversity. The few studies which have examined the effect of fishing on coral reefs are equivocal, however, with some finding changes in prey communities (Claro 1991) while others found no effect (Jennings et al. 1995, Jennings & Polunin 1997).

Thesis Synopsis

The main aim of this thesis was to investigate how piscivorous coral reef fish responded to fluctuations in the abundance of their prey and to use this information to predict their impact on prey populations. In the first part of the thesis I examine a broad suite of piscivorous species at Lizard Island on the Great Barrier and describe their distribution and abundance and how this relates to prey abundance. In the second part I concentrate on how prey abundance effects the ecology of two common species of piscivorous fish, the rock-cods *Cephalopholis cyanostigma* and *C. boenak*. Rock-cods of the genus *Cephalopholis* were considered ideal for study due to their piscivorous diet (Shpigel & Fishelson 1989, Martin 1994), territorial nature (Shpigel & Fishelson 1991b, Mackie 1993) and proven suitability for laboratory and field experimentation (Mackie 1993, Martin 1994, Beukers & Jones 1997).

In chapter 2, I aim to describe patterns of spatial variation in the abundance of piscivorous fish at Lizard Island. This includes testing a new baited census technique to determine if this improves the accuracy of censuses of cryptic species. This was particularly important for the planned study as the two target species, *Cephalopholis cyanostigma* and *C. boenak* were known to be cryptic (Randall et al. 1990) and difficult to census.

In the third chapter I investigate the reciprocal effect of prey abundance on predator abundance and predator abundance on prey mortality. I test 2 hypotheses: (1) that predators aggregate in areas of high prey abundance and (2) that this aggregation causes density-dependent mortality of prey. This was done by monitoring predator and prey abundance in two habitats, patch and contiguous reef, over an 18 month period. I also investigate patterns of predator and prey recruitment and the long and short term movement of *Cephalopholis cyanostigma* and *C. boenak* as potential mechanisms responsible for these patterns.

Chapter 4 is concerned with how prey abundance effects the feeding ecology of the two rock-cod species. This includes examining how patterns of spatial and temporal variation in diet and feeding rates are effected by fluctuations in prey abundance. Using this information and densities of the rock-cods from the previous 2 chapters I also assess their impact on standing stocks of prey.

The fifth chapter describes the life-history characteristics and population structures of *Cephalopholis cyanostigma* and *C. boenak* and compares them between patch and contiguous reef. I test the hypothesis that patterns will be related to differences in the abundance of prey, competitors and predators between the 2 reef types.

Finally, in chapter 6 I draw on the results of the previous chapters and describe a field experiment examining the effect of prey abundance on the movement, diet and growth of *Cephalopholis boenak*. I test the hypotheses that (1) *C. boenak* will move from areas of low to high prey density and (2) that feeding and growth rates of *C. boenak* will be higher in areas of high prey density. Small patch reefs used in the experiment were equivalent in terms of habitat type, isolation and competitor and predator density, but prey abundance varied naturally between reefs.

Chapter 2

New technique improves the accuracy of censuses of cryptic piscivorous fish on coral reefs

Abstract:

Piscivorous fish appear to play an important role in determining the structure of coral reef fish communities. Estimates of their abundance and distribution may therefore provide an insight into their impact on prey populations. Many piscivorous reef fish are cryptic, however, making them difficult to census with traditional techniques. This study tested a new visual census technique which used bait to bring cryptic species into view. Results from this census were then compared to those from a traditional survey using strip transects. The baited technique produced significantly higher density estimates for 3 of the 4 most abundant cryptic species. A subsequent patch reef experiment on 3 of these cryptic species demonstrated the baited technique accounted for 85% to 96% of fish present. Censuses without bait observed only 40 to 61% of fish present. For mobile species, on the other hand, the baited census appeared to overestimate abundance, due to movement of fish into the census area. I therefore recommend combining baited censuses of cryptic species with traditional censuses of mobile species to gain an accurate picture of piscivorous reef fish communities. Using this approach at Lizard Island on the Great Barrier Reef, the proportion of cryptic piscivores in the community was found to be almost double that which would have otherwise been observed. I also found considerable spatial variation in the abundance and distribution of piscivorous fish. These patterns would have been quite different had the survey been based on strip transects alone. Previous studies may therefore have underestimated the importance of cryptic piscivorous species in communities of coral reef fish.

Introduction:

Predation by piscivorous fish appears to play an important role in determining the structure of coral reef fish communities (Hixon 1991, Jones 1991). This may occur in several different ways. Firstly, if predation causes density-dependent mortality of newly recruited fish then large peaks in recruitment will be dampened (Caley et al. 1996). Recruitment patterns will also be altered if there is spatial or temporal variation in predation pressure (ie. the likelihood of a recruit being eaten by a predator) and thirdly, if predators selectively consume some species more than others (Caley et al. 1996). In order to measure predation pressure it is necessary to have information on a variety of factors. These include both the abundance of predators and the rates at which they are consuming fish prey. Prey consumption rates will in turn depend on the biomass of predators present, the degree of piscivory they exhibit and their ability to capture prey in the habitat present.

Despite recent increased emphasis on the role of predation in structuring coral reef fish communities (Hixon 1991, Caley 1993, Connell 1996, Hixon & Carr 1997) there is very little quantitative data on predation pressure in these areas. Even information on patterns of abundance and distribution of piscivorous fish species, seemingly the most straight-forward data to collect, is largely lacking (with some notable exceptions eg. (Williams & Hatcher 1983, Newman et al. 1997, Connell & Kingsford 1998)). In this study I aimed to examine the distribution, abundance and species composition of piscivorous fish in the waters around Lizard Island on the Great Barrier Reef, Australia. Lizard Island has been used as a site for numerous ecological studies examining the effects of recruitment and post-settlement mortality on populations of coral reef fish eg. (Aldenhoven 1986, Meekan 1988, Caley 1995, Beukers 1996). On experimental reefs, Caley (1995), found piscivore abundance and mortality of prey to be higher at Lizard Island than One Tree Island, in the southern Great Barrier Reef. It was hoped that the availability of information on predation pressure in natural communities at Lizard Island may shed some light on the results of these previous studies.

The ability to carry out accurate and precise censuses was considered essential for obtaining a meaningful picture of piscivorous fish abundance. In general, coral reef fishes can be censused either visually or destructively. Visual censuses are the most commonly used as they are rapid, cause little disturbance and can produce accurate measures of relative density (Sale & Douglas 1981). The major disadvantage of visual censuses, however, is that they tend to underestimate the abundance of small, cryptic and flighty species (Brock 1954, Brock 1982). Destructive censuses involving the use of chemicals such as rotenone (Brock 1982) or explosives (Williams & Hatcher 1983), are less favoured than visual censuses as they are non-selective, vary in effectiveness for different species, are difficult to quantify and cause considerable disturbance to the community in question (Thresher & Gunn 1986). On the other hand, destructive sampling is generally thought to be the only technique suitable for estimating the abundance of small and cryptic fish. A third alternative is to estimate density by tagging all fish in an area so that they can be individually recognised (Thresher & Gunn 1986). This can produce very accurate estimates but has rarely been used as it is an extremely labour intensive and time consuming process. Rates of tag loss and tagging induced mortality also need to be quantified, which can prove difficult in some cases.

As many piscivorous fish species, particularly of the family Serranidae, are cryptic by nature (Randall et al. 1990), the potential inability of visual censuses to accurately determine the abundance of such fish was of particular concern to this study. To this end I tested a new technique for censusing coral reef fish. This consisted of a variation on the point census method developed by Bohnsack and Bannerot (1986), whereby bait was used to attract cryptic species into view. The effectiveness of this technique was examined in two ways: firstly by comparison with the results from a survey of quadrats (divided into strip transects) at the same sites around Lizard Island and secondly by an experiment comparing the two methods on patch reefs.

Methods:

1. Identification of Piscivorous Species

A total of 48 species of fish from 8 families were included in the censuses as piscivores, (see Table 1). Determination of these species as piscivores was based on published dietary analyses. Species were then further divided into confirmed and opportunistic piscivores. Confirmed piscivores are known to include fish as a regular part of their diet while opportunistic piscivores only occasionally eat fish. If there was any possibility of two species being confused they were pooled for analysis (see Table 1). Nocturnally active piscivores (eg. Holocentridae) were not included in the study as all censuses were conducted in daylight hours. Highly active pelagic fish such as the family Carangidae were also not counted as such fish generally require specialised census techniques (Thresher & Gunn 1986).

2. Baited Point Censuses (BPC)

Baited point censuses of piscivorous fish were conducted in December 1994 and January 1995 at nine different sites around Lizard Island (14°40' S; 145°28' E) on the Great Barrier Reef (Fig. 1). These sites represented three different zones of exposure to the prevailing weather conditions: Exposed (3 sites), Sheltered (3 sites) and Lagoonal (3 sites). To carry out baited point censuses fluorescent tape was used to mark out ten points around the circumference of a 5 m radius circle, generally centred on the slope of the reef. A mesh bag containing four pilchards, which were pulverised with a hammer at the start of each observational period, was then placed in the middle of the circle. This bait was intended to bring into view cryptic species whose abundance may have otherwise have been underestimated. All piscivorous fish observed during a 15 minute search of this circle were counted. Observers were careful not to count the same individual more than once. Six censuses were conducted at each site, a total of 54 overall.

3. Quadrat Censuses (QC)

Quadrat censuses of piscivorous fish species were conducted in January 1995 at the same 9 sites around Lizard Island as above (see Fig. 1). At each site an 18 m x 30 m quadrat was set up using measuring tapes, parallel to the reef edge and centred on the slope (as for the baited point censuses). With additional measuring tapes, quadrats were then divided into 6 strip transects, each 30 m long and 3 m wide. Each tape had been marked every 3 m to effectively divide the quadrat into a grid consisting of 60 3 x 3 m squares.

To carry out fish counts a diver swam up and back each transect in turn. Mobile species were generally counted on the way out and cryptic species on the return. All habitat was intensively searched, including any caves or ledges present which were examined with a flashlight. On average it took approximately 90 minutes to census a quadrat in this way. Any piscivorous fish observed were plotted on the grid in the position at which they were first seen. Mapping fish positions in this way improved the fish counts in several ways. Firstly, it helped ensure that individual fish were not counted more than once, which is a potential risk when censusing adjacent transects. Secondly, it enabled flighty species to be plotted on the grid well ahead of the diver, hence reducing the likelihood that their numbers would be underestimated.

4. Patch Reef Experiment

To examine the relative accuracy of the two different census techniques, an experiment involving three cryptic, piscivorous species of rock-cod, *Cephalopholis cyanostigma, C. boenak* and *C. microprion* (Serranidae), was conducted on six adjacent patch reefs (mean size 165 m^2) in February 1995. These fish species are known to rarely move between these patch reefs (Chapter 3) and so were ideal for the study. Firstly, to simulate the quadrat censuses, a diver counted numbers of the target species while swimming around each reef in a spiral-like fashion, starting at the base and working up to the top. All caves and ledges on the reef were again intensively searched with a flashlight. On average, it took approximately 30 minutes to census a reef in this way. Within one to three days the same reefs were again censused in a similar fashion, but this time four crushed pilchards were placed on each reef to attract fish (simulating the baited point census method). Finally, as part of another study on the same reefs (Chapters 3 to 5), an intensive tag and release program was undertaken over the next 7 days for the same three species of rock-cod. At the conclusion of this exercise nearly all individuals had been tagged and it was possible to give accurate estimates of absolute density for each species.

5. Data analysis

a) Comparison of Baited Point and Quadrat Censuses:

For the baited point census (BPC) the mean number of each species counted per census (78.5 m^2) was calculated and converted to a mean density per 100 m^2. For the quadrat census (QC) the mean number of fish per transect (90 m^2) was calculated and again expressed as a mean number of fish per 100 m^2. Data was then transformed to $\sqrt{x}+\sqrt{x+1}$ to improve normality and heterogeneity (Underwood 1981). Differences between the BPC and QC were examined by a one factor ANOVA comparing the total density of piscivores estimated by the two methods and by a two factor ANOVA comparing the methods at species level. The two fixed factors were census method and species. Differences between densities estimated for each species by the two methods were examined by Tukey's honestly significant difference (HSD) method (Day & Quinn 1989).

b) Patch Reef Experiment

For each patch reef the number of fish counted by both the visual and baited visual censuses was calculated as a percentage of the number determined from the tagging study. These percentages were then averaged for the six reefs. This was deemed to represent the accuracy of each technique for measuring the absolute density of each species. Data was then arcsine transformed to allow parametric tests. Differences between the percentage accuracy of the two techniques were examined by a two factor ANOVA. The two fixed factors were census method and species. The percentage difference between densities estimated by the two census methods was also calculated for both the experiment and the natural censuses. To do this for the natural censuses, six sites were chosen at random and for each method the censuses at each site were pooled for comparison. Data was again arcsine transformed and compared with a two factor ANOVA (factors as above). This addressed the question of whether or not the experiment was representative of the natural situation.

c) Spatial Variation in the Abundance of Piscivorous Fish

Patterns of spatial variation in the abundance of piscivorous fish were examined for all families and the 20 most abundant species. Analysis was restricted to this number of species in order to reduce the chance of a Type 1 error. Differences between the mean total number of piscivorous fish observed at each site and between zones were also examined. Data was again transformed to $\sqrt{x}+\sqrt{x+1}$ to improve normality and heterogeneity. The significance of differences was tested by two factor nested ANOVA. The two factors were zone (fixed) and site nested within zone (random).

Results:

1. Comparison of Baited Point and Quadrat Censuses

Overall, the baited point census (BPC) estimated a mean density of 37.37 piscivores / 100 m^2 (± 2.76 SE) at Lizard Island, more than double the number observed in the quadrat census (QC), (18.09 piscivores / 100 m^2 (± 1.75 SE)), (Table 2a). Comparing the two techniques at species level showed a significant interaction between census method and species (Table 2b). Post hoc analysis (Table 3) revealed that the BPC produced significantly higher density estimates for 9 of the 12 most abundant species of fish. These included *Pseudochromis fuscus*, *Cephalopholis cyanostigma* and *C. boenak*, which were 3 of the 4 most abundant cryptic species. The BPC also produced a higher density estimate for the fourth abundant cryptic species, *C. microprion*, but this was not significant. For mobile fish the BPC produced significantly higher density estimates for 6 of the 8 most abundant species. These included 4 labrids, *Thalassoma lunare*, *T. hardwicke, Cheilinus chlorourus* and *C. digrammus* and also *Lutjanus carponatatus* and *Plectropomus leopardus*. The QC produced a significantly higher estimate for only 1 mobile species, *Lutjanus quinquelineatus*. This result was probably due to several chance encounters with schools of this species during the QC. The total number of species observed, on the other hand, was quite similar for the QC and BPC (38 and 37 species respectively), although 8 species were exclusive to the QC and 7 species to the BPC. All of these species, however, were in low abundance (see Table 3).

2. Patch Reef Experiment

In the patch reef experiment the baited visual censuses were shown to produce a significantly more accurate measure of absolute density (between 85 and 96 %) than the standard visual censuses (between 40 and 61 %), (Table 4a, Fig. 2a). The general trend was for the standard visual census to be least accurate for *Cephalopholis boenak* but slightly more accurate for *C. cyanostigma* and *C. microprion*. These trends appeared to be repeated in the natural censuses (Fig 2b) indicating the patch reef experiment was probably quite representative of what was occurring in the natural situation. The percentage differences between the densities estimated for each species by the two techniques in the experiment were not significantly different from those observed in the natural censuses (Table 4b). In general 30 to 55 % of fish sighted when bait was present were not seen in the standard visual censuses.

3. Community Structure of Piscivorous Fish at Lizard Island

Based on the comparison between the baited point census (BPC) and the quadrat census (QC) and the results of the patch reef experiment I decided that cryptic species were more accurately estimated by the BPC. For the mobile species on the other hand, personal observations indicated that large numbers of these fish were moving into the census areas during the BPC. The BPC therefore probably overestimated the abundance of these species. Hence mobile species appeared to be more accurately estimated by the QC. I therefore combined the BPC density estimates for cryptic species with the QC density estimates for mobile species to produce an overall picture of the community structure of piscivorous fish at Lizard Island. The use of BPC density estimates for cryptic species almost doubled their representation in the piscivorous fish community from 17.61% (in the quadrat census) to 32.19% (in the combined census). When only confirmed piscivores (see Table 1) were considered, cryptic species increased in proportion from 53.37% to 74.56% of the community.

At the family level, with all species included (Fig. 3a), Labridae was most highly represented, followed by Serranidae, Psuedochromidae and Lutjanidae. The four other families, Synodontidae, Pinguipedidae, Lethrinidae and Cirrhitidae made up only a small proportion of the remainder. When the analysis was restricted to confirmed piscivores, (Fig. 3b), however, Serranidae became the dominant family with Labridae being reduced to the fourth most common family. These patterns can be explained by examining the relative densities of each species censused (Fig. 4). Many of the most abundant species belonged to the genus *Thalassoma* (Labridae), which are opportunistic feeders that only occasionally prey on fish (Randall et al. 1990). The high abundance of rock-cods (genus: *Cephalopholis*) largely accounts for Serranidae being the most common family of confirmed piscivores.

4. Spatial Variation in the Abundance of Piscivorous Fish

Using the combined census (as above) I also examined spatial variation in the abundance of piscivorous fish at Lizard Island. The total number of piscivorous fish belonging to 3 families showed significant variation between zones (Fig. 5, Table 5a). Labrids were more abundant in the exposed zone than the lagoon, while Serranids were more abundant in the sheltered zone than the lagoon (Table 5b). Pseudochromids were more abundant in the sheltered zone than either the exposed zone or the lagoon. Three families, Labridae, Serranidae and Lutjanidae also varied significantly at site level (Table 5a). These patterns can be further explained by examining patterns of spatial variation for each species (Fig. 6, Table 6a). Four species, *Thalassoma lunare*, *Pseudochromis fuscus*, *Cephalopholis boenak* and *Epibulus insidiator*, varied significantly at zone level. *T. lunare* was more abundant in the exposed zone than the lagoon, *P. fuscus* and *C. boenak* were more abundant in the sheltered zone than either the exposed zone or the lagoon and *E. insidiator* was more abundant in the lagoon than either the exposed or sheltered zones (Table 6b). In addition, 11 of the 20 most abundant species also showed significant variation in abundance at site level (Table 6a).

Patterns of spatial variation in total numbers of piscivorous fish changed according to which species were included in the analysis. At the site level there was significant variation in piscivore abundance when all species were included (Fig. 7a, Table 7a), but not quite (p=0.053) when analysis was restricted to confirmed piscivores (Fig. 7b,Table 7b). Relative patterns of abundance between sites also depended on which species were included in the analysis (Fig. 7). There was no significant variation in total numbers of piscivorous fish at zone level (Table 7).

Discussion:

The significantly higher piscivore densities estimated by the baited point census (BPC) were almost certainly due to the presence of bait within the census area. For the mobile species it was quite likely that many of the fish counted were attracted from outside the census area during the observational period. This method is therefore only effective for measuring relative densities of mobile species. For cryptic piscivorous species, however, it is my argument that the difference between the BPC and quadrat census (QC) density estimates was almost solely due to these fish being brought into view by the attraction of the bait and not by extra fish migrating into the census area. The cryptic species I censused were all relatively sedentary and territorial. For example, two of the largest and most common cryptic species we censused, *Cephalopholis cyanostigma* and *Cephalopholis boenak* patrol relatively small and discrete home ranges and display intra and interspecific territoriality (Mackie 1993, Chapter 3). Another of the most common piscivores at Lizard Island, *Cephalopholis microprion*, was found to move only a few metres, even over a period of 2 years (Stewart, unpubl. data). Hence the BPC appears to be an effective technique for estimating the absolute density of these cryptic species.

The results from the patch reef experiment further support the effectiveness of the BPC. When compared to the tagging density estimates (my measure of absolute density), the baited census was found to be 85 to 96 % accurate compared with 40 to 61% accuracy when bait was not present. In addition, differences between the two techniques in the experiment were similar to those observed in the natural situation. Other research on the central Great Barrier Reef (Samoilys 1992), also suggests that traditional visual censuses are ineffective for estimating the density of cryptic piscivorous species. In her study visual censuses underestimated the absolute density of cryptic serranids by more than five times when compared with explosive sampling.

This ability of the baited census technique to improve the accuracy of abundance estimates for cryptic species is a significant breakthrough. In the past, such species have been largely ignored in visual censuses as it was considered impossible to accurately estimate their abundance (for exceptions see Russ and Alcala 1989, 1996). The use of the BPC in this study showed that such species made up almost double the proportion of the piscivorous fish community than would have been indicated by traditional census methods. Previous studies may therefore have underestimated the abundance of cryptic piscivorous species. My results place greater importance on the role of cryptic species in trophic dynamics.

Although destructive sampling also has the potential to produce very accurate estimates of density for some cryptic fish species, the baited point census technique offers several major advantages. Most importantly it is non-destructive. Not only does this ensure minimal disturbance to the habitat and the community in question, but it also allows repeated censuses to be conducted in order to examine such factors as temporal variation in abundance or the effects of fishing. In addition, several species which are not effected by explosives, such as moray eels and larger fish, are included in visual censuses. Tag and release programs such as used in this study may also provide accurate estimates of absolute density but are extremely labour intensive. In this case it took 2 people 7 days to tag only three species on six relatively small patch reefs.

For the more mobile species, previous work (eg. Brock 1982, Thresher & Gunn 1986, Samoilys 1992) suggests that traditional visual censuses are adequate. For example, Samoilys (1992) found that visual estimates were very similar to the results from explosives for roving serranids (eg. *Plectropomus leopardus*) and lutjanids. These results justify combining QC estimates for mobile species with the BPC estimates for cryptic species in order to gain an accurate picture of piscivorous fish communities.

Based on the combined census my study indicates that the piscivorous fish community at Lizard Island is dominated by small species belonging to the families Labridae, Serranidae and Pseudochromidae. This is in direct contrast to One Tree Island in the southern Great Barrier Reef where piscivorous fish below 20 cm in length are uncommon (Connell & Kingsford 1998). Several studies have indicated that small piscivorous coral reef fish prey heavily on newly recruited fish (Sweatman 1984, 1993, Martin 1994). In a recent study at Lizard Island by Beukers (1996), experimentally released new recruits of a damselfish, *Pomacentrus moluccensis*, were consumed exclusively by small piscivores such as *Pseudochromis fuscus* and *Thalassoma lunare*. Given the high abundance of small piscivores in the natural community at Lizard Island, mortality rates of newly settled fish could be higher there than at other areas such as One Tree Island. In support of this notion, this was exactly the pattern found by Caley (1995) when he compared fish communities on experimental patch reefs at the two locations.

The combined census also indicated considerable spatial variation in piscivore densities at both site and zonal level. Such variability could potentially translate to spatial variation in the mortality rates of prey fish and hence affect the distribution and abundance of such species. In support of this, both Aldenhoven (1986) and Beukers (1996) found spatial variation in the mortality rates of prey fish at Lizard Island. Connell (1996) linked mortality of a coral reef fish at One Tree Island with the abundance of predatory fish. The abundance of piscivorous species is not likely to be the sole factor affecting the impact of predators on prey fish, however. It is also necessary to have information on the availability of refuges for prey, the biomass of predators present and the degree of piscivory exhibited by these predators. Some of the species counted in this study, eg. *Synodus variegatus*, are known to be almost 100% piscivorous (Sweatman 1984), while others such as *Thalassoma lunare* only occasionally consume fish (Randall et al. 1990, Martin 1994, Connell 1998a). By restricting analysis to confirmed piscivores (those species which normally consume fish) I observed different patterns in the abundance and distribution of piscivorous fish. Given that these species seem likely to have a greater impact on prey fish populations it may be more meaningful to examine these patterns when investigating predator-prey relationships. Alternatively, although opportunistic piscivores may not consume many fish individually, due to their high abundance at Lizard Island (eg. *Thalassoma lunare*) their combined impact on prey fish populations may be quite considerable (see also Parrish et al. 1986). A further understanding of this question can only be obtained by detailed diet analysis of the predatory species in question.

Spatial variation in the abundance and distribution of piscivorous coral reef fish has been reported in several other studies (eg. Williams & Hatcher 1983, Newman et al. 1997, Connell & Kingsford 1998). Such variation may be due to patterns of larval supply (Doherty 1981, Doherty & Fowler 1994), habitat selection at the time of settlement (Williams 1991), or post-settlement processes such as differential survival of recruits (Hixon 1991) or movement of piscivores to areas of optimal habitat and food supply (Robertson 1988, Lewis 1997). Given the potential role of piscivorous fish in influencing the community structure of prey fishes and that many piscivorous coral reef fish are of commercial and recreational importance (Russ 1991), further understanding of the factors controlling the distribution and abundance of these fish is a prime area for further research.

Table 1. List of species censused as piscivores at Lizard Island.

Species Censused	**Max. Size (tot. length)**	**Behaviour (mobility)**	**Piscivore category**	**Ref.**
Synodontidae (Lizardfishes)				
*Synodus spp.**	28cm	Mobile	Confirmed	1,6
Scorpaenidae (Scorpionfishes)				
Pterios volitans	38cm	Cryptic	Confirmed	4,6
Seranidae (Groupers)				
Anyperodon leucogrammicus	52cm	Cryptic	Confirmed	5, 6
Cephalopholis boenak	24cm	Cryptic	Confirmed	2, 6
Cephalopholis cyanostigma	35cm	Cryptic	Confirmed	2, 6
Cephalopholis microprion	23cm	Cryptic	Confirmed	2, 6
Cephalopholis urodeta	27cm	Cryptic	Confirmed	5, 6
Cromileptes altivelis	66cm	Cryptic	Confirmed	6
Epinephelus caeruleopunctatus	60cm	Cryptic	Confirmed	6
Epinephelus corallicola	31cm	Cryptic	Confirmed	6
Epinephelus fasciatus	35cm	Cryptic	Confirmed	4, 6
Epinephelus howlandi	45cm	Cryptic	Confirmed	6
*Epinephelus spp.***	35cm	Cryptic	Confirmed	4, 6
Epinephelus ongus	40cm	Mobile	Confirmed	6
Plectropomus leopardus	75cm	Mobile	Confirmed	8, 9
Pseudochromidae (Dottybacks)				
Psuedochromis fuscus	9cm	Cryptic	Confirmed	2, 6
Lutjanidae (Snappers)				
Lutjanus bohar	75cm	Mobile	Confirmed	6, 10
Lutjanus carponotatus	40cm	Mobile	Confirmed	6, 7
Lutjanus fulviflamma	35cm	Mobile	Confirmed	6, 7
Lutjanus fulvus	40cm	Mobile	Confirmed	6, 10
Lutjanus gibbus	50cm	Mobile	Confirmed	6, 11
Lutjanus monostigma	50cm	Mobile	Confirmed	6, 11
Lutjanus quinquelineatus	38cm	Mobile	Confirmed	6, 12
Lutjanus russeli	45cm	Mobile	Confirmed	6
Lutjanus vitta	40cm	Mobile	Confirmed	5, 6
Lethrinidae (Emperors)				
Lethrinus harak	60cm	Mobile	Confirmed	6
Lethrinus nebulosus	86cm	Mobile	Confirmed	6
Lethrinus obsoletus	40cm	Mobile	Confirmed	6
Monotaxis grandoculis	60cm	Mobile	Confirmed	6
Cirrhitidae (Hawkfishes)				
Paracirrhites forsteri	22cm	Cryptic	Confirmed	1,6
Pinguipedidae (Sandperches)				
Parapercis hexopthalma	23cm	Cryptic	Opportunistic	6

Table 1. (Continued)

Species censused	Max. Size (tot. length)	Behaviour (mobility)	Piscivore category	Ref.
Labridae (Wrasses)				
Bodianus axillaris	20cm	Mobile	Oportunistic	6
Bodianus mesothorax	20cm	Mobile	Oportunistic	6
Cheilinus chlorourus	36cm	Mobile	Confirmed	6, 13
Cheilinus digrammus	30cm	Mobile	Confirmed	6, 7, 13
Cheilinus trilobatus	40cm	Mobile	Confirmed	6
Cheilinus undulatus	230cm	Mobile	Confirmed	6
Choerodon fasciatus	30cm	Mobile	Oportunistic	6
Epibulus insidiator	35cm	Mobile	Confirmed	1, 6, 13
Halichoeres prosopeion	13cm	Mobile	Oportunistic	6
Thalassoma amblycephalum	16cm	Mobile	Oportunistic	6
Thalassoma hardwicke	18cm	Mobile	Oportunistic	6
Thalassoma jansenii	20cm	Mobile	Oportunistic	6
Thalassoma lunare	25cm	Mobile	Oportunistic	2, 6, 7
Thalassoma lutescens	25cm	Mobile	Oportunistic	6

* *Synodus spp.* includes *Saurida gracilis*, *Synodus dermatogenys* and *Synodus variegatus*
** *Epinephelus spp.* includes *Epinephelus merra* and *Epinephelus quoyanus*

References

1. Parrish et al. (1986)
2. Martin (1994)
3. Sweatman (1984)
4. Harmelin - Vivien and Bouchon (1976)
5. Hiatt and Strasburg (1960)
6. Randall et al. (1990)
7. Connell (1998a)
8. Kingsford (1992)
9. St John (1995)
10. Miles (1963)
11. Randall and Brock (1960)
12. Sweatman (1993)
13. Gottleib (1992)

Table 2.

a) Results of ANOVA comparing the density of total numbers of piscivorous fish estimated by the baited point and quadrat census methods (* indicates significant difference).

SOURCE	SS	DF	MS	F	Sig of F
Method	10042.05	1	10042	34.89	0.000*
Error	30511.31	106	287.84		

b) Results of ANOVA comparing the density of each species of piscivorous fish estimated by the baited point and quadrat census methods (* indicates significant difference).

SOURCE	SS	DF	MS	F	Sig of F
Species	3148.90	44	71.57	88.21	0.000*
Method	77.72	1	77.72	95.79	0.000*
Species*Method	330.50	44	7.51	9.26	0.000*
Within	3870.14	4770	0.81		

Table 3. Density (mean no. / 100m^2) of each piscivorous species estimated by the baited point (BPC) and quadrat (QC) censuses and the results of Tukey's (HSD) multiple comparison of means. NS indicates no significant difference and BPC or QC singularly indicates the species was exclusive to that census.

Species censused	**BPC**	**(SE)**	**QC**	**(SE)**	**Tukey's**
Thalassoma lunare	15.33	1.57	6.65	0.94	BPC>QC
Thalassoma hardwicke	2.45	0.31	1.38	0.36	BPC>QC
Thalassoma amblycephalum	2.43	1.65	0.99	0.60	NS
Psuedochromis fuscus	2.05	0.30	1.03	0.18	BPC>QC
Cephalopholis cyanostigma	1.93	0.23	0.91	0.17	BPC>QC
Lutjanus carponotatus	1.65	0.21	0.06	0.03	BPC>QC
Thalassoma jansenii	1.56	0.32	1.09	0.39	NS
Cheilinus chlorourus	1.44	0.21	0.39	0.15	BPC>QC
Cephalopholis microprion	1.08	0.23	0.76	0.22	NS
Plectropomus leopardus	0.94	0.15	0.19	0.07	BPC>QC
Cephalopholis boenak	0.90	0.21	0.23	0.06	BPC>QC
Cheilinus digrammus	0.64	0.12	0.29	0.10	BPC>QC
Choerodon fasciatus	0.59	0.18	0.62	0.17	NS
Lutjanus fulviflamma	0.57	0.27	0.76	0.50	NS
*Epinephelus spp.***	0.47	0.12	0.21	0.07	NS
*Synodus spp.**	0.40	0.13	0.31	0.09	NS
Parapercis hexophtalma	0.38	0.15	0.04	0.03	NS
Epinephelus fasciatus	0.33	0.09	0.02	0.02	NS
Lutjanus bohar	0.33	0.12	0.02	0.02	NS
Cephalopholis urodeta	0.28	0.11	0.00	0.00	BPC
Bodianus axillaris	0.26	0.08	0.25	0.09	NS
Epibulus insidiator	0.26	0.07	0.39	0.11	NS
Cheilinus trilobatus	0.24	0.07	0.08	0.04	NS
Monotaxis grandoculis	0.17	0.07	0.16	0.06	NS
Lutjanus gibbus	0.12	0.05	0.02	0.02	NS
Paracirrhites forsteri	0.09	0.06	0.04	0.03	NS
Halichoeres prosopeion	0.09	0.05	0.00	0.00	BPC
Lutjanus fulvus	0.07	0.05	0.00	0.00	BPC
Lutjanus quinquelineatus	0.07	0.05	0.60	0.19	BPC<QC
Lethrinus nebulosus	0.07	0.05	0.00	0.00	BPC
Lutjanus monostigma	0.05	0.03	0.00	0.00	BPC
Cheilinus undulatus	0.05	0.03	0.04	0.03	NS
Epinephelus howlandi	0.02	0.02	0.00	0.00	BPC
Lethrinus harak	0.02	0.02	0.00	0.00	BPC
Bodianus mesothorax	0.02	0.02	0.16	0.06	NS
Thalassoma lutescens	0.02	0.02	0.04	0.03	NS
Pterios volitans	0.00	0.00	0.06	0.05	QC
Anyperodon leucogrammicus	0.00	0.00	0.02	0.02	QC
Cromileptes altivelis	0.00	0.00	0.02	0.02	QC
Epinephelus corallicola	0.00	0.00	0.02	0.02	QC
Epinephelus ongus	0.00	0.00	0.02	0.02	QC
Lutjanus russeli	0.00	0.00	0.16	0.07	QC
Lutjanus vitta	0.00	0.00	0.02	0.02	QC
Lethrinus obsoletus	0.00	0.00	0.02	0.02	QC

Table 4.

a) Results of ANOVA examining the accuracy of the visual and baited visual census methods in the patch reef experiment (* indicates significant difference)

SOURCE	SS	DF	MS	F	Sig of F
Species	0.03	2	0.01	0.12	0.890
Method	4.08	1	4.08	34.03	0.000*
Species*Method	0.49	2	0.24	2.04	0.148
Error	3.60	30	0.12		

b) Results of ANOVA comparing the difference between the visual and baited visual density estimates in the experimental and natural censuses

SOURCE	SS	DF	MS	F	Sig of F
Species	0.79	2	0.40	2.61	0.090
Census	0.001	1	0.001	0.007	0.933
Species*Census	0.02	2	0.01	0.07	0.931
Error	4.56	30	0.15		

Table 5. a) Results of nested ANOVAs examining spatial variation in total numbers of piscivorous fish belonging to the four most abundant families (* indicates significant difference)

Labridae

SOURCE	SS	DF	MS	F	Sig of F
Site (Zone)	144.3	6	24.06	12.14	0.000*
Zone	295.8	2	147.9	6.15	0.035*
Error	89.2	45	1.98		

Serranidae

SOURCE	SS	DF	MS	F	Sig of F
Site (Zone)	27.84	6	4.64	3.71	0.004*
Zone	62.71	2	31.35	6.76	0.029*
Error	56.23	45	1.25		

Pseudochromidae

SOURCE	SS	DF	MS	F	Sig of F
Site (Zone)	11.72	6	1.95	1.97	0.090
Zone	63.11	2	31.55	16.15	0.004*
Error	44.6	45	0.99		

Lutjanidae

SOURCE	SS	DF	MS	F	Sig of F
Site (Zone)	40.45	6	6.74	3.19	0.011*
Zone	38.37	2	19.18	2.85	0.135
Error	95.16	45	2.11		

b) Results of Tukeys test (honestly significant difference method) showing significant differences in the mean density of families of piscivorous fish between the three zones of exposure

Family	**Result**
Labridae	Exposed > Lagoon
Serranidae	Sheltered > Lagoon
Pseudochromidae	Sheltered > Exposed and Lagoon

Table 6. a) Results of nested ANOVAs examining spatial variation in the abundance of the 20 most common species of piscivorous fish. Results are only shown for species which varied significantly. (* indicates significant result).

Thalassoma lunare

SOURCE	SS	DF	MS	F	Sig of F
Site (Zone)	54.97	6	9.16	3.57	0.006*
Zone	146.7	2	73.34	8	0.020*
Error	115.6	45	2.57		

Pseudochromis fuscus

SOURCE	SS	DF	MS	F	Sig of F
Site (Zone)	11.72	6	1.95	1.97	0.090
Zone	63.11	2	31.55	16.15	0.004*
Error	44.6	45	0.99		

Cephalopholis cyanostigma

SOURCE	SS	DF	MS	F	Sig of F
Site (Zone)	16.55	6	2.76	2.48	0.037*
Zone	22.98	2	11.49	4.17	0.073
Error	49.96	45	1.11		

Thalassoma hardwicke

SOURCE	SS	DF	MS	F	Sig of F
Site (Zone)	55.05	6	9.18	8.22	0.000*
Zone	44.53	2	22.27	2.43	0.169
Error	50.22	45	1.12		

Thalassoma janseni

SOURCE	SS	DF	MS	F	Sig of F
Site (Zone)	54.22	6	9.04	8.59	0.000*
Zone	38.6	2	19.3	2.14	0.199
Error	47.36	45	1.05		

Cephalopholis microprion

SOURCE	SS	DF	MS	F	Sig of F
Site (Zone)	43.06	6	7.18	9.55	0.000*
Zone	17.85	2	8.92	1.24	0.353
Error	33.83	45	0.75		

Cephalopholis boenak

SOURCE	SS	DF	MS	F	Sig of F
Site (Zone)	8.88	6	1.48	1.36	0.251
Zone	29.32	2	14.66	9.91	0.013*
Error	48.98	45	1.09		

Choerodon fasciatus

SOURCE	SS	DF	MS	F	Sig of F
Site (Zone)	14.65	6	2.44	2.69	0.026*
Zone	5.85	2	2.92	1.2	0.365
Error	40.86	45	0.91		

Table 6. (Continued)

Lutjanus quinquelineatus

SOURCE	SS	DF	MS	F	Sig of F
Site (Zone)	15.97	6	2.66	3.75	0.004*
Zone	14.27	2	7.14	2.68	0.147
Error	31.9	45	0.71		

Epinephelus spp.

SOURCE	SS	DF	MS	F	Sig of F
Site (Zone)	14.63	6	2.44	4.88	0.001*
Zone	5.61	2	2.81	1.15	0.377
Error	22.46	45	0.5		

Epibulus insidiator

SOURCE	SS	DF	MS	F	Sig of F
Site (Zone)	1.65	6	0.28	0.41	0.871
Zone	5	2	2.5	9.09	0.015*
Error	30.52	45	0.68		

Epinephelus fasciatus

SOURCE	SS	DF	MS	F	Sig of F
Site (Zone)	9.12	6	1.52	3.42	0.007*
Zone	1.52	2	0.76	0.5	0.629
Error	20.02	45	0.44		

Bodianus axillaris

SOURCE	SS	DF	MS	F	Sig of F
Site (Zone)	6.63	6	1.1	2.78	0.022*
Zone	6.54	2	3.27	2.96	0.127
Error	17.91	45	0.4		

Cephalopholis urodeta

SOURCE	SS	DF	MS	F	Sig of F
Site (Zone)	24.03	6	4.01	155.9	0.000*
Zone	8.01	2	4.01	1	0.422
Error	1.16	45	0.03		

b) Results of Tukey's test (honestly significant difference method) showing significant differences in the mean density of species of piscivorous fish between the three zones of exposure.

Species	**Result**
Thalassoma lunare	Exposed > Lagoon
Pseudochromis fuscus	Sheltered > Exposed and Lagoon
Cephalopholis boenak	Sheltered > Exposed and Lagoon
Epibulus insidiator	Lagoon > Exposed and Sheltered

Table 7. Results of nested ANOVAs examining spatial variation in total numbers of piscivorous fish (* indicates significant difference).

a) All species

SOURCE	SS	DF	MS	F	Sig of F
Site (Zone)	3015.18	6	502.53	8.65	0.000*
Zone	3313.81	2	1656.9	3.3	0.108
Error	2615.08	45	58.11		

b) Confirmed piscivores only

SOURCE	SS	DF	MS	F	Sig of F
Site (Zone)	367.01	6	61.17	2.27	0.053
Zone	494.83	2	247.42	4.04	0.077
Error	1211.72	45	26.93		

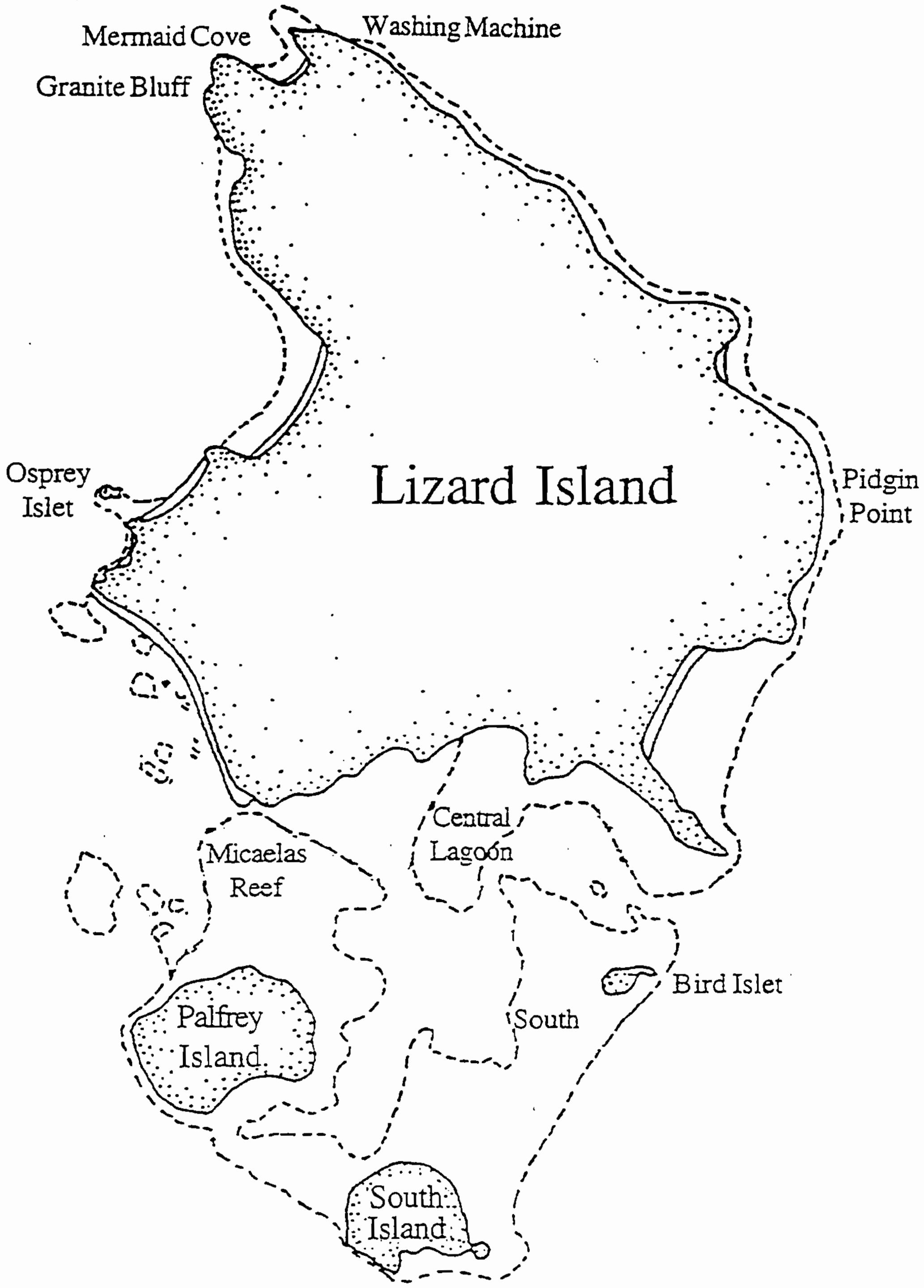


Fig 1 Map of Lizard Island showing study sites

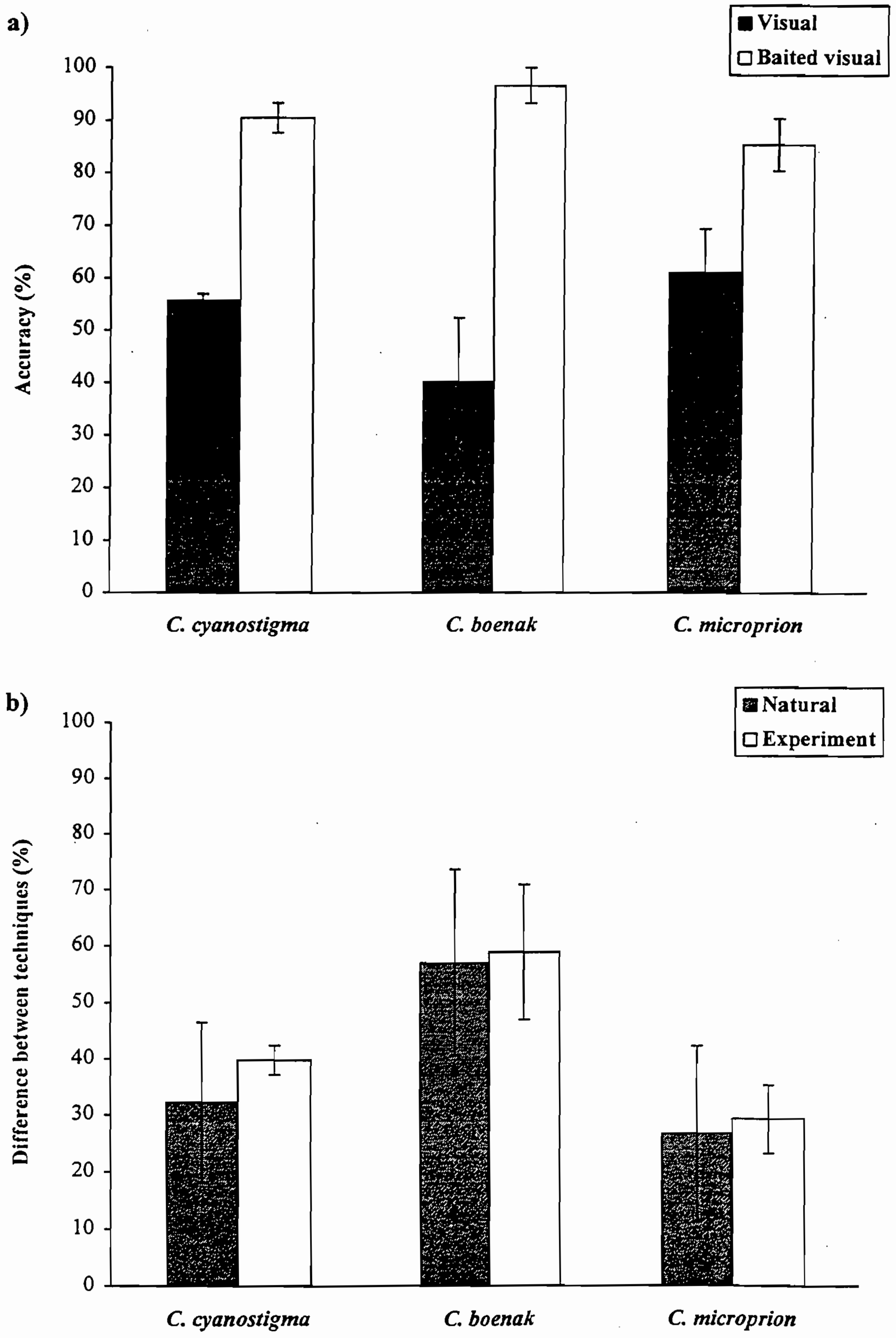


Figure 2. a) Percentage accuracy (mean +/- SE) of the visual and baited census techniques for the three rock-cod species in the patch reef experiment (n=6) and **b)** Difference between the two techniques (mean percentage +/-SE of fish not seen without bait) in the natural censuses (n=6) and the patch reef experiment (n=6).

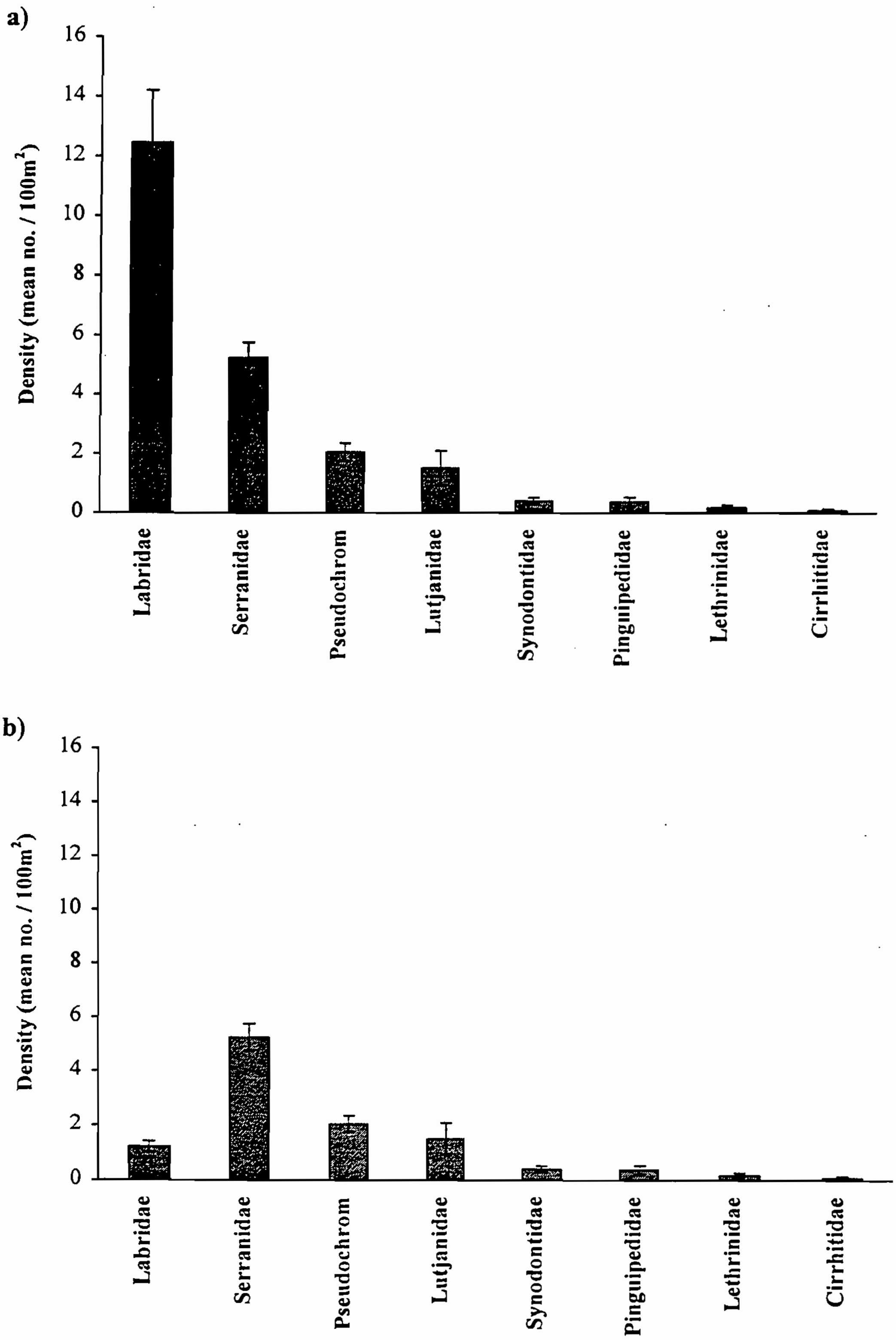


Figure 3. Density (mean +/- SE) of families of piscivorous fish at Lizard Island estimated by the combined census (cryptic species - baited point census; mobile species - quadrat census; n=54); **a)** all species, **b)** confirmed piscivores only (Pseudochrom = Pseudochromidae).

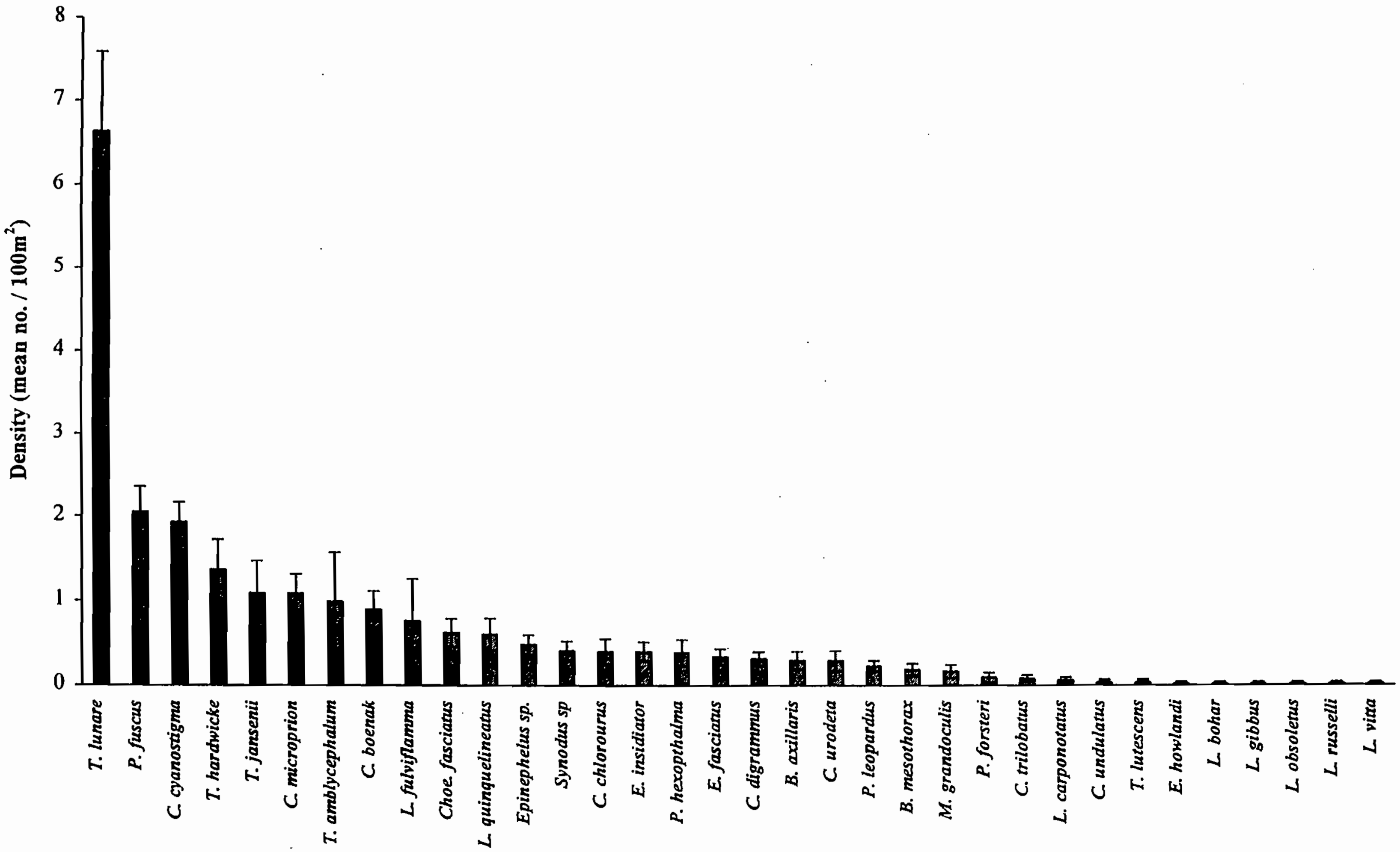


Figure 4. Density (mean +/-SE) of piscivorous species of fish at Lizard Island estimated by the combined census (cryptic species - baited point census; mobile species - quadrat census; n=54)

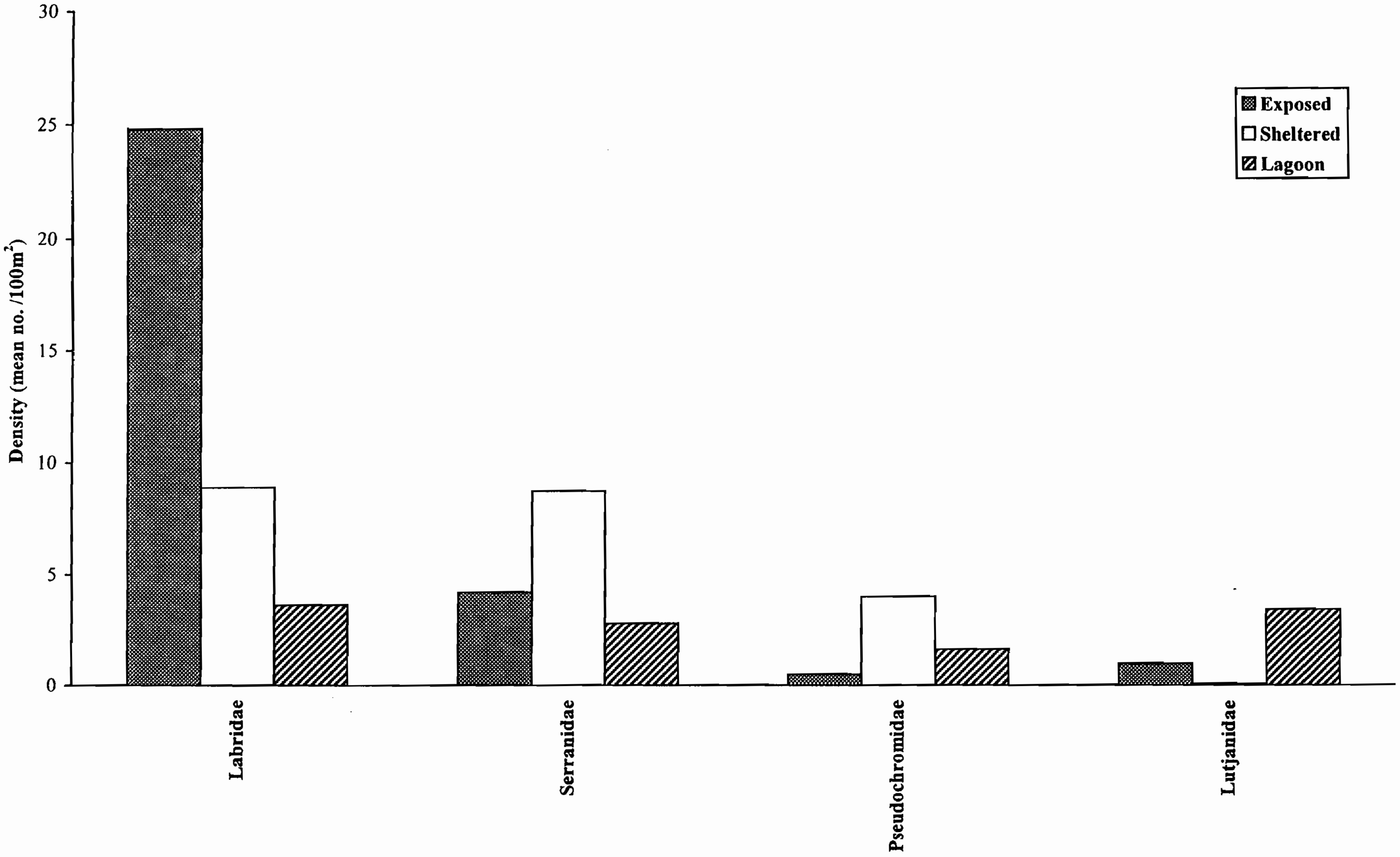


Figure 5. Density (mean +/- SE) of the four most common families of piscivorous fish in each of the three zones of exposure at Lizard Island (combined census; n=18 per zone).

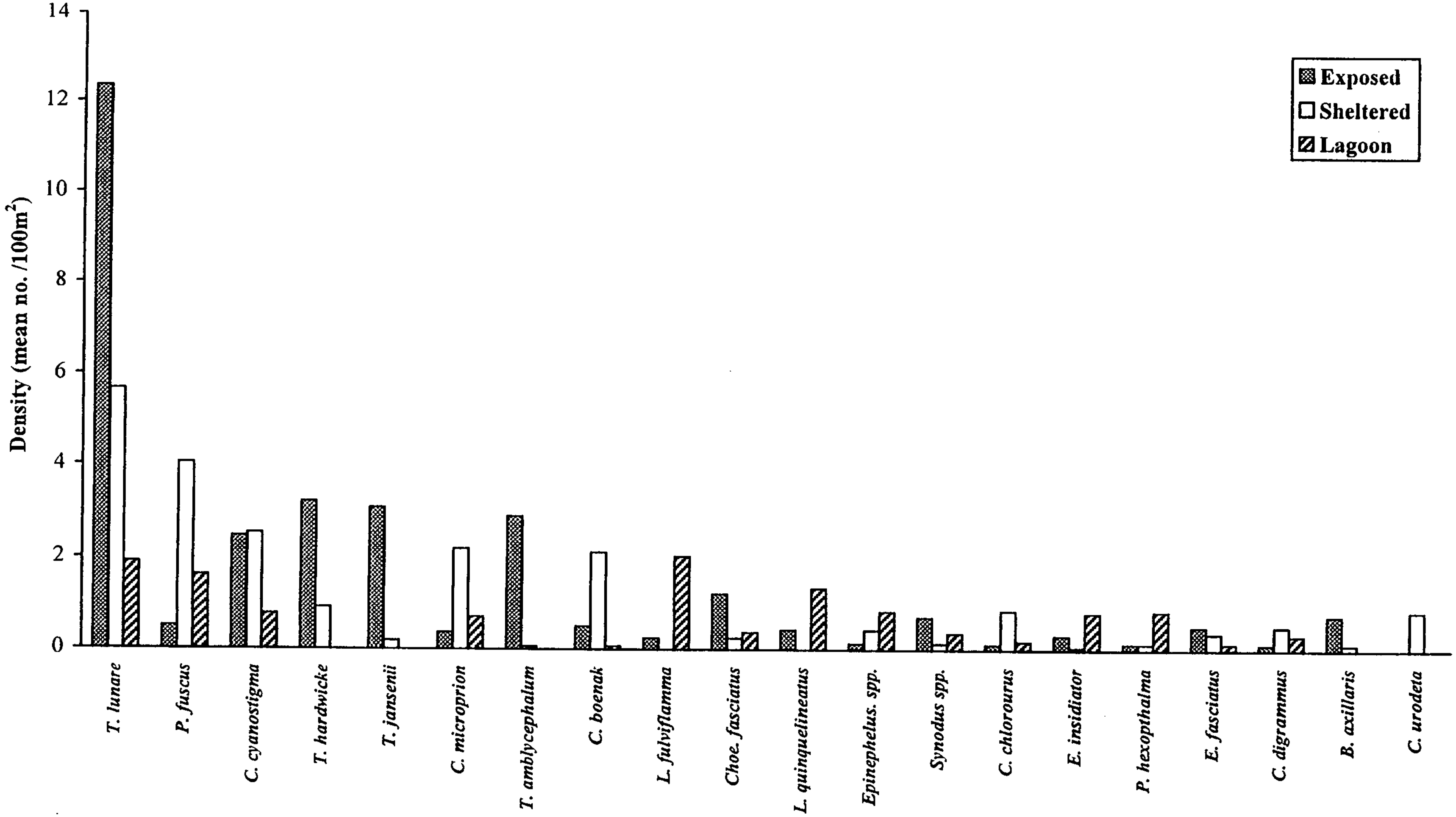


Figure 6. Density (mean +/- SE) of the 20 most abundant species of piscivorous fish in each of the three zones of exposure at Lizard Island (combined census; n=18 per zone).

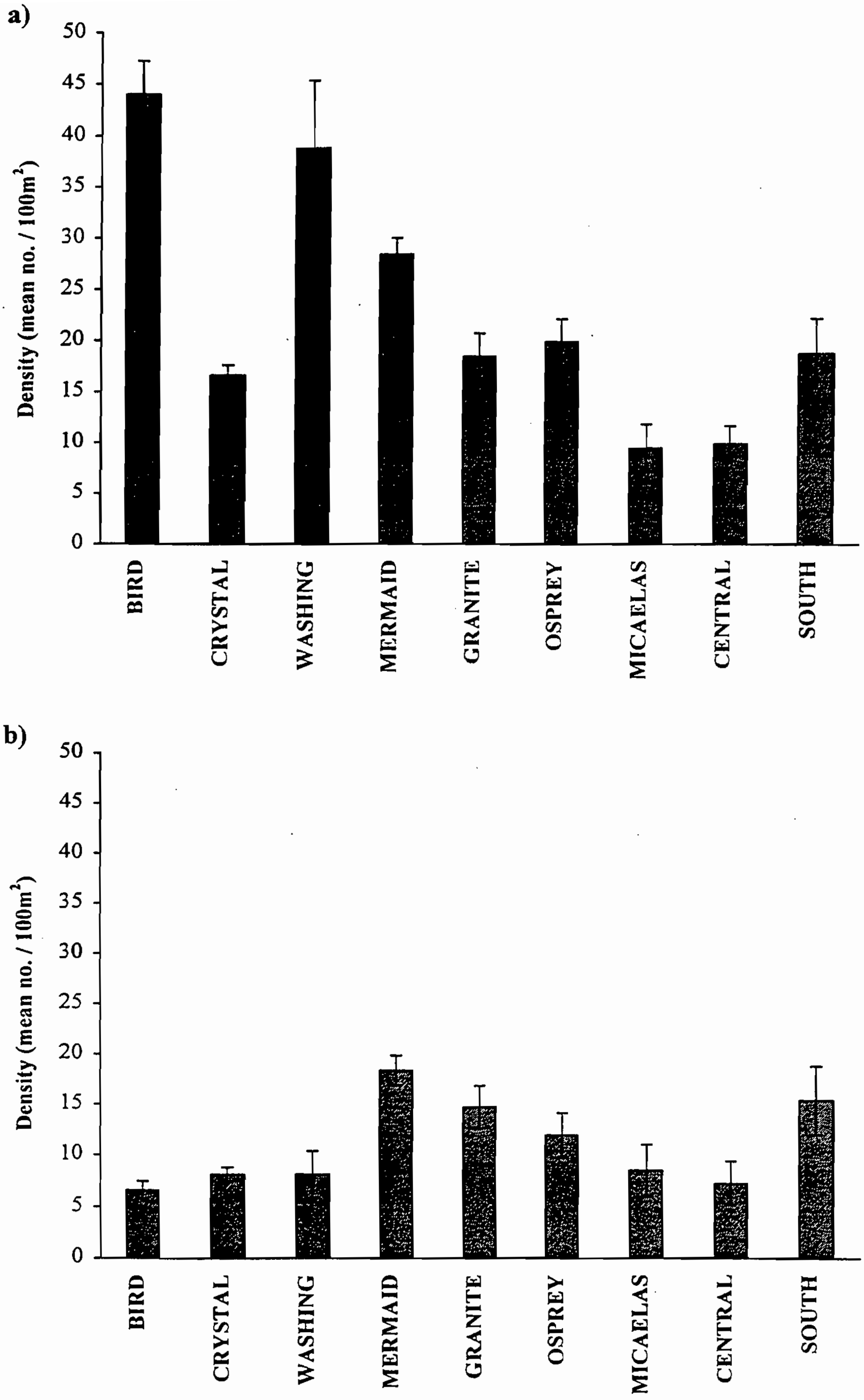


Figure 7. Density (mean +/- SE) of the total number of piscivorous fish at each site censused at Lizard Island (combined census; n=6); **a)** all species, **b)** confirmed piscivores only.

Chapter 3

Interactions determining the abundance of piscivorous fishes and their prey on coral reefs

Abstract:

Few studies have examined the interactions that determine the distribution and abundance of piscivorous coral reef fishes and their prey populations. Here I examined patterns of spatial and temporal association between predator and prey fish at Lizard Island on the Great Barrier Reef, Australia. I tested two predictions that follow if piscivore abundance is limited by prey availability and populations of prey species are limited by piscivore predation. These were: (1) The abundance of predators should be positively related to the abundance of prey, and (2) Prey populations should exhibit density-dependent mortality, due to the aggregation of predators in areas of high prey abundance. Strong positive relationships between prey and piscivore abundance were maintained throughout the study. Greater densities of both predators and prey were found on patch reef habitats, compared with contiguous reef slope habitats. Loss rates of prey fish were density-dependent and strongly correlated with the densities of predators. However, there was also a positive relationship between the ratio of prey to predators and prey loss, suggesting predator abundance only partially explained patterns of prey loss. The relative roles of recruitment and piscivore movement in determining these patterns were assessed from surveys of recruit densities and an intensive program of tagging two species of rock-cod, *Cephalopholis cyanostigma* and *C. boenak* (Serranidae), over two years. Patterns of recruitment explained little of the variation in the abundance and distribution of piscivorous fish. If movement explains large scale patterns of distribution this was not evident from the tagging study. The two rock-cod species were highly sedentary, with individuals on patch reefs seldom moving among reefs. Individuals on reef slopes were also highly site-attached, although moved greater distances than those confined to patch reefs. Within contiguous reef sites and individual patch reefs, however, prey abundance appeared to have a strong effect on the movement of the rock-

cods. The size of territories maintained by these fish was inversely proportional to the density of prey available. Local scale variation in prey distribution induced by currents also resulted in a corresponding movement of the rock-cods. Hence, although the mechanisms remain to be fully determined, this study demonstrated that the abundance and distribution of the predator and prey fishes on coral reefs was strongly linked, with the abundance of predators determined by prey numbers and numbers of prey at least partially controlled by predators.

Introduction:

Temporal and spatial variation in abundance and distribution is characteristic of organisms and one of the central goals in ecology is to determine the causes of this variation (Menge & Sutherland 1987). Predator-prey interactions can potentially determine the abundance of both predators and prey (Hunter & Price 1992, Menge 1992). It has been argued as a general rule that in benign habitats predators will be limited by prey availability and prey abundance will be limited by predators (Hairston et al. 1960, Menge & Sutherland 1976). Numerous studies, on a wide range of taxa have shown that predators tend to be concentrated in areas of greatest food or prey availability (Krebs & Davies 1978; Werner et al. 1983a; Begon et al. 1986; Eklov 1997). Aggregation of predators in areas of high prey abundance may be maintained by the continual re-location of predators as prey abundance fluctuates in space and time (Hassell & May 1974). The effects of predators on prey mortality or abundance have been demonstrated many times (Sih et al. 1985). The effects of predators on prey and the reciprocal effects of prey on predators have been recognised most readily in low diversity communities where food chains are relatively simple (e.g., Menge 1992). Whether or not the generalisation can be extended to complex communities made up by diverse assemblages of predator and prey species is unknown.

Patterns in the distribution and abundance of fishes in highly diverse coral reef habitats have been well-documented (Goldman & Talbot 1976; Williams & Hatcher 1983; Williams 1991). Most of the studies investigating the factors controlling variation in the abundance of coral reef fish concentrated on small species (Doherty & Williams 1988; Jones 1991). This work has highlighted the importance of a number of interacting processes, including levels of recruitment (Doherty 1981; Victor 1983, 1986; Doherty and Fowler 1994), competition (Jones 1987, 1990, 1991; Robertson 1996) and predation (Doherty & Sale 1985; Hixon & Beets 1993; Hixon & Carr 1997). Mortality of small fishes is thought to be primarily due to piscivorous fishes as they can be a diverse and abundant component of the reef fish fauna (Hixon 1991). Piscivorous species exhibit considerable spatial and temporal variation in their abundance (e.g., Williams and Hatcher 1983; Connell & Kingsford 1998; Chapter 2). However, the factors affecting the distribution and abundance of piscivorous fishes are poorly understood. Likewise, few workers have set out to examine the reciprocal effects of predator-prey interactions on both predatory fishes and their prey populations on coral reefs.

If populations of piscivores are limited by the availability of prey, their abundance should be correlated with prey densities (Hassell & May 1974). There is some evidence that piscivorous reef fish tend to be concentrated in areas of live coral (Huntsman & Waters 1987) and of high relief such as caves and ledges (Hobson 1965; Parrish 1987) as these provide suitable shelter holes. It would also seem likely that attraction of predators to these areas is linked to the high abundance of prey fishes which are concentrated in similar habitats (Bell & Galzin 1984; Roberts & Ormond 1987; Ault & Johnson 1998). However, of the few studies that have examined the relationship between piscivore and prey density in coral reef fish, two found piscivore abundance was positively related to the abundance of prey (Kock 1982; Beukers 1996), while three found a negative relationship (Thresher 1983; Hixon & Beets 1989, 1993).

The processes establishing these different patterns may relate to the patterns of recruitment and behaviour of different predatory species. Piscivorous fish rarely recruit in high numbers (Shpigel & Fishelson 1991a, Beets & Hixon 1994; Lewis 1997) and it is unknown whether or not they preferentially settle at sites of high prey density. The high mobility of many piscivorous species (e.g., Sweatman 1984; Samoilys 1986; Davies 1995; Zeller 1997a,b,

1998) raises the potential for predators to aggregate at sites of high prey density. On the other hand, interactions among predators may limit their densities at these sites (Begon et al. 1986). Many predators undergo gradual shifts in their use of habitats as they grow (Eggleston 1995; Light & Jones 1997). While there is increasing evidence that patterns of distribution and abundance of reef fishes can be determined by movement, even on isolated reefs (Robertson 1988; Lewis 1997; Ault & Johnson 1998) this is likely to be more important for larger, predatory species. This needs to be substantiated by intensive tag and release programs.

The relationship between predator and prey abundance may also be influenced by the degree to which piscivores impact on the abundance of their prey. If predators are food-limited, prey mortality should vary in response to predator densities. Patterns of mortality in coral reef fish populations have been linked with variation in predator abundance (eg. Caley 1995; Connell 1996). Where predator-induced mortality is density-dependent, predators can regulate prey numbers (Forrester 1995, Caley et al. 1996).

This study examined the numerical relationships between piscivorous reef fishes and their prey at Lizard Island on the Great Barrier Reef, Australia. The spatial and temporal association between predators and prey was examined both within and among patch reef and contiguous reef slope habitats. I predicted that if predator populations are food-limited there would be a positive relationship between predator and prey numbers. I also predicted that if predators are food-limited, prey would exhibit density-dependent mortality due to predator aggregation at sites of high prey density. Patterns of recruitment of piscivores and prey and movement of two piscivorous species of rock-cod, *Cephalopholis cyanostigma* and *C. boenak* (Serranidae) were then examined in detail to investigate their influence on their abundance and distribution and how this related to prey density. Rock-cods of the genus *Cephalopholis* are known to be protogynous hermaphrodites which are territorial and maintain a haremic social system (Shpigel & Fishelson 1991b; Mackie 1993). Little is known about long term movement, however, or how the size and location of territories may be effected by factors such as prey density.

Methods:

The study was conducted on the western (predominantly sheltered) side of Lizard Island ($14^0$40'S; $145^0$28'E) on the northern Great Barrier Reef, Australia between February 1995 and March 1997. Six sites were selected in 5 to 10m of water depth, 3 on contiguous reef and 3 on patch reefs. Each site on contiguous reef was situated on the slope of the fringing reef and measured 30 m x 30 m (area 900 m^2). Each of the patch reef sites consisted of 6 reefs, ranging in size from 40 m^2 to 306 m^2 (mean 114 m^2). Total area of reef at each of the patch reef sites ranged from 506 m^2 to 960 m^2. Patch reefs were situated on sand and were separated from each other and contiguous reef by at least 10m and more commonly 20 to 30 m. All censuses and observations were conducted on SCUBA.

1. Spatial and temporal variation in the distribution and abundance of piscivores and their prey

Piscivorous fish and their prey were censused at 2 patch and 2 contiguous reef sites approximately once every 3 months between August 1995 and February 1997 (a total of 7 censuses covering 2 winters and 2 summers). A third contiguous reef site was censused 6 times, commencing in November 1995 and a third patch reef site censused 5 times, commencing in February 1996. Fish were identified as piscivores on the basis of published dietary analysis (see Table 1). Piscivores were also classified as either mobile or relatively site-attached (sedentary). Prey censuses included all fish less than 5 cm in standard length belonging to the families Pomacentridae, Apogonidae, Clupeidae, Caesionidae and Atherinidae. This size and type of fish are the main prey of many common piscivores on the Great Barrier Reef such as *Pseudochromis fuscus*, (Martin 1994), *Cephalopholis cyanostigma* and *C. boenak* (Martin 1994; Chapter 4), *Plectropomus leopardus* (Kingsford 1992; St John 1995), *Synodus variegatus* (Sweatman 1984), and *Lutjanus carponatatus* and *L. fulviflamma* (Connell 1998a).

Censuses were conducted slightly differently on contiguous and patch reefs. On contiguous reefs the corner of each site was permanently marked out by small sub-surface buoys. To census fish, the corners of each site were joined up by tapes to form a quadrat and this area was then divided into 10 transects (each 3 m x 30 m). All piscivores and prey were censused along every second transect (ie 5 transects per site, each 3 m apart). To carry out a census a diver swam along each transect 3 times. Firstly, as tapes were laid out, mobile piscivores were counted, on the return an intensive search for cryptic piscivores was conducted using a flashlight, and on the final swim prey fish were counted. Censuses were conducted at haphazardly selected times of the day. Chapter 2 has shown that this census technique underestimates the abundance of cryptic piscivorous species. In this study, however, I was mainly interested in relative differences in abundance between sites and times, so an accurate estimate of absolute density was not necessary.

On patch reefs, piscivores were censused by swimming around each reef in a spiral like fashion. Mobile species were counted first and this was again followed by an intensive search with a flashlight for cryptic species. It was not practical to use transects to count piscivores on patch reefs. Prey, on the other hand, were again censused along permanent transects 3 m wide. One transect was run across the longest axis of each reef and therefore varied in length from 6 m to 18 m, according to the size of each reef. Censuses were again conducted at haphazardly selected times of the day.

On a few occasions large schools of lutjanids (predominantly *Lutjanus fulviflamma*) of 50 to 100 individuals passed through the census areas. These fish were not included in the censuses as they almost exclusively feed at night, far from their daytime resting positions (Connell 1998a).

Spatial and temporal variation in both piscivore and prey density and the ratio of prey to piscivores was examined by partly nested ANOVA. Census date and reef type were treated as fixed factors and site (nested within reef type) as a random factor. Date was fixed to enable comparisons between the two years of the study. Raw data was transformed (Ln x) when necessary (Cochrans C Test $p < 0.05$) to improve normality and heterogeneity (Underwood 1981). Spatial and temporal variation in the abundance of two species of rock-cod, *Cephalopholis cyanostigma* and *C. boenak* (both separately and combined) was also analysed in the same way.

The local scale relationship between piscivore and prey density was then examined at each census date, using transects (on contiguous reef) and individual patch reefs as replicates. This investigated whether or not piscivores were aggregated at areas of high prey abundance. This relationship was also investigated separately for mobile and sedentary piscivorous species, and for the combined density of *C. cyanostigma* and *C. boenak.*

2. Prey loss in relation to prey and predator densities

Percentage loss rates of all prey fish, from peaks of abundance in February 1996 to low points in August 1996 were then calculated and related to initial prey density. These loss rates should not have been affected by additional recruitment as fish recruitment is rare between February and August on the Great Barrier Reef (Doherty 1991). Transects and individual patch reefs were again used as replicates. The density of piscivores and the ratio of prey to piscivores in February 1996 was also related to these estimates of prey loss. These analyses were also done using patch reefs only as prey may have been able to move between transects on contiguous reef and hence effect estimates of loss. Loss rates were also calculated separately for each family. In this case sites were used as replicates. The percentage of each family remaining in August 1996 was compared by one way ANOVA, with the fixed factor being family. Data was arcsine transformed.

3. Recruitment of piscivores and prey

Recruitment of piscivores and prey was estimated in February 1996 and 1997 as part of the above piscivore / prey censuses. All piscivores estimated to be less than 5 cm standard length (SL) were regarded as having recruited that summer (with the exception of

Pseudochromis fuscus - which was counted when less than 2.5 cm SL). Recruitment rates of prey were calculated by subtracting the density of fish counted in November (at the start of the recruitment season) from the density of fish counted in February (at the end of recruitment season). These measures of recruitment can therefore only be seen as relative and approximate. Some recruits would have suffered mortality between the two census dates and others may have migrated into or out of the different sites. This study was only concerned with detecting relative differences in recruitment, however, so these measures were deemed sufficient. Differences in the density of piscivore and prey recruits at different sites and reef types over the 2 years were examined by partly nested ANOVA. Factors were year of census (fixed), reef type (fixed) and sites nested within reef types (random). Raw data was transformed (Ln x+1). The local scale relationship (ie using transects and patch reefs as replicates) between the density of piscivore and prey recruits was examined to determine if similarity in these patterns explained the relationships between the abundance of all piscivores and prey.

4. Movement of piscivores (*Cephalopholis cyanostigma* and *C. boenak*)

To further assess the influence of movement and prey abundance on patterns of abundance and distribution of piscivorous fish, the long and short term movement of two piscivorous species of rock-cod (*C. cyanostigma* and *C. boenak*) was examined. Between February 1995 and November 1996 a total of 271 *C. cyanostigma* and 157 *C. boenak* were tagged at the six study sites. Fish tagged ranged in total length from 12.6 cm to 31.4 cm for *C. cyanostigma* and from 9.8 cm to 21.4 cm for *C. boenak*. These fish were initially captured underwater on SCUBA using a baited hook and line. After being taken to a nearby dinghy for tagging and measurement they were returned to within a metre of where they were originally captured. In this way they were not displaced from their normal home ranges. Each fish was tagged in the dorsal musculature with 2 "Hallprint" T-bar anchor tags. Two tag colours and sizes were used, and each tag was placed in one of three different positions on either side of the fish. This produced a large number of combinations which allowed each fish to be recognised underwater.

a) Long term movement

During each piscivore / prey census, the position of any tagged fish recognised was plotted on a map of each site (to the nearest 3 m). On contiguous reef, all 10 transects at each site were searched for tagged fish. At the end of each census the area within 15 m on each side of the quadrat was also searched for tagged fish (ie a total area of 3600 m^2 was searched). On patch reefs, a 15 m wide strip of the nearest surrounding contiguous reef was searched at the end of each census, giving total search areas similar to those at the contiguous reef sites. A wider ranging search did not locate any tagged fish outside these areas. In addition to these censuses, the position of any tagged fish recaptured during the tagging process (approximately 2 days per site during each census month) was also recorded. When combined, these observations gave a large number of estimates on the movement of fish over periods ranging from 3 months to 2 years. Differences in the distance moved on each reef type were compared by chi-squared analysis. It was predicted that fish would move away from areas where prey density decreased and towards areas where prey increased. This was expected to be reflected in movements between either transects on contiguous reef or between patch reefs.

b) Short term movement.

The short term movements of *Cephalopholis cyanostigma* and *C. boenak* were examined during February and March 1997. During this period each site was censused between 10 and 15 times, and the position of any tagged fish recognised was plotted to the nearest metre. Otherwise, censuses were conducted in the same way as during the long term movement study. Within each month, censuses were conducted on at least 3 different, haphazardly selected, days. Any censuses conducted on the same day were separated by at least 2 hours to improve independence. Censuses were done haphazardly between 8 am and 6 pm.

Home ranges for each fish were calculated with the CALHOME program (Kie et al. 1996), using the minimum convex polygon method. The relationship between the number of times each fish was observed and home range calculated was investigated to determine the minimum number of observations needed to plot accurate home ranges. Home range data was only presented for fish fulfilling this criteria. Ten percent of observations furthest from the activity centre of each fish were also excluded from the analysis. This reduced the likelihood of home ranges being overestimated by unusual excursions of fish (Brown and Orians 1970). For each species, the mean size of home ranges on patch and contiguous reef was compared by ANOVA. Due to variable sample sizes, data was pooled between sites within each reef type, and sample size was randomly reduced on patch reefs so that it matched that on contiguous reef. Data for *Cephalopholis cyanostigma* was Ln(x) transformed due to heterogenous variances. The relationship between fish size (weight) and home range size was then examined for each species on the two reef types. The relationship between home range size and prey density (from the February 1997 censuses) and between home range / fish weight ratio and prey density at the local scale of individual patch reefs was also investigated to ascertain if this relationship explained patterns of rock-cod abundance. Home range / fish weight ratio was used to take account of the possible effect of fish weight on home range size.

Finally, the response of piscivores and prey to current direction was investigated. Two of the patch reef sites were subject to medium strength tidal currents which flow predominately from the south (Zeller 1997b). During March 1997, the presence of cyclone "Justin" near Lizard Island and associated strong northerly winds caused a reversal of this pattern. On four of the patch reefs (2 at one site and 2 at another) and on two occasions in each current direction, I plotted the distribution of the rock-cods and their prey. Using measuring tapes a grid of 3 m x 3 m squares was placed over each reef. The rock-cods and their prey were then plotted in the square in which they were first seen. The percentage of rock-cods and their prey on each side of the patch reefs (either north or south) was then calculated for both northerly and southerly currents. A two way ANOVA was performed on this data comparing the proportion of each fish type on the south side of reefs in the two current directions. The two factors were direction of current and fish type (both fixed). Data was arcsine transformed. If piscivores move in response to the distribution of their prey then any movement of prey in response to current direction should have been reflected by a similar movement of piscivores.

Results:

1. Spatial and temporal variation in the distribution and abundance of piscivores and their prey

Sixty three species of piscivores, belonging to 19 families, were observed in the census areas over the course of the study (Table 1). Counts were dominated by small species (maximum size 9 to 35 cm total length) belonging to the families Serranidae (*Cephalopholis cyanostigma*, *C. boenak*, *C. microprion*), Labridae (*Cheilinus chlorourus*) and Pseudochromidae (*Pseudochromis fuscus*). Piscivore density was found to be significantly higher on patch reefs than on contiguous reef (Fig. 1a, Table 2a). There was also significant temporal variation with small increases in piscivore density over the summer months (November to February) of each year. Prey densities followed a similar pattern to piscivore densities, although differences were more dramatic. Prey density was significantly higher on patch reefs than contiguous reefs (Fig 1b, Table 2b) and, particularly on patch reefs, there were large increases in prey densities over the summer months. Corresponding to these patterns, the ratio of prey to piscivores was generally higher on patch reefs than contiguous reef (Fig 1c, Table 2c) and peaked during the summer months. There was a significant interaction between time and reef type, however, with no significant difference between the two reef types during the first two censuses. Ratios were also significantly variable between sites within each reef type.

Similar to the total density of piscivores, both *Cephalopholis cyanostigma* and *C. boenak* appeared to be more abundant on patch reefs than contiguous reef (Fig. 2, Table 3). This difference was not significant for *C. boenak*, however, due to significant variation at site level (Table 3). The combined density of the two species, however, was consistently higher on patch reefs than on contiguous reef (Fig. 2, Table 3). The changes in density between November 1995 and February 1996 were largely due to the addition of two new sites.

The family composition of prey varied between patch and contiguous reefs (Fig 3). On both reef types, pomacentrids, followed by apogonids, were consistently the most abundant type of prey. Apogonids made up a much higher proportion of the prey available on patch reefs, however. In the summer of 1995 / 96 there was a large increase in the density of clupeids on patch reefs, however there was only a small increase in the summer of 1996 / 97. The other 2 families, Caesionidae and Atherinidae, only made up a small proportion of the remainder.

At each census date there was a strong logarithmic relationship between prey density and the density of all piscivore species at the local scale of patch reefs and transects (Fig. 4, Table 4). These relationships tended to be relatively linear in August and November of each year, but were more asymptotic in February and May after increases in prey density. The strength (R^2) of the relationships were reduced in 6 out of 7 censuses when analysis was restricted to mobile piscivorous species and further reduced in 6 out of 7 censuses when analysis was restricted to sedentary species (Table 4). The strength of the relationships between prey and sedentary piscivores were even lower in February and May each year. In two cases (August and November 1995) the relationships between prey and sedentary piscivore density were linear rather than logarithmic. Relationships between prey density and the combined of *Cephalopholis cyanostigma* and *C. boenak* were similar to those between prey and sedentary piscivores (Fig. 5).

2. Prey loss in relation to prey and piscivore density

Loss rates of prey, from February to August 1996, appeared to be density-dependent (Fig. 6). This was more obvious when analysis was restricted to patch reefs. In addition, there was a significant positive relationship between piscivore density and prey loss (Fig. 7), which again was more evident on patch reefs. Piscivore abundance did not fully explain prey loss however, as there was also a significant positive relationship between the ratio of prey to predators and prey loss (Fig. 8).

Loss rates of prey also differed between families (Fig. 9, Table 5). Clupeids suffered the highest rate of loss, having completely disappeared by August, while only 22% of apogonids remained, significantly less than 65% of pomacentrids.

3. Recruitment of piscivores and prey

Recruitment of piscivores was relatively low in both years and there were no significant differences in the density of recruits on patch and contiguous reefs (Fig. 10a, Table 6a), although there were differences at site level. Recruitment rates of prey were also relatively consistent across the two years, however, prey recruitment was substantially higher on patch reefs than contiguous reef (Fig 10b, Table 6b). There were significant linear relationships between prey and piscivore recruit density in both February 1996 and 1997 (Fig. 7). However, these relationships were strongly influenced by a school of 30 to 40 *Lutjanus quinquelineatus* recruits which appeared on the same patch reef in both years. When this reef was excluded from analysis the R^2 of the regression was reduced from 0.63 to 0.38 ($p<0.05$) in 1996 and from 0.25 to 0.05 ($p=0.20$) in 1997.

4. Movement of piscivores (*Cephalopholis cyanostigma* and *C. boenak*)

a) Long term movement

Of the 271 *C. cyanostigma* and 157 *C. boenak* tagged during the study, 174 *C. cyanostigma* (64.2%) and 92 *C. boenak* (58.6%) were resighted or recaptured at least once. Many fish were seen more than once and several on every census date. In total there were 431 resightings or recaptures of *C. cyanostigma* and 187 of *C. boenak*. A number of other tagged fish were resighted but could not be identified due to the loss of one tag. Tag loss was not quantified in this study as tagging data was not used to estimate abundance or mortality rates. Perusal of the data did not indicate any difference in the distance moved with increased time at liberty, therefore I calculated the maximum distance between any 2 observations for each fish. Both *C. cyanostigma* (k^2=104.70, df=3, $p<0.05$) and *C. boenak* (k^2=27.30, df=2, $p<0.05$) tended to move further on contiguous reef than on patch reefs (Fig. 12).

Movements of both species were generally within the patch reef on which they were captured. Only 4 tagged *C. cyanostigma* individuals moved between patch reefs (one twice) and one of those individuals subsequently moved to the nearby contiguous reef. Three of these movements were to reefs which had increased in prey density while the other 2 were not. The distances moved across open sand in these instances ranged from 10 m to 20 m. Only 3 tagged *C. boenak* individuals moved from patch reefs, in all cases to other smaller patch reefs approximately 10 m away On contiguous reef, a reasonable number of tagged *C. cyanostigma* individuals had moved maximum distances between 21 and 48 m (Fig 12a) while several *C. boenak* individuals had moved as far as 27 to 33 m (Fig 12b). Only 8 tagged *C. cyanostigma* (one twice) moved between the transects on contiguous reef on which prey density was being monitored. Half of the movements were to transects which had increased in prey density while the other half were not. Only 4 *C. boenak* moved between the same transects and again only half of the movements were towards transects which had increased in prey density.

b) Short term movement

The minimum number of observations needed to calculate accurate home ranges was determined to be 8. Of the tagged fish resighted, 75 *Cephalopholis cyanostigma* and 27 *C. boenak* fulfilled this criteria. The mean number of observations for these fish was 9.69 for *C. cyanostigma* and 9.85 for *C. boenak*. Home ranges generally consisted of a central area exclusive to each fish surrounded by an area which was shared between neighbours. For both *C. cyanostigma* and *C. boenak*, home ranges were significantly larger on contiguous reef than on patch reefs (Table 7), although the difference was much greater for *C. cyanostigma*. Reducing the sample sizes on patch reefs had little effect on the means and standard errors, indicating sample sizes were adequate.

There was no relationship between fish weight and home range size of *Cephalopholis cyanostigma* on patch reefs (Fig. 13a), however there was a strong relationship on contiguous reef (Fig. 13b). There was a weak relationship between fish weight and home range size of *C. boenak* on patch reefs (Fig. 13c) but a stronger relationship on contiguous reef (Fig 13d).

At the local scale of individual patch reefs there was a weak relationship between prey density and home range size for *Cephalopholis cyanostigma* (Fig. 14a) but no relationship for *C. boenak* (Fig. 14c). Dividing home range size by fish weight had little effect on the relationship for *C. cyanostigma* (Fig. 14b) but produced a weak relationship for *C. boenak* (Fig 14d).

Plotting the two rock-cod species and their prey on the four patch reefs subject to current flow indicated both the rock-cods and prey tended to accumulate on the upcurrent side of patch reefs (Fig. 15, Table 8). A change in current direction resulted in a shift in the distribution of both types of fish.

Discussion:

This study showed strong positive relationships between the density of prey and piscivores, both between and within patch and contiguous reef habitats. These relationships were also maintained over time, despite sometimes dramatic fluctuations in the abundance of prey. Hence the data would appear to support the hypothesis that the abundance of the piscivores was prey-limited, causing them to aggregate in areas of high prey density.

Interestingly, while the relationship between prey and piscivore density was almost linear at lower prey densities (ie in August and November of each year) it became more asymptotic when prey density increased in February. This also accounted for the ratio of prey to piscivores being higher on patch reefs than contiguous reef, particularly in February of each year. This suggests that the maximum number of piscivores an area of reef could support was limited not only by prey abundance, but also by other factors such as the habitat available. For example, the number of shelter holes could have been limiting (see Hixon and Beets 1989, 1993). Interactions between piscivores may have helped to establish this upper limit. Several of the most common piscivores on the reefs (eg. *Cephalopholis cyanostigma* and *C. boenak*) were territorial species which are known to be aggressive towards conspecifics and mobile piscivores such as *Cheilinus chlorourus*, *Lutjanus carponatatus* and *Plectropomus leopardus* (Mackie 1993; pers. obs.). These territorial fish may therefore have kept the number of conspecifics and mobile species in an area below a certain level.

Alternatively, or in addition, the total abundance of piscivores at Lizard Island could have been limited by the low levels of prey available during the winter months (see Kock 1982), or by low levels of recruitment (Doherty 1981). If this was the case there may have been insufficient numbers of piscivores present to respond proportionally to very high levels of prey recruitment. Certainly, this study indicated that piscivore recruitment at Lizard Island was very low, but it must be remembered that recruitment was only monitored over two summers. In addition, newly settled piscivores are often cryptic and difficult to census (Eggleston 1995; Chapter 2) so this study would have underestimated their true abundance. The question of how much influence recruitment has on overall piscivore abundance can only really be addressed by a long term study which uses either bait (Chapter 2) or suction pumps (Eggleston 1995) to accurately census piscivore recruits.

Along with several other recent studies (Forrester 1995; Hixon and Carr 1997), including two at Lizard Island (Caley 1995; Beukers and Jones 1997), this study also found loss rates of coral reef prey fish to be density-dependent. Although both mortality and migration may have contributed to this loss, migration from one area would have been likely to result in increases in other areas. This was not observed, suggesting mortality was the key factor influencing loss rates. In addition, patterns of prey loss were positively correlated with piscivore abundance, hence the data also appears to support the hypothesis that aggregation of piscivores in areas of high prey density caused density-dependent mortality of prey.

Interestingly, however, there was also a positive correlation between the ratio of prey to piscivores and prey loss. This was due to the fact that piscivore abundance, prey abundance, prey to piscivore ratio and prey loss were all positively related to one another. Contrary to the observed pattern of prey loss, this suggests that prey recruiting in high density would actually have swamped piscivores and been afforded some protection from predation. Hence although piscivore abundance appeared to contribute to prey mortality it did not fully explain patterns of prey loss.

Several other factors may have contributed to the density-dependent loss of prey. For example, Hixon and Carr (1997), found that only the combined effect of both resident and transient (pelagic) piscivores produced density-dependent mortality. Although transient piscivores were censused in this study (eg. Carangidae, Sphyraenidae and Scombridae), their high mobility meant that the census method I used may have underestimated their abundance (Thresher and Gunn 1986). Personal observations suggest that such transient piscivores may also play a large role in predation at Lizard Island. For example, on one occasion I observed a large school (approximately 100 individuals) of *Carangoides fulvoguttatus* and *C. ferdau* (Carangidae) feeding repeatedly on newly recruited Clupeids and Apogonids at one of the patch reef sites. This continued for over an hour, during which time the resident piscivores also fed heavily. Even if such events are rare they will still have a dramatic effect on prey communities. Caley (1995), also suggested that pelagic species may be important predators at Lizard Island.

A functional response by piscivores may also have contributed to density-dependent mortality of prey. For example, in areas where the ratio of prey to piscivores was higher than others, each piscivore may have fed at a higher rate. If this was a type 3 functional response (ie if consumption rate increased disproportionately with increasing prey density, Holling 1959) then density-dependent mortality of prey would be even more likely

(Murdoch and Oaten 1975). Finally, increased piscivory by species which do not normally consume fish, may also have caused greater prey loss in areas of high prey abundance. The importance of these last two mechanisms can only be examined by detailed dietary analysis of the species in question.

Patterns of prey fish loss also indicated differences between families. Migration may have accounted for some of the loss of Clupeids as they are highly mobile (Randall et al. 1990) and may have moved away from the study sites altogether. There is strong evidence, however, that Clupeids were highly preyed upon and selected for by at least some of the piscivores present (see Chapter 4). Several other studies have reported differences in mortality rates for different species (Sale and Ferrell 1988; Carr and Hixon 1995), suggesting species level variation was probably responsible for the family level differences seen in this study. In general, loss rates appeared to be related to the habitat which prey fish occupied with the pelagic Clupeids suffering the highest loss, followed by Apogonids which hover above the reef, followed by Pomacentrids which are generally closely associated with the substrate. Overall, observations that prey loss was both density-dependent and varied between families illustrates that post-settlement mortality patterns may have a large influence on the abundance and composition of prey communities.

Despite density-dependent mortality of prey, however, the higher prey densities observed on patch reefs over the two years of the study did appear to be maintained by higher recruitment. The reasons for this pattern of recruitment are unknown, however, they are likely to have been a combination of patterns of hydrodynamic activity (Milicich 1994) and habitat selection by larval fish (Sweatman and St John 1990; Carr 1991). The patch reefs in this study were all of relatively high relief, rising 3 to 5 m from the substrate, and in combination with the flat sandy areas which surrounded them, this feature may have concentrated larval fish about to settle. By contrast, the substrate at the contiguous reef sites was much less heterogeneous.

Neither recruitment or movement appeared to fully explain the variation in the abundance of piscivorous fish. Firstly, there was no difference in piscivore recruitment to patch and contiguous reef, and secondly there were only weak relationships between the recruitment patterns of piscivores and prey. This initially suggested that post-settlement processes, such as predator mortality and movement, may have been responsible for the observed patterns. I did not examine predator mortality, but the tagging study of *Cephalopholis cyanostigma* and *C. boenak* revealed very little post-settlement movement between patch and contiguous reef or between individual patch reefs, even over periods of up to 2 years. It is possible that ontogenetic shifts (eg. Eggleston 1995; Light & Jones 1997) may have contributed to the observed patterns, but this explanation must remain speculative as I only tagged a few juvenile rock-cods and none were recovered.

Movement may have been more important for the larger, more mobile species. For example, correlations between prey and mobile piscivorous species were stronger than those between prey and sedentary piscivores. A recent study at the same sites I used (Zeller 1997a,b) showed that the large piscivore, *Plectropomus leopardus*, moved between patch reefs and between patch and contiguous reef, on a daily basis. Unfortunately, how these movements related to fluctuations in prey abundance was not examined. Hence, the mechanisms responsible for the between habitat relationships between prey and piscivore density remain to be determined. The most likely explanation is that they were result of complex interactions between recruitment, and post-settlement mortality and movement, with the importance of each process varying between species.

Within contiguous reef sites and within individual patch reefs, however, movement of the rock-cods did appear to have a large influence on their distribution. Several lines of evidence suggest this movement was in response to the amount of prey available. Firstly, the mean size of home ranges was significantly smaller on patch reefs where high densities of prey were available than on contiguous reef where prey were much less common. This also allowed for the high numbers of rock-cods present on patch reefs to co-exist. Secondly, on contiguous reef where prey density was relatively uniform, home range size increased linearly with increasing fish size. Numerous studies, (Krebs and Davies 1978, Schoener 1983), have shown that larger individuals maintain larger territories in response to their increased food requirements.

There were also significant relationships between home range size and prey density at the local scale of individual patch reefs, although only a small proportion (11 to 14%) of the variation was explained. The most likely explanation for this was that both prey density and the availability of suitable habitat varied within patch reefs.

The distribution of the rock-cods and their prey on the patch reefs subject to current flow confirmed that prey abundance varied within patch reefs and suggested that piscivores were responding to this variation. Similar responses to current direction have also been reported for another coral reef piscivore, *Plectropomus leopardus* (Kingsford 1992, Zeller 1997b). Many of the prey fish counted in this study are planktivorous and therefore are likely to have orientated themselves in the direction of the current for feeding purposes (Bray 1981). It appeared that the piscivores responded to this in turn by moving into position to feed on the planktivores.

Overall, the behaviour of the *Cephalopholis cyanostigma* showed a high degree of plasticity in response to prey abundance. For example, one *C. cyanostigma* individual patrolled a home range of 3.2 m^2 on a patch reef of high prey density while another of similar size patrolled a home range of 264.2 m^2 on a low prey density area of contiguous reef. Shpigel and Fishelson (1991b), also suggested prey density had a strong influence on the territory size of other *Cephalopholis* species in the Red Sea, although they did not have quantitative data. *C. boenak* behaviour, on the other hand, did not respond quite so strongly to differences in prey abundance. *C. boenak* reaches a smaller maximum size than *C. cyanostigma* (Randall et al. 1990) and therefore may have been under increased pressure from predators (Milinski 1986) and competitors (Krebs and Davies 1978) which prevented it from maintaining territories as large as *C. cyanostigma*. For example, *C. cyanostigma* individuals less than 20 cm TL (ie similar in size to *C. boenak*) were also only able to maintain small home ranges less than $10m^2$.

There have been no studies examining if the feeding rates and growth of coral reef piscivores are limited by the abundance of prey or if they are able to feed to satiation. Food-limitation has been shown for planktivorous (Jones 1986) and herbivorous (Clifton 1995; Van Rooij et al. 1995; Hart and Russ 1996) coral reef fish, however. If piscivores are food-limited then the rock-cods on patch reefs might be expected to show higher feeding and growth rates. Although *C. cyanostigma* home ranges were approximately 4 times larger on contiguous reef, prey abundance was approximately 6 times higher on patch reefs. For *C. boenak* the difference could be even more pronounced as home ranges were only 1.5 times larger on contiguous reef than patch reefs. In addition, as home ranges were smaller on patch reefs, much less energy would be expended on travelling in search of prey and defending such large territories from competitors (Krebs and Davies 1978). Possibly compensating for this, however, was the fact that density of competitors was higher on patch reefs as was the density of potential predators of the rock-cods themselves, such as large *Plectropomus leopardus* individuals (St John 1995). Both factors may have inhibited feeding rates (Milinski 1986; Holbrook and Schmitt 1988). The question of whether or not the rock-cods gain an advantage on patch reefs can therefore only be determined by detailed examination of their feeding and growth rates.

In summary, this study demonstrated that variation in prey abundance was a key factor influencing predator abundance and behaviour, suggesting that the predators were limited by the abundance of prey. The abundance and mortality of prey also appeared to be at least partly controlled by the abundance of predators. The abundance and distribution of both predators and prey at Lizard Island therefore appears to be strongly linked.

Table 1. Density (mean no./100m^2 +/- SE) of species censused as piscivores during the study (n=214).

Species	**Behaviour**	**Density**	**SE**	**Rank**	**Ref.**
Hemiscyllidae (Bamboo sharks)					
Hemiscyllium ocellatum	Mobile	0.005	0.005	63	1
Muraenidae (Morays)					
Gymnothorax javanicus	Mobile	0.020	0.009	60	1
Synodontidae (Lizardfishes)					
Saurida gracilis	Mobile	0.019	0.008	47	2
Synodus dermatogenys	Mobile	0.125	0.039	24	3
S. variegatus	Mobile	0.426	0.057	16	4, 3
Holocentridae (Squirrelfishes)					
Myripristis murdjan	Sedentary	0.922	0.130	9	1
Sargocentron spiniferum	Sedentary	0.417	0.052	18	2
Fistularidae (Flutemouths)					
Fistularia commersonii	Mobile	0.010	0.010	58	2
Scorpaenidae (Scorpionfishes)					
Pterios volitans	Sedentary	0.006	0.006	61	6
Platycephalidae (Flatheads)					
Thysanophrys arenicola	Mobile	0.016	0.012	51	1
Centropomidae (Barramundi)					
Psammoperca waigiensis	Mobile	0.029	0.011	43	1
Seranidae (Groupers)					
Anyperodon leucogrammicus	Mobile	0.053	0.017	32	5
Cephalopholis argus	Sedentary	0.010	0.007	57	6, 7
C. boenak	Sedentary	1.879	0.212	4	3
C. cyanostigma	Sedentary	3.329	0.207	1	3
C. microprion	Sedentary	1.740	0.157	5	3
Cromileptes altivelis	Mobile	0.010	0.007	56	1
Epinephelus cyanopodus	Mobile	0.038	0.018	38	1
E. fasciatus	Sedentary	0.016	0.009	50	6
E. howlandi	Sedentary	0.002	0.002	64	1
E. maculatus	Mobile	0.023	0.011	45	1
E. merra	Sedentary	0.063	0.020	29	6
E. quoyanus	Sedentary	0.042	0.015	36	8
E. ongus	Mobile	0.053	0.019	31	1
Plectropomus leopardus	Mobile	1.035	0.107	7	9, 10
P. maculatus	Mobile	0.014	0.008	54	1
Diploprion bifasciatum	Mobile	0.005	0.005	62	1
Pseudochromidae (Dottybacks)					
Ogilbyina queenslandiae	Sedentary	0.043	0.019	35	1
Psuedochromis fuscus	Sedentary	2.257	0.133	3	3
Priacanthidae (Bigeyes)					
Priacanthus hamrur	Mobile	0.506	0.077	14	1
Apogonidae (Cardinalfishes)					
Cheilodipterus macrodon	Mobile	0.192	0.044	22	1

Table 1. (Continued)

Species	**Behaviour**	**Density**	**SE**	**Rank**	**Ref.**
Carangidae (Trevallies)					
Carangoides ferdau	Mobile	0.120	0.041	25	1
C. fulvoguttatus	Mobile	0.034	0.020	40	1
Caranx melampygus	Mobile	0.061	0.026	30	1
Scomberoides lysan	Mobile	0.012	0.007	55	1
Lutjanidae (Snappers)					
Lutjanus argentimaculatus	Mobile	0.016	0.008	49	1
L. bohar	Mobile	0.165	0.035	23	11
L. carponotatus	Mobile	0.930	0.074	8	8
L. fulviflamma	Mobile	0.466	0.144	15	8
L. fulvus	Mobile	0.032	0.012	42	11
L. gibbus	Mobile	0.047	0.023	34	12
L. monostigma	Mobile	0.048	0.019	33	12
L. quinquelineatus	Mobile	0.861	0.213	10	13
L. russeli	Mobile	0.289	0.060	20	1
L. sebae	Mobile	0.015	0.010	52	1
Symphorus nematophorus	Mobile	0.014	0.008	53	1
Lethrinidae (Emperors)					
Gymnocranius sp.	Mobile	0.027	0.011	44	1
Lethrinus atkinsoni	Mobile	0.108	0.024	27	1
L. harak	Mobile	0.419	0.074	17	1
L. lentjan	Mobile	0.118	0.038	26	1
L. obsoletus	Mobile	0.256	0.049	21	1
L. olivaceus	Mobile	0.022	0.015	46	1
L. nebulosus	Mobile	0.667	0.101	12	1
Monotaxis grandoculis	Mobile	1.414	0.169	6	1
Cirrhitidae (Hawkfishes)					
Parracirrhites forsteri	Sedentary	0.068	0.025	28	2
Sphyraenidae (Barracudas)					
Sphyraena flavicuda	Mobile	0.019	0.011	48	1
Labridae (Wrasses)					
Cheilinus chlorourus	Mobile	2.306	0.156	2	14
C. digrammus	Mobile	0.301	0.048	19	14, 8
C. trilobatus	Mobile	0.039	0.016	37	1
C. undulatus	Mobile	0.032	0.011	41	1
C. fasciatus	Mobile	0.515	0.057	13	14
Epibulus insidiator	Mobile	0.760	0.067	11	2, 14
Hologymnosus doliatus	Mobile	0.010	0.010	59	1
Scombridae (Mackerals)					
Grammatorcynus bicarinatus	Mobile	0.035	0.024	39	1

References:
1. Randall et al. (1990), 2. Parrish et al. (1986), 3. Martin (1994), 4. Sweatman (1984), 5. Hiatt and Strasburg (1960), 6. Harmelin-Vivien and Bouchon (1976), 7. Shpigel and Fishelson (1989), 8. Connell (1998a), 9. Kingsford (1992), 10. St John (1995), 11. Miles (1963), 12. Randall and Brock (1960), 13. Sweatman (1993), 14. Gottlieb (1992).

Table 2. Results of ANOVA examining spatial and temporal variation in piscivore and prey density and the ratio of prey to piscivores. Data was Ln(x) transformed. (*indicates significant result).

a) Piscivore density

SOURCE	SS	DF	MS	F	Sig of F
Time	7.25	6	1.21	15.36	0.000*
Reef	17.98	1	17.98	304.32	0.000*
Site (Reef)	0.24	4	0.06	0.31	0.874
Reef by Time	0.20	6	0.03	0.43	0.847
Site (Reef) by Time	0.94	12	0.08	0.41	0.959
Within + Residual	34.59	179	0.19		

b) Prey density

SOURCE	SS	DF	MS	F	Sig of F
Time	20.13	6	3.35	27.16	0.000*
Reef	58.92	1	58.92	180.13	0.000*
Site (Reef)	1.31	4	0.33	1.47	0.214
Reef by Time	2.08	6	0.35	2.80	0.061
Site (Reef) by Time	1.48	12	0.12	0.55	0.876
Within + Residual	39.88	179	0.22		

c) Ratio of prey to piscivores

SOURCE	SS	DF	MS	F	Sig of F
Time	9.80	6	1.63	13.36	0.000*
Reef	11.81	1	11.81	23.80	0.008*
Site (Reef)	1.98	4	0.50	5.72	0.000*
Reef by Time	3.24	6	0.54	4.41	0.014*
Site (Reef) by Time	1.47	12	0.12	1.41	0.165
Within + Residual	15.53	179	0.09		

Table 3. Results of ANOVA examining spatial and temporal variation in the density of *Cephalopholis cyanostigma*, *C. boenak* and the two species combined. Data was Ln (x+1) transformed. (* indicates significant result).

a) *C. cyanostigma*

SOURCE	SS	DF	MS	F	Sig of F
Time	1.57	6	0.26	0.78	0.598
Reef	23.33	1	23.33	26.93	0.007*
Site (Reef)	3.47	4	0.87	2.79	0.028*
Reef by Time	0.38	6	0.06	0.19	0.974
Site (Reef) by Time	4.01	12	0.33	1.07	0.384
Within + Residual	55.61	179	0.31		

b) *C. boenak*

SOURCE	SS	DF	MS	F	Sig of F
Time	0.88	6	0.15	1.25	0.349
Reef	17.34	1	17.34	2.40	0.197
Site (Reef)	28.95	4	7.24	21.10	0.000*
Reef by Time	0.43	6	0.07	0.60	0.723
Site (Reef) by Time	1.41	12	0.12	0.34	0.980
Within + Residual	61.39	179	0.34		

c) Combined

SOURCE	SS	DF	MS	F	Sig of F
Time	2.45	6	0.41	1.42	0.286
Reef	38.01	1	38.01	18.98	0.012*
Site (Reef)	8.01	4	2.00	5.23	0.001*
Reef by Time	0.33	6	0.05	0.19	0.974
Site (Reef) by Time	3.47	12	0.29	0.75	0.697
Within + Residual	68.60	179	0.38		

Table 4. Temporal variation in the local scale relationships between prey and piscivore density (all relationships are significant, $p < 0.05$)

a) All piscivorous species combined

Date	**n**	**Relationship**	**R^2**
Aug-95	22	Pisc. density=10.860Ln(Prey density)-50.476	0.715
Nov-95	27	Pisc. density=11.656Ln(Prey density)-53.533	0.786
Feb-96	33	Pisc. density=13.999Ln(Prey density)-72.384	0.708
May-96	33	Pisc. density=11.540Ln(Prey density)-50.734	0.705
Aug-96	33	Pisc. density=13.444Ln(Prey density)-61.230	0.782
Nov-96	33	Pisc. density=15.261Ln(Prey density)-72.671	0.753
Feb-97	33	Pisc. density=11.675Ln(Prey density)-53.743	0.682

b) Mobile piscivorous species only

Date	**n**	**Relationship**	**R^2**
Aug-95	22	Pisc. density=5.714Ln(Prey density)-26.187	0.476
Nov-95	27	Pisc. density=6.540Ln(Prey density)-29.689	0.560
Feb-96	33	Pisc. density=8.891Ln(Prey density)-48.885	0.715
May-96	33	Pisc. density=7.334Ln(Prey density)-35.343	0.623
Aug-96	33	Pisc. density=8.037Ln(Prey density)-37.748	0.636
Nov-96	33	Pisc. density=8.280Ln(Prey density)-39.796	0.632
Feb-97	33	Pisc. density=8.135Ln(Prey density)-40.933	0.644

c) Sedentary piscivorous species only

Date	**n**	**Relationship**	**R^2**
Aug-95	22	Pisc. density=0.009(Prey density)+1.772	0.574
Nov-95	27	Pisc. density=0.009(Prey density)+2.115	0.557
Feb-96	33	Pisc. density=5.097Ln(Prey density)-23.402	0.375
May-96	33	Pisc. density=4.179Ln(Prey density)-15.269	0.373
Aug-96	33	Pisc. density=5.439Ln(Prey density)-23.705	0.438
Nov-96	33	Pisc. density=6.954Ln(Prey density)-32.707	0.500
Feb-97	33	Pisc. density=3.488Ln(Prey density)-12.490	0.358

Table 5. Results of ANOVA comparing percentage loss rates of pomacentrids and apogonids from February to August 1996. Data was arcsine transformed (* indicates significant result).

SOURCE	SS	DF	MS	F	Sig of F
Family	0.52	1	0.52	11.04	0.008*
Within + Residual	0.47	10	0.05		

Table 6. Results of ANOVA examining spatial and temporal variation in the density of piscivore and prey recruits in February 1996 and 1997. Data was Ln(x+1) transformed (* indicates significant result).

a) Density of piscivore recruits

SOURCE	SS	DF	MS	F	Sig of F
Year	0.01	1	0.01	0.01	0.925
Reef	0.25	1	0.25	0.13	0.737
Site (Reef)	7.73	4	1.93	3.34	0.016*
Reef by Year	0.45	1	0.45	0.35	0.613
Site (Reef) by Year	2.57	2	1.29	2.22	0.118
Within + Residual	32.42	56	0.58		

b) Density of prey recruits

SOURCE	SS	DF	MS	F	Sig of F
Year	3.49	1	3.49	0.96	0.431
Reef	113.6	1	113.6	41.42	0.003*
Site (Reef)	10.97	4	2.74	1.39	0.249
Reef by Year	4.06	1	4.06	1.11	0.402
Site (Reef) by Year	7.28	2	3.64	1.85	0.167
Within + Residual	110.3	56	1.97		

Table 7. Spatial variation in home range size of *Cephalopholis cyanostigma* and *C. boenak*.

a) *C. cyanostigma* home ranges (m^2)

Patch Reefs

Site	**Total n**	**Mean**	**SE**	**Reduced n**	**Mean**	**SE**
Casuarina	25	14.82	2.68	10	15.62	3.96
Corner Beach	15	21.49	4.02	9	22.56	4.62
South Bay Pt	8	21.78	5.05	8	21.78	5.05
Total	48	18.07	2.07	27	19.76	2.57

Contiguous Reef

Site	**Total n**	**Mean**	**SE**
Osprey	6	54.56	10.09
Chinamans	12	77.33	14.86
Mermaid	9	75.50	24.50
Total	27	71.66	10.52

b) Results of ANOVA comparing home range size of *C. cyanostigma* on patch and contiguous reef. Data was Ln(x) transformed. (* indicates significant result).

SOURCE	SS	DF	MS	F	Sig of F
Reef Type	21.99	1	21.99	41.17	0.000*
Within + Residual	27.77	52	0.53		

c) *C. boenak* home ranges (m^2)

Patch Reefs

Site	**Total n**	**Mean**	**SE**	**Reduced n**	**Mean**	**SE**
Casuarina	7	3.16	0.62	5	3.01	0.43
South Bay Pt	10	7.02	1.10	5	6.94	1.68
Total	17	5.43	0.83	10	4.98	1.05

Contiguous Reef

Site	**Total n**	**Mean**	**SE**
Chinamans	6	7.68	1.01
Mermaid	4	8.78	0.83
Total	10	8.12	0.68

d) Results of ANOVA comparing home range size of *C. boenak* on patch and contiguous reef. (* indicates significant result).

SOURCE	SS	DF	MS	F	Sig of F
Reef Type	49.28	1	49.28	6.33	0.021*
Within + Residual	140.12		18	7.78	

Table 8. Results of ANOVA comparing the proportion of rock-cods and their prey on the south side of patch reefs in southerly and northerly currents. Data was arcsine transformed (* indicates significant result).

SOURCE	SS	DF	MS	F	Sig of F
Current Direction	2.26	1	2.26	26.52	0.000*
Fish Type	0.12	1	0.12	1.44	0.254
Fish Type by Direction	0.12	1	0.12	1.38	0.263
Within + Residual	1.02	12	0.09		

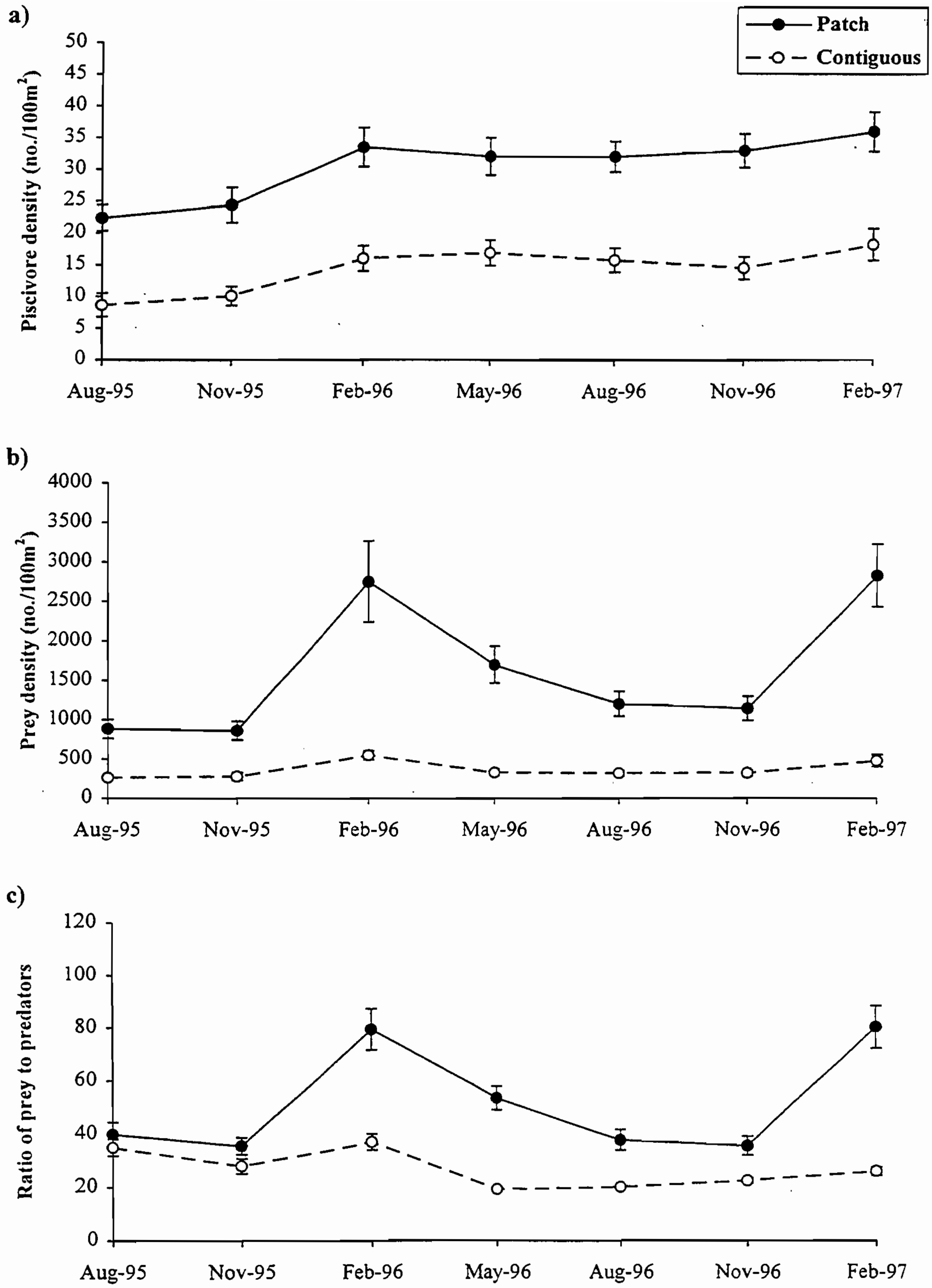


Figure 1. Temporal and spatial variation in the **a)** density of piscivores (mean+/-SE), **b)** density of prey (mean+/-SE) and **c)** the ratio of prey to piscivores (mean+/-SE) on patch and contiguous reefs (n=18 on patch reefs, except Aug-95 and Nov-95 n=12, and n=15 on contiguous reef, except Aug-95 and Nov-95 n=10).

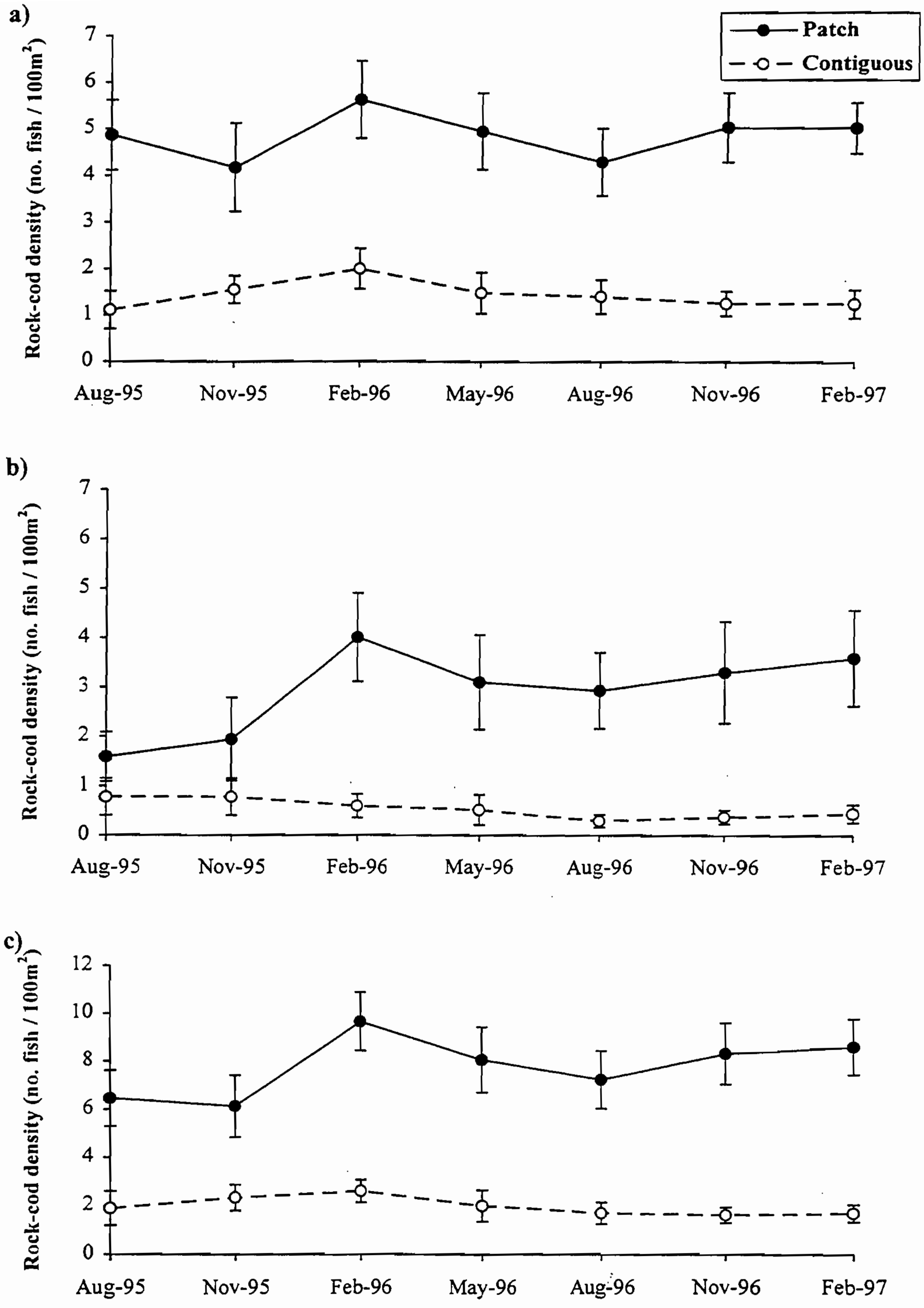


Figure 2. Temporal and spatial variation in the density (mean+/- SE) of **a)** *C. cyanostigma*, **b)** *C. boenak* and **c)** both species combined, on patch and contiguous reef (n=18 on patch reefs, except Aug-95 and Nov-95, n=12 and n=15 on contiguous reef except Aug-95 and Nov 95, n=10)

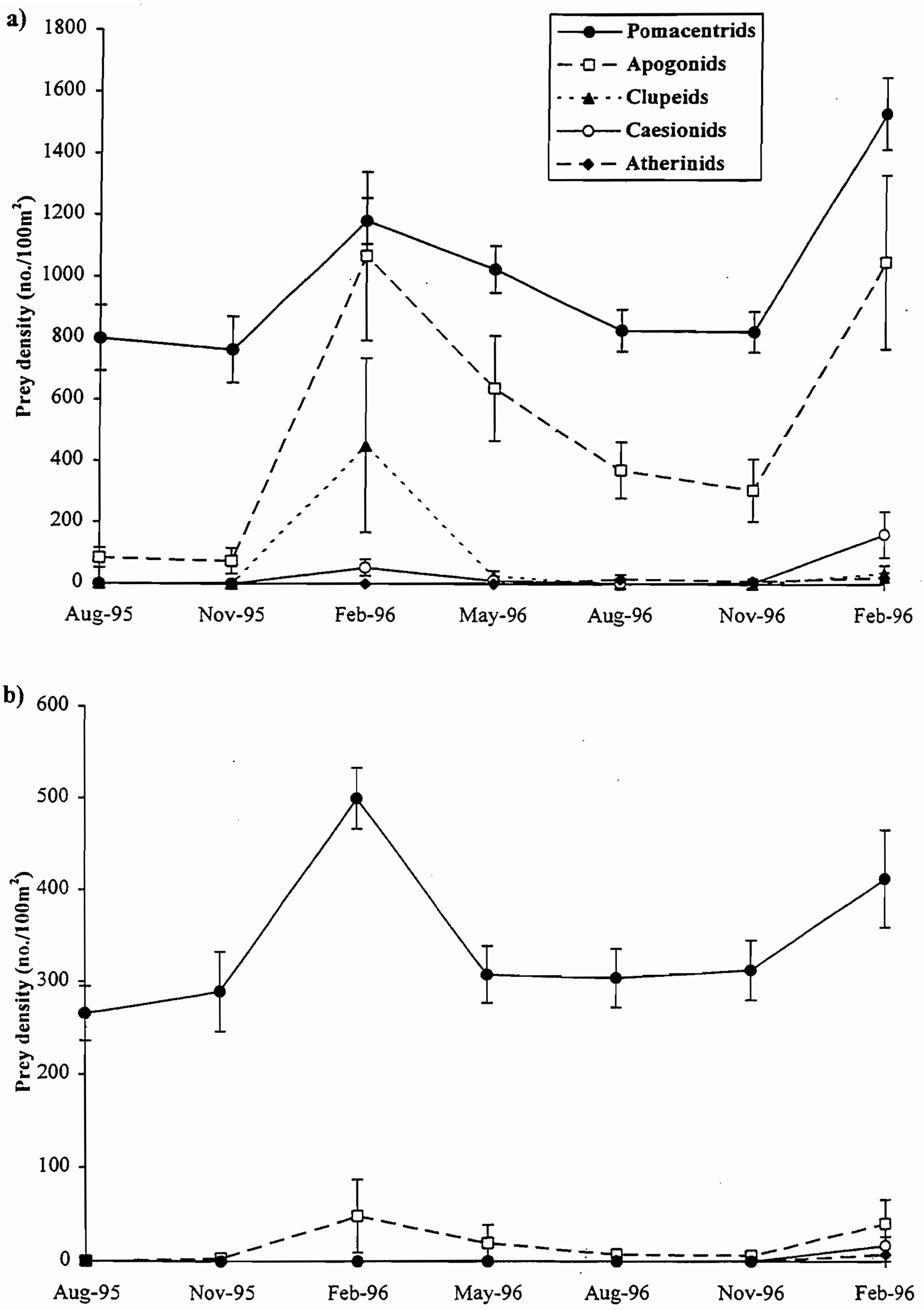


Figure 3. Temporal variation in the density (mean+/-SE) of families of prey fish on **a)** patch reefs (n=18, except Aug-95 and Nov-95 n=12) and **b)** contiguous reef (n=15, except Aug-95 and Nov 95 n=10)

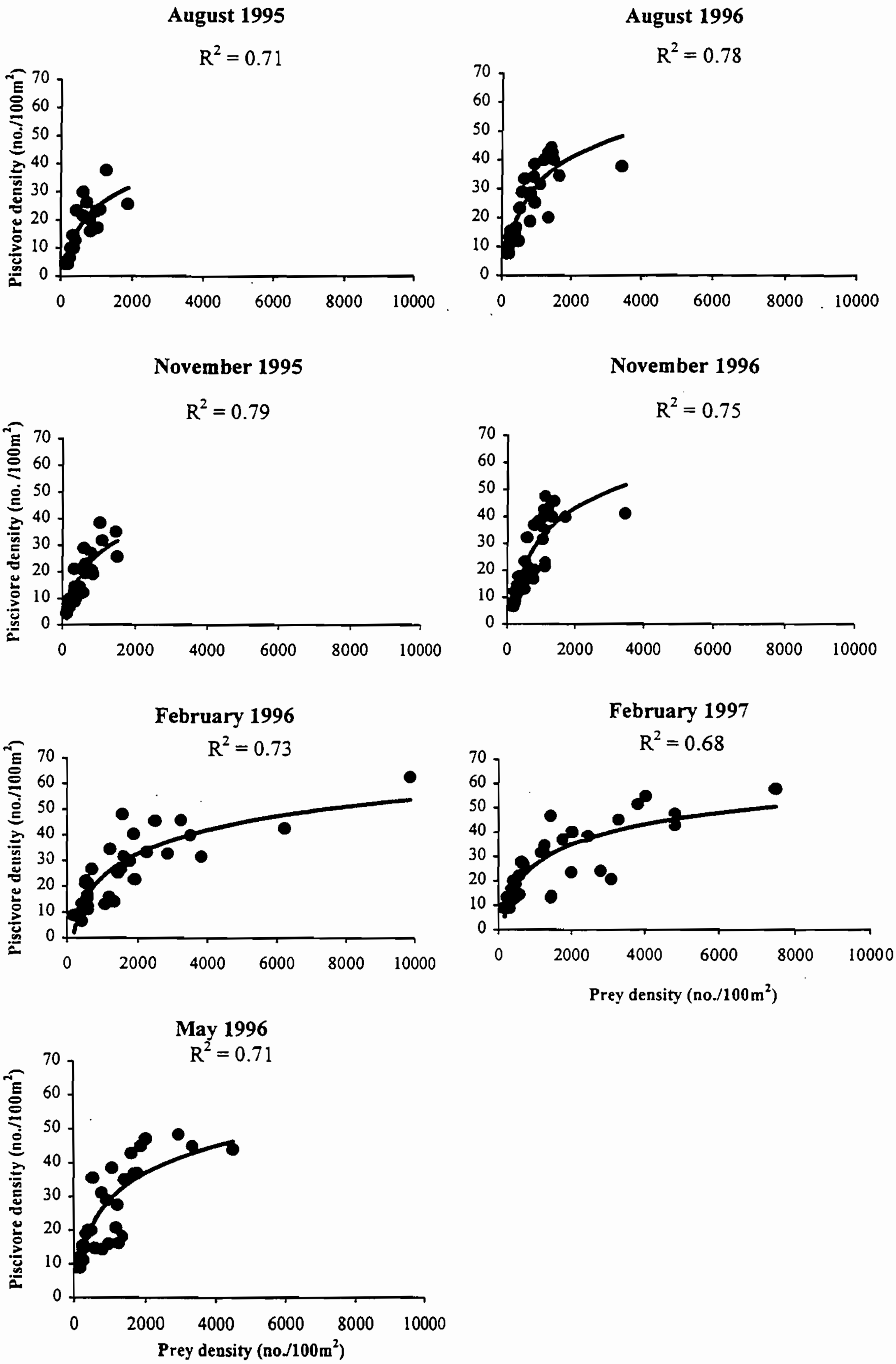


Figure 4. Temporal variation in the relationship between prey density and the combined density of all piscivorous species (see Table 4 for sample sizes and equations).

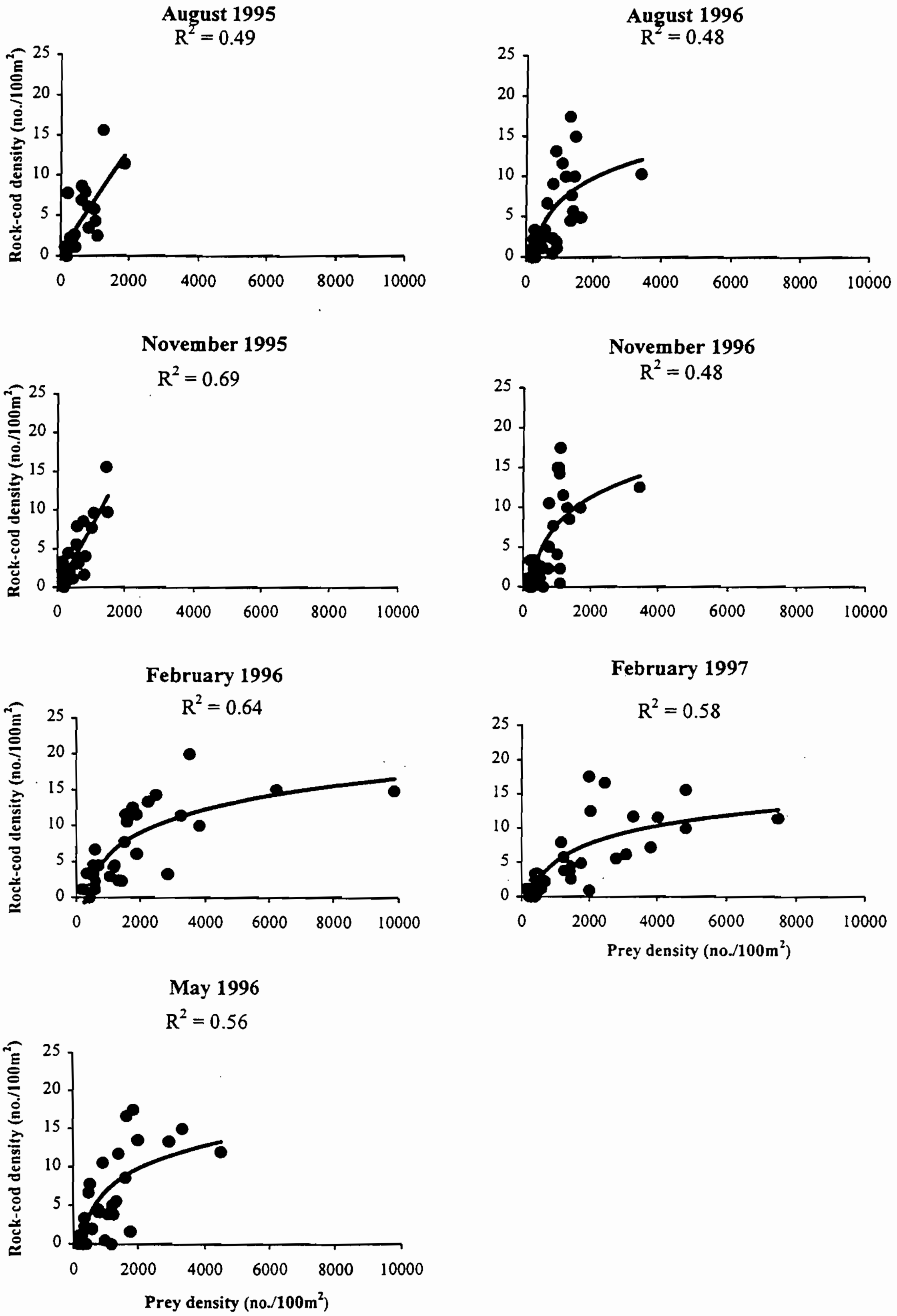
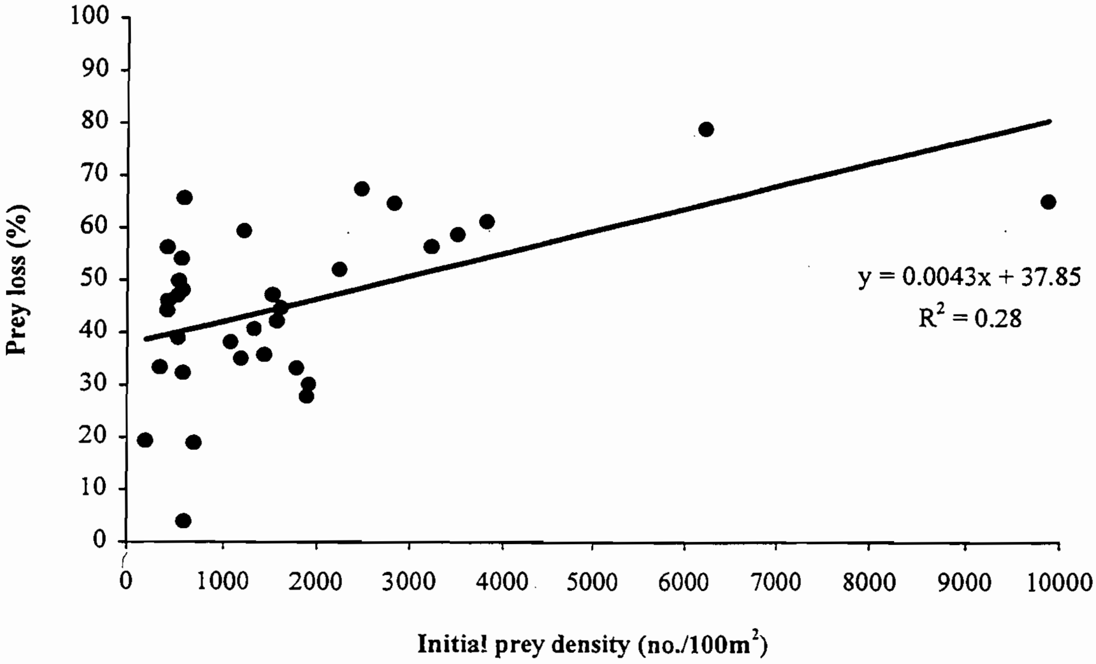


Figure 5. Temporal variation in the relationship between prey density and the combined density of *C. cyanostigma* and *C. boenak* (n=33, except August and November 1995 n=22, $p<0.05$ in all cases).

a)



b)

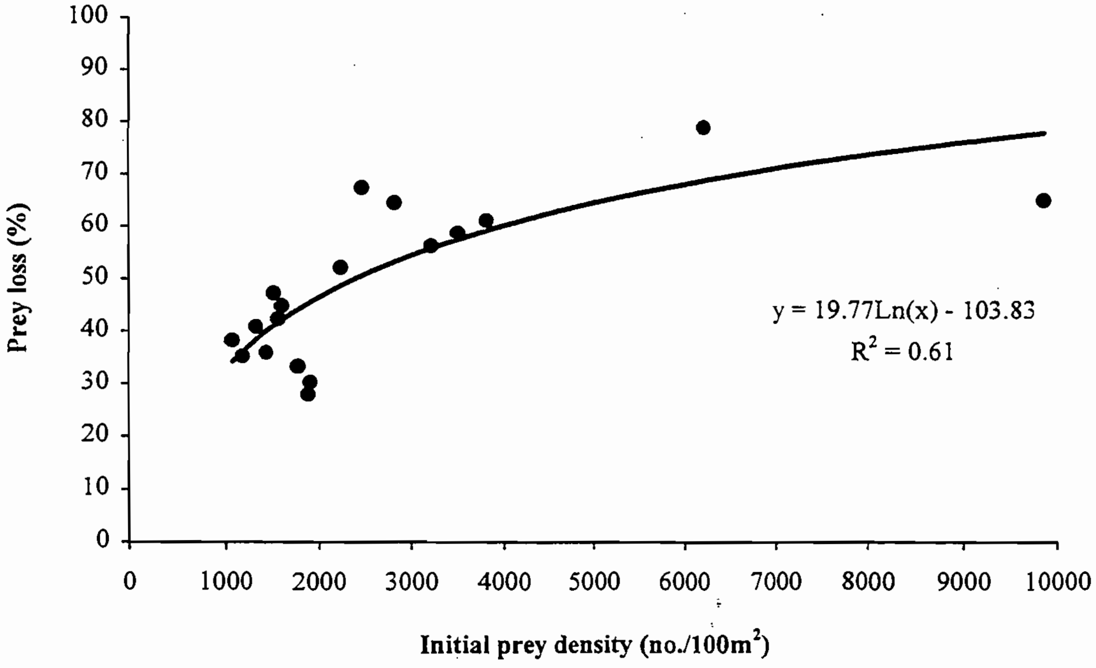
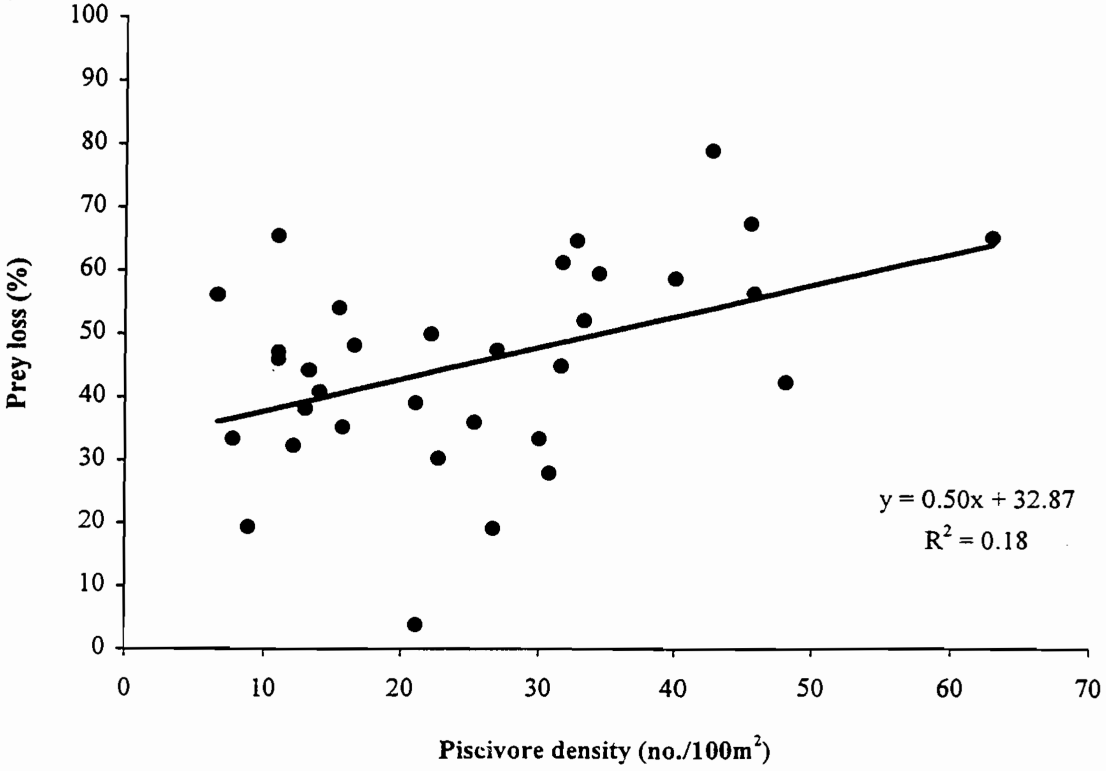


Figure 6. The relationship between initial prey density and percentage loss of prey from February to August 1996, **a)** contiguous and patch reefs (n=33), **b)** patch reefs only (n=18). $P<0.05$ in both cases.

a)



b)

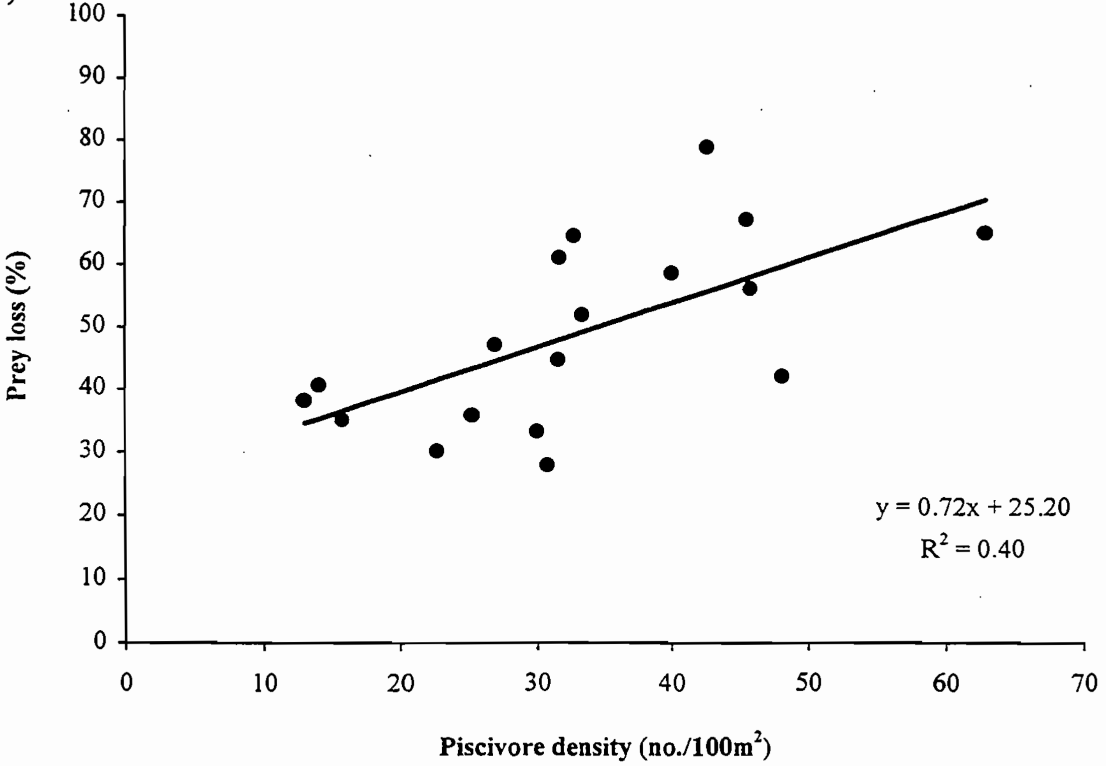
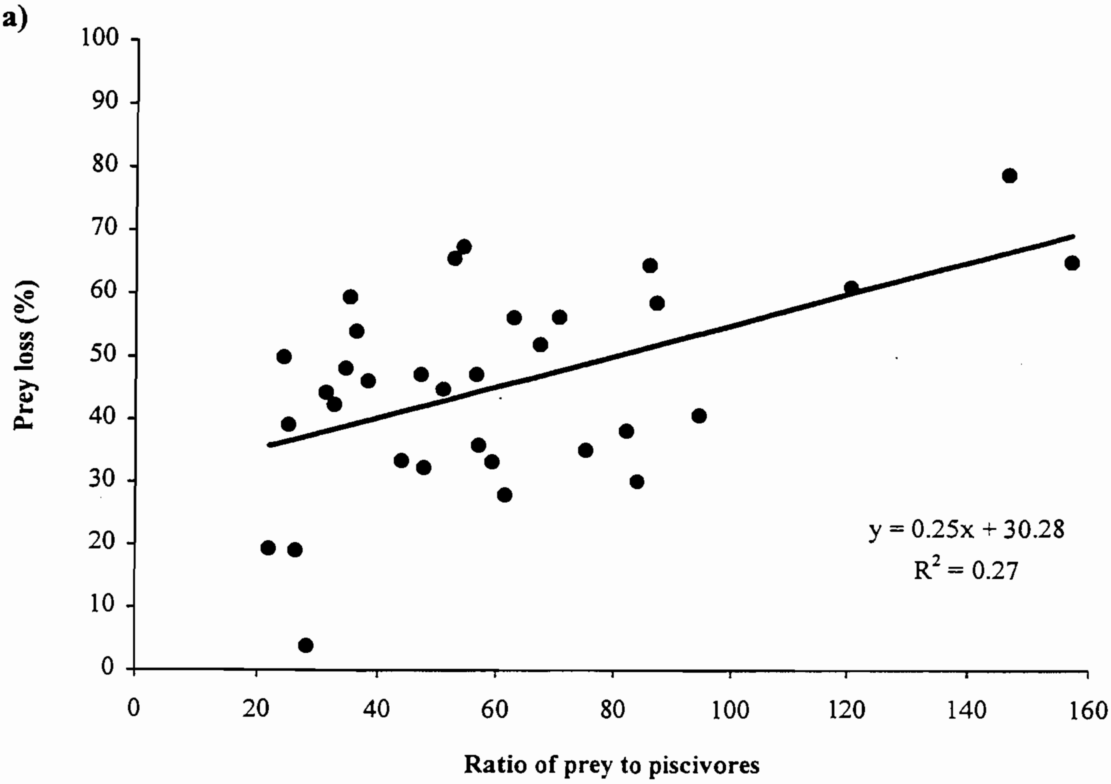


Figure 7. The relationship between piscivore density in February 1996 and percentage loss of prey from February to August 1996 **a)** contiguous and patch reefs (n=33), **b)** patch reefs only (n=18). $P < 0.05$ in both cases.

a)



b)

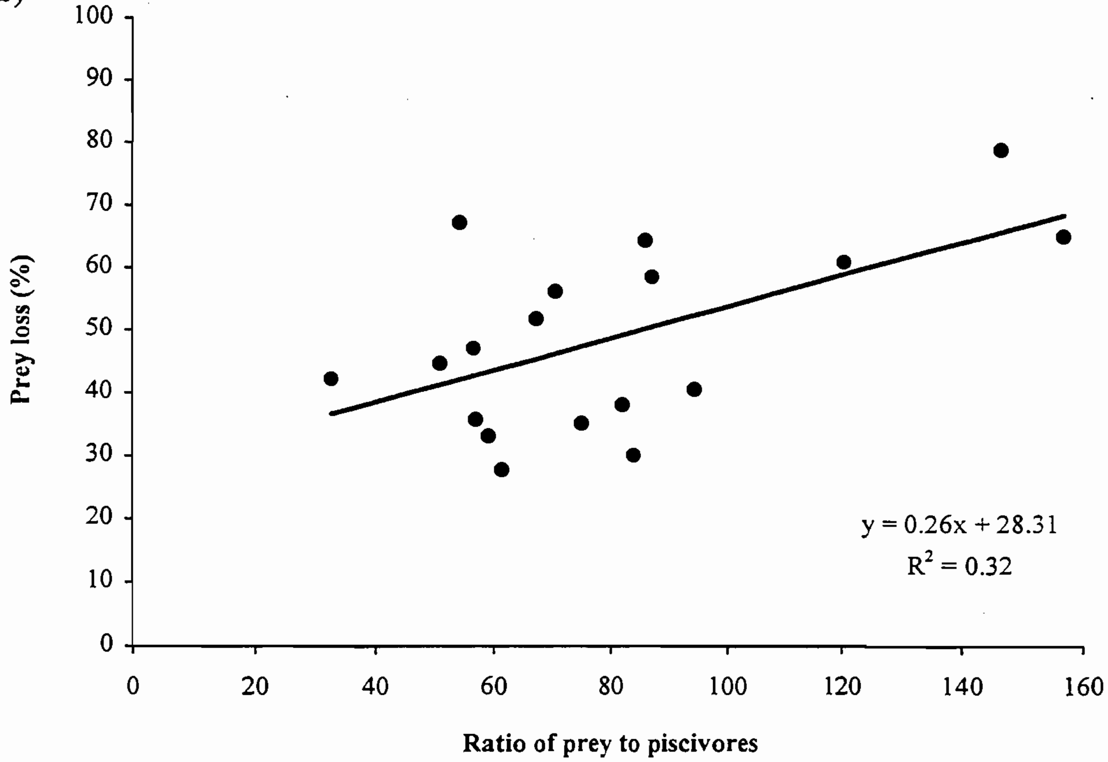


Figure 8. The relationship between the ratio of prey to piscivores in February 1996 and the percentage loss of prey from February and August 1996, **a)** contiguous and patch reefs (n=33), **b)** patch reefs only (n=18). $P < 0.05$ in both cases.

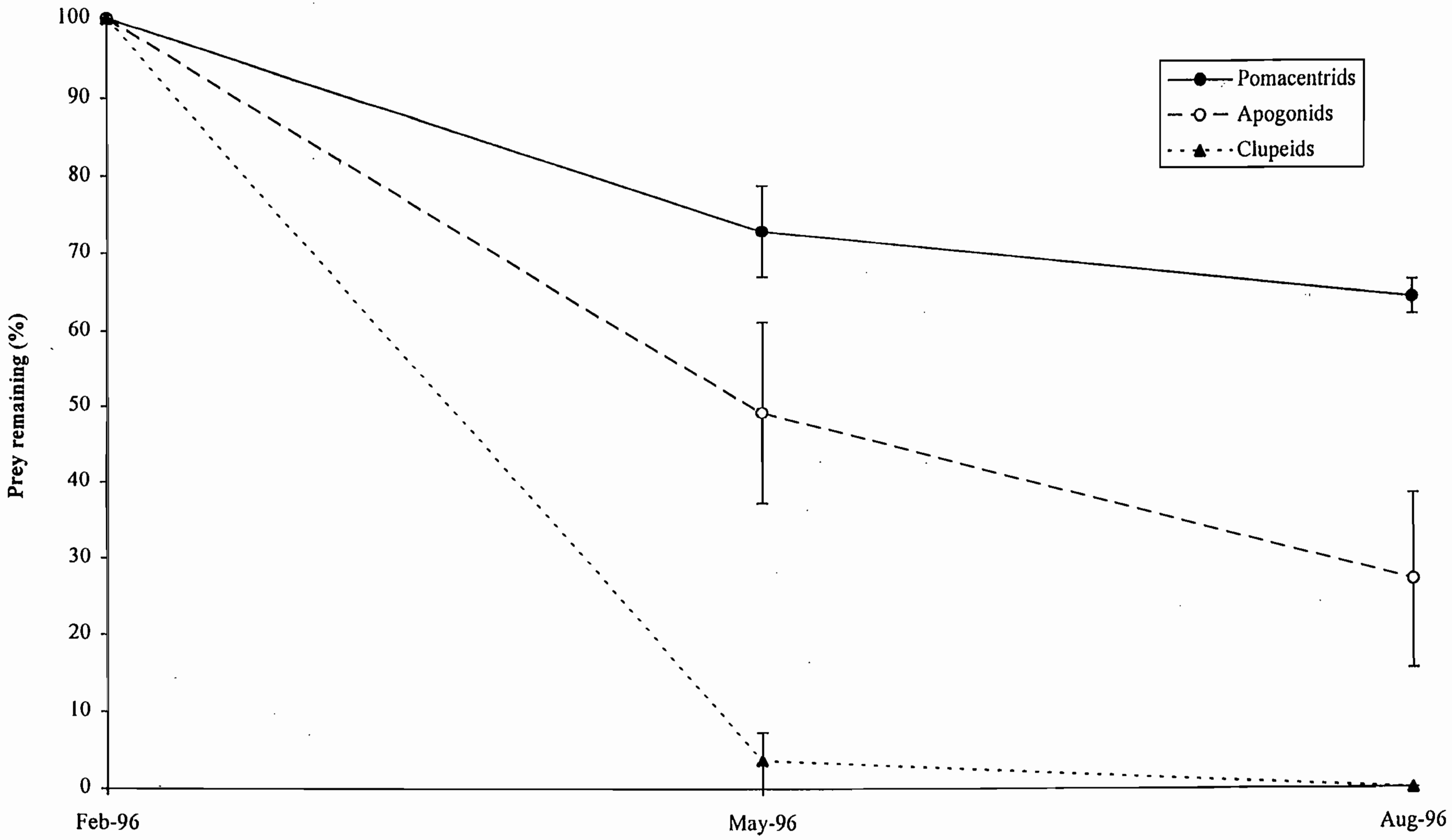


Figure 9. Percentage loss rates (mean+/-SE) of pomacentrids, apogonids and clupeids during 1996 (n=6 sites, except for clupeids n=3 sites)

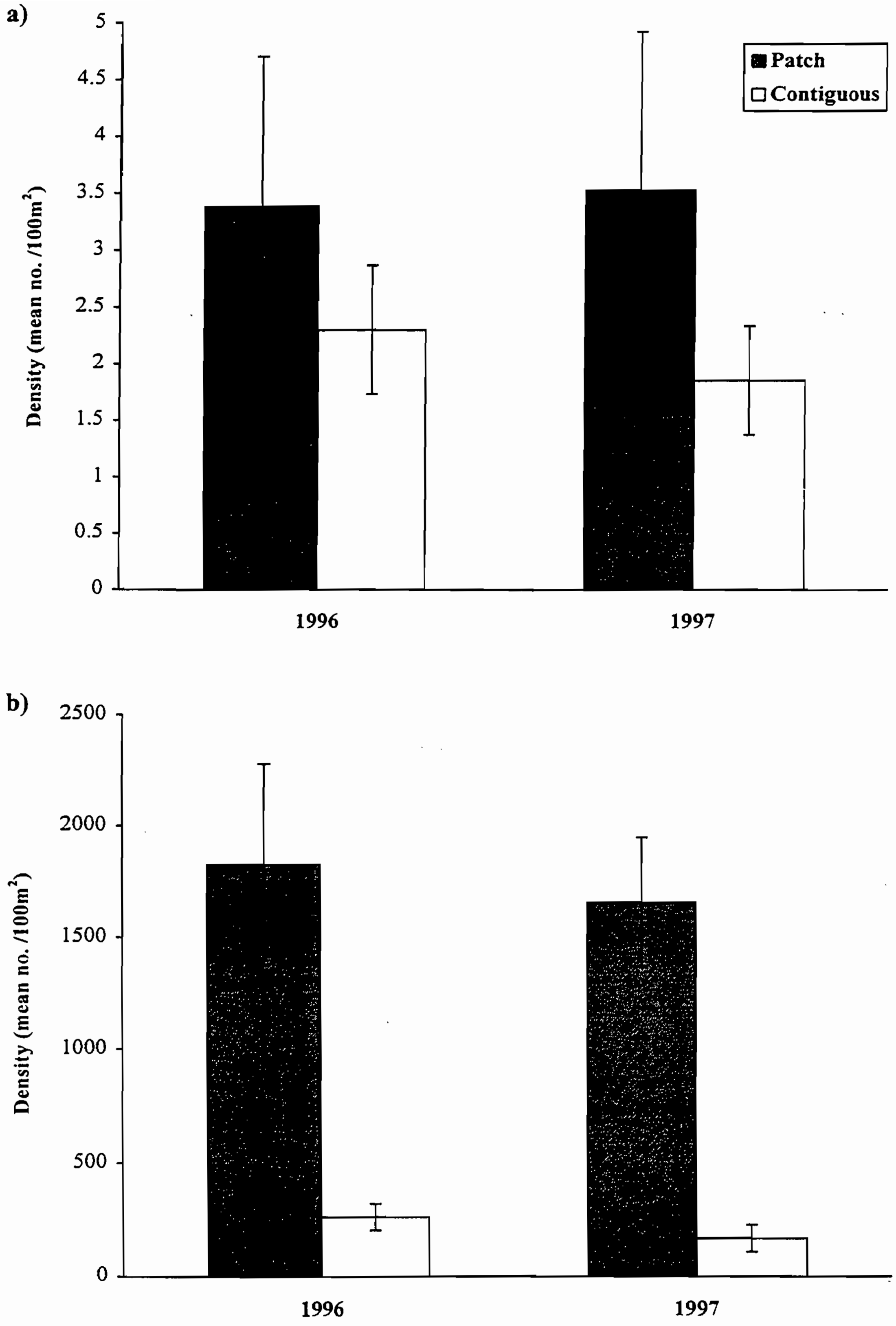


Figure 10. Temporal and spatial variation in the density (mean+/-SE) of **a)** piscivore and **b)** prey recruits on patch and contiguous reef in February 1996 and 1997 (n=18 on patch reef and n=15 contiguous reef).

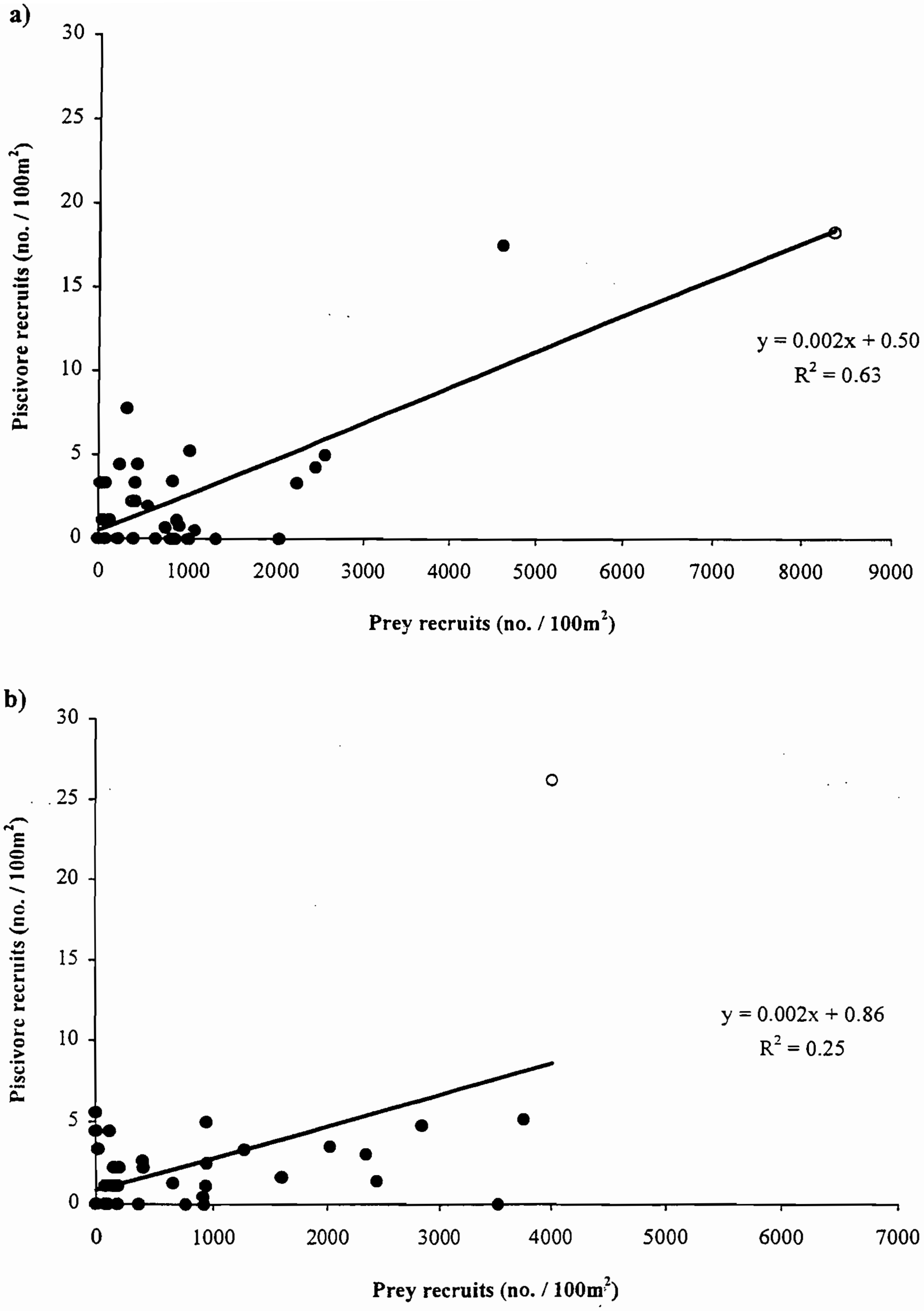


Figure 11. The relationship between prey and piscivore recruit density in **a)** February 1996 (n=33) and **b)** February 1997 (n=33). $P<0.05$ in both years, however, one patch reef (denoted by an open circle) had a large influence on the strength of the relationship in both years (see text for details).

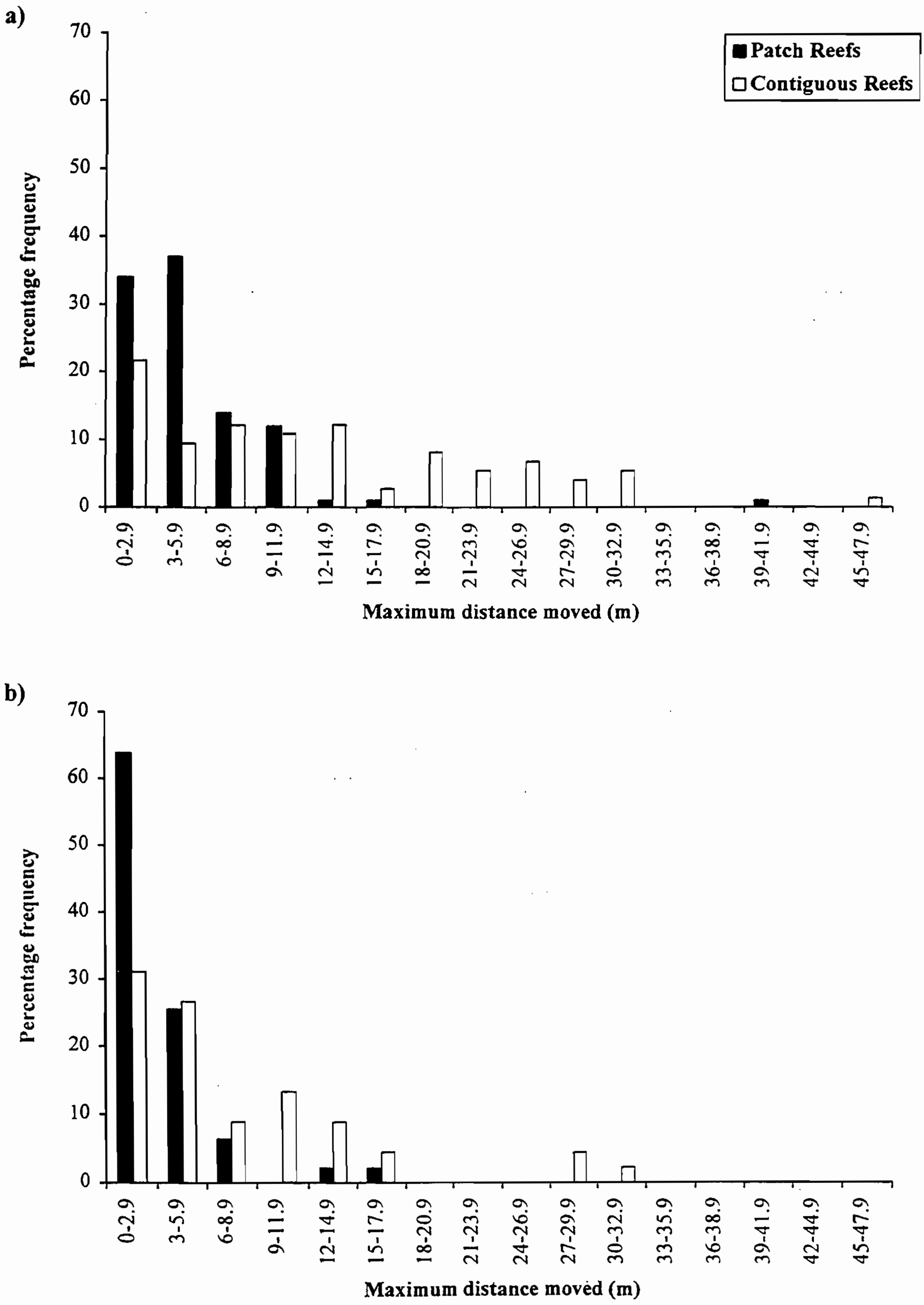


Figure 12. A comparison of the maximum distances moved by **a)** *C. cyanostigma* on patch (n=100) and contiguous reefs (n=74) and **b)** *C. boenak* on patch (n=47) and contiguous reefs (n=45)

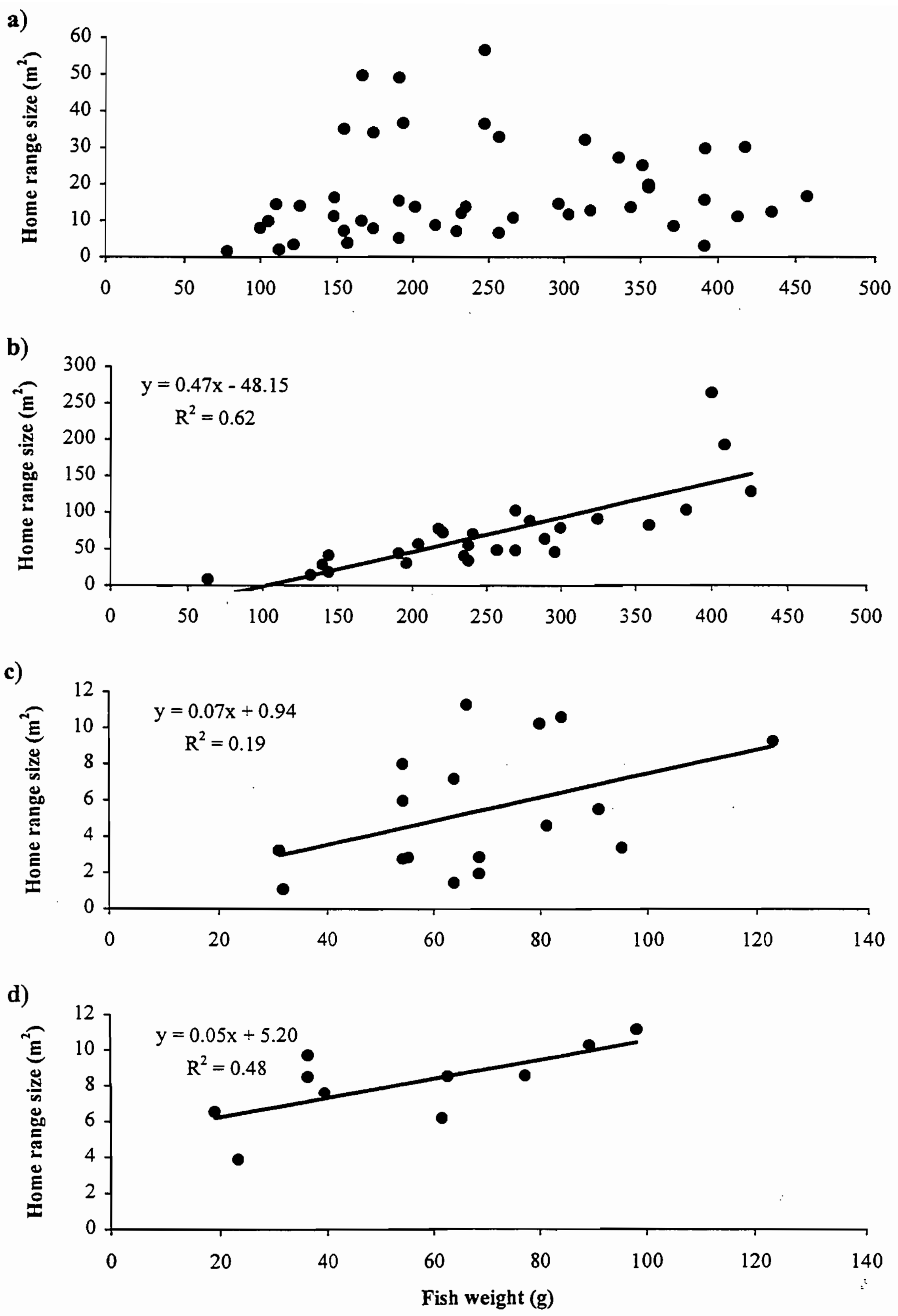


Figure 13. The relationship between fish weight and home range size for *C. cyanostigma* on **a)** patch reef (n=48) and **b)** contiguous reef (n=27) and *C. boenak* on **c)** patch reef (n=17) and **d)** contiguous reef (n=10). All relationships (except **a)**) significant ($p<0.05$).

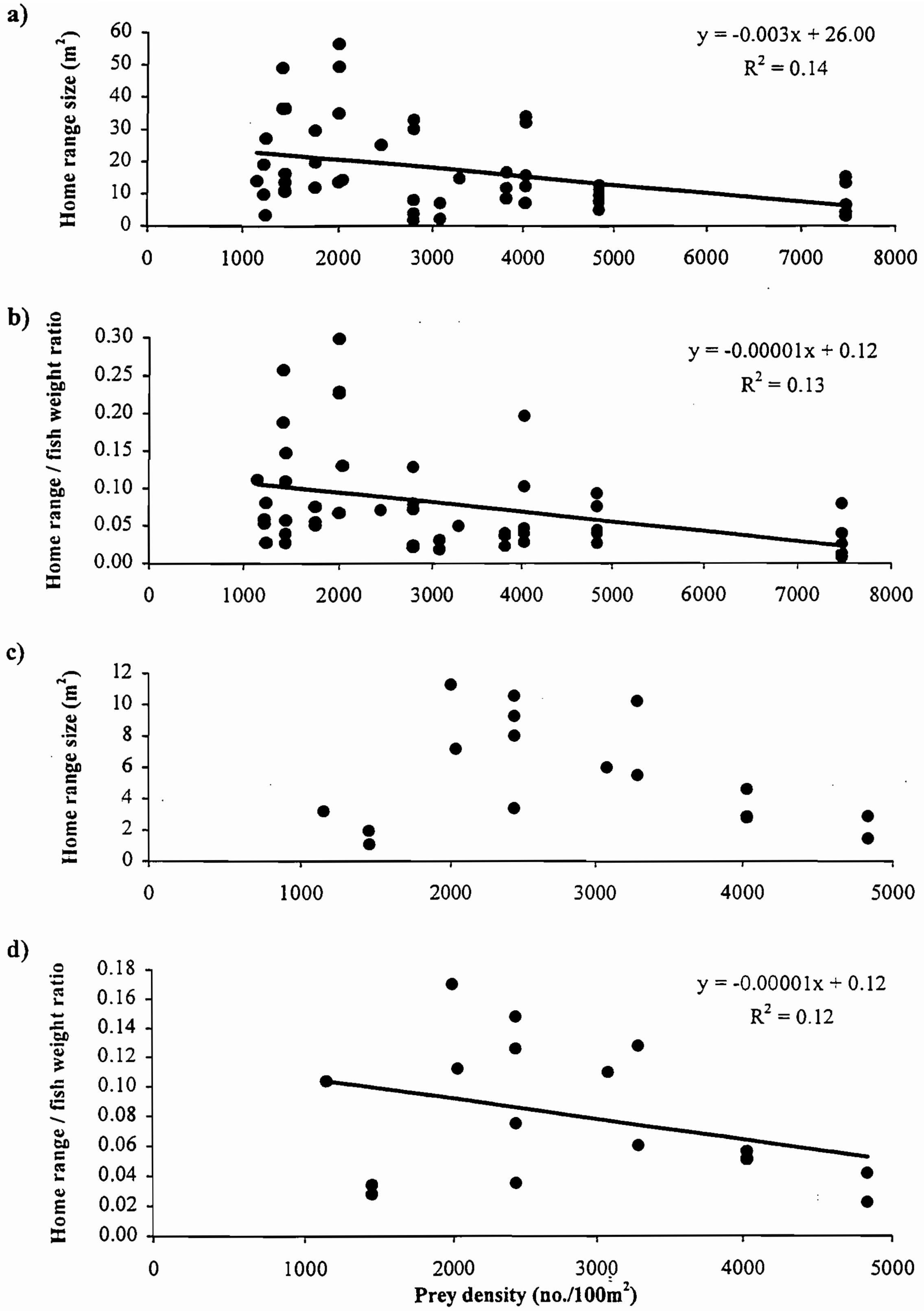


Figure 14. The relationship between prey density on patch reefs and **a)** home range size of *C. cyanostigma* (n=48), **b)** home range size / fish weight ratio of *C. cyanostigma* (n=48), **c)** home range size of *C. boenak* (n=17) and **d)** home range size / fish weight ratio of *C. boenak* (n=17). All relationships (except **c)**) significant ($p<0.05$).

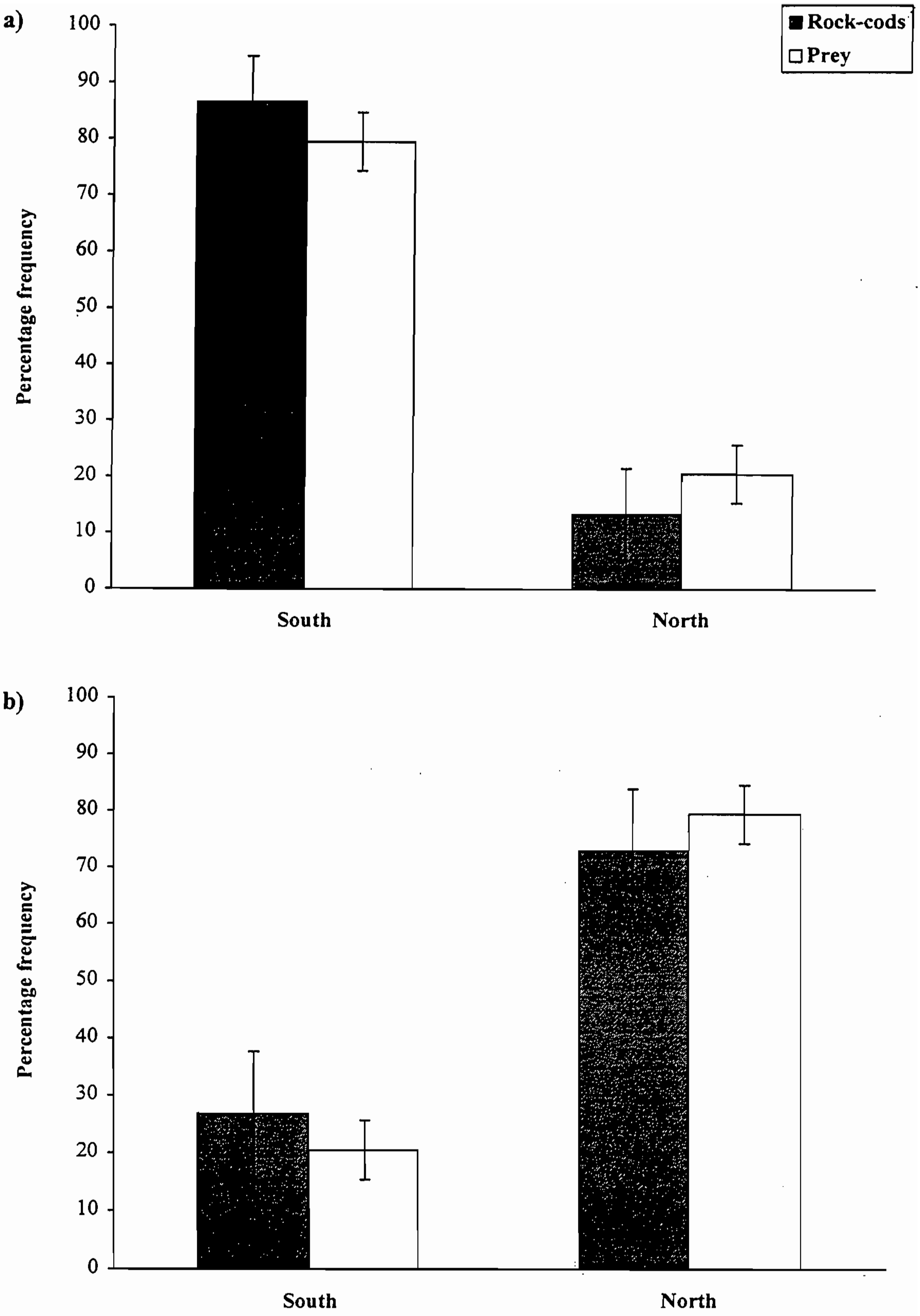


Figure 15. The proportion (mean+/-SE) of rock-cods (*C. cyanostigma* and *C. boenak*) and prey sighted on the south and north sides of patch reefs (n=4) in **a)** southerly and **b)** northerly currents.

Chapter 4

The influence of prey abundance on the feeding ecology of two piscivorous coral reef fishes

Abstract:

Despite the potential importance of predation as a process structuring coral reef fish communities, few studies have examined how the diet of piscivorous fish responds to fluctuations in the abundance of their prey. This study focused on two species of rock-cod, *Cephalopholis cyanostigma* and *C. boenak* (Serranidae) and monitored their diet in two different habitats (patch and contiguous reef) at Lizard Island on the northern Great Barrier Reef, Australia, over a two year period. The abundance and family composition of their prey was monitored at the same time. Dietary information was collected largely from regurgitated samples, which were found to represent 60 % of the prey consumed and were unbiased in composition. A laboratory experiment showed that fish were digested approximately four times faster than crustaceans, leading to gross overestimation of the importance of crustaceans in the diet. When this was taken into account fish were found to make up over 90% of the diet of both species. Prey fish of the family Apogonidae, followed by Pomacentridae and Clupeidae, were found to dominate the diet of both species of rock-cod. The interacting effect of fluctuations in prey abundance and patterns of prey selection caused dietary composition to vary both temporally and spatially. Mid-water schooling prey belonging to the families Clupeidae and to a lesser extent Caesionidae were selected for over other families. In the absence of these types of prey apogonids were selected for over the more reef-associated pomacentrids. A laboratory experiment supported the hypothesis that such patterns were largely due to prey behaviour. Feeding rates of both species of rock-cod were much higher in summer than in winter, and in summer they concentrated on small recruit sized fish. There was little variation in feeding rates between habitats, however, despite apparent differences in prey abundance. The combination of high densities, high feeding rates and selection for certain sizes and types of fish suggested that the two rock-cod

species were having a considerable impact on populations and communities of their prey. Removal of large numbers of piscivorous coral reef fish (such as occurs with overfishing) may have significant effects which flow on to entire coral reef communities.

Introduction:

Predation is one of the most important processes influencing the dynamics of population (Murdoch & Oaten 1975; Taylor 1984) and the structure of ecological communities structure (Paine 1966; Connell 1975; Menge & Sutherland 1987). The most direct way in which predators impact prey populations is by consuming individuals. This may lead to the local extinction of prey populations (Murdoch and Bence 1987), or the reduction of prey population size to a point below the carrying capacity of the environment (Menge and Sutherland 1987). Consequently, predators may effect the species diversity and composition of prey communities (Menge and Sutherland 1987). In addition, predators may also have indirect effects on prey morphology, physiology, chemistry, life history and behaviour (Sih 1987). In prey populations subject to high predation pressure this may lead to effects on habitat selection, feeding rates, growth and reproductive success (Milinski 1986; Sih 1987; Holbrook & Schmitt, 1988).

Despite a long history of research in other ecosystems, until recently predation received relatively little attention as a process which may be structuring coral reef fish communities (Hixon 1991). In the last 7 years a number of researchers (Caley 1993; Hixon & Beets 1993; Carr & Hixon 1995; Connell 1996, 1997, 1998b; Beets 1997; Beukers & Jones 1997; Eggleston et al. 1997; Hixon & Carr 1997) have attempted to redress this situation and have focused their attention on manipulating densities of piscivorous fish as a means to examining the importance of predation. Predator densities were manipulated either by the habitat provided (Hixon & Beets 1993), by selectively removing predators (Caley 1993; Carr & Hixon 1995; Beets 1997; Eggleston et al. 1997) by caging (Connell 1996, 1997, 1998b; Hixon and Carr 1997), or by transplanting known densities of predators (Beukers & Jones 1997). All of these studies showed reduced prey abundance in the presence of predators, along with a range of other effects such as decreased species diversity (Caley 1993, Beets

1997, Eggleston 1997), variation between species (Carr & Hixon 1995), mediation by habitat structure (Hixon & Beets 1993, Beukers & Jones 1997; Eggleston et al. 1997), effects of prey density (Hixon & Carr 1997, Connell 1998b) and the role of different types of predators (Hixon & Carr 1997). In all of these studies, however, information on the identity of the species responsible for predation and the rates at which they were consuming prey was either lacking or sparse.

Clearly, a full understanding of the role of predation on coral reefs requires detailed descriptions of spatial, temporal and ontogenetic changes in diet, prey selection and feeding rates of piscivorous fish and how these interact with prey dynamics (Jones 1991). The most common method for elucidating the identity and diet of coral reef piscivores has been the study of gut contents. Such work commenced in the 1960s (Hiatt & Strasburg 1960; Miles 1963; Randall 1967), but has been less common in more recent years (Hobson 1974; Harmelin-Vivien & Bouchon 1976; Norris & Parrish 1988; Shpigel & Fishelson 1989; Connell 1998a). Many of these studies examined a large number of potentially piscivorous species and so were very useful for identifying piscivores, however, this meant samples sizes for individual species were often low (less than 50). Low samples sizes, combined with a large number of empty stomachs and advanced digestion of prey has generally prevented detailed description of diet for individual species (for exceptions see Kingsford 1992 and St John 1995). In addition, lack of information on digestion rates has also often prevented conversion of stomach content data into estimates of daily feeding rates.

Another problem with gut content studies is that they generally require the removal of large numbers of the piscivorous species in question from study sites. This makes it difficult, if not impossible, to examine temporal variation in diet without spatial variation potentially confounding results. One way to bypass this problem is to remove gut contents from live fish (Hyslop 1980) so that repeated sampling of the same individuals becomes possible. This has been achieved by stomach flushing in some freshwater and temperate fish (Andreasson 1971; Meehan & Miller 1978), but has very rarely been attempted for coral reef fish (Light 1995).

Direct observation of predatory behaviour is an alternative approach to assessing the impact of piscivores on prey. This was used successfully by Sweatman (1984), who estimated that prey fish had a 65% chance of being consumed in one year by a single species of piscivore. In general, however, direct observation is difficult due to the high mobility of piscivorous species (Samoilys 1986; Zeller 1997), the infrequent and unpredictable nature of predatory strikes (Samoilys 1986; Martin 1994) and the difficulty of determining outcomes (Martin 1994).

Some predatory coral reef fish have been shown to mainly eat crustaceans when they are young, switching to a more piscivorous diet as they grow older and larger (Harmelin-Vivien & Bouchon 1976; Parrish 1987; St John 1995). The nature of this change may be important for predator / prey interactions. For example, variation in the age / size composition of predatory individuals in the community may effect the impact of piscivores on prey (Kingsford 1992).

Piscivorous coral reef fish are often considered to be generalist, opportunistic predators, whose diet reflects the abundance of prey available (Harmelin-Vivien & Bouchon 1976; Parrish 1987). This common perception is surprising given that only one study on coral reefs (Shpigel & Fishelson 1989) has compared predator diet to the availability of prey at the same place and time. This is despite the widespread use of this approach for examining prey selection in other fish communities (Laur & Ebeling 1983; Jones 1984; Schmitt & Holbrook 1984; Cowen 1986). The predators studied by Shpigel and Fishelson (1989) did appear to concentrate on the most common prey available, although results were only reported in general terms.

A more detailed study of the prey available to predators would provide information on several important factors. Firstly, it would give details on the vulnerability of different prey types to predators. If some species suffer proportionally higher predation than others this will have important implications for community structure (Carr & Hixon 1995). Secondly, it would provide information on how different size classes of prey are impacted by predation. Mortality of coral reef fish is often highest during the early period after settlement (Doherty

& Sale 1985; Eckert 1987; Meekan 1988), but the role of predation in producing this pattern is not clear. Thirdly, it would give insights into how predators respond to variations in the abundance of their prey. If, for example, predators consume proportionally higher numbers of prey during pulses of recruitment then this will dampen these peaks in abundance and change the relative numbers of prey surviving to maturity (Caley et al. 1996). The ideal situation would be to compare data on consumption rates of predators with patterns of mortality of their prey in order to determine the relative importance of different predatory species.

This study examined the diet and feeding rates of two piscivorous species of rock-cod, *Cephalopholis cyanostigma* and *C. boenak* (Serranidae) at Lizard Island on the northern Great Barrier Reef, Australia. Dietary information was collected mainly from regurgitated samples so that the same populations could be monitored over time. This data was then related to information on the family composition and abundance of prey communities monitored at the same sites and times (see Chapter 3). It was therefore possible to measure prey selectivity and to investigate how predator feeding rates responded to fluctuations in the abundance of prey. The two target species were ideal for the planned study as they are among the most common piscivores at Lizard Island (Chapters 2 and 3) and were relatively site attached during the study (Chapter 3). This made monitoring of the prey available to these species relatively simple compared to more mobile piscivores. Finally, consumption rates of the two rock-cod species were used to assess their impact on standing stocks of prey. This was related to known loss rates of prey during the same period (see Chapter 3) to determine the relative contribution of each piscivorous species to patterns of mortality.

Methods:

The study was conducted between February 1995 and April 1997 on the western (predominantly sheltered) side of Lizard Island ($14^0$40'S; $145^0$28'E) on the northern Great Barrier Reef, Australia. Six sites were selected in 5 to 10m of water depth, 3 on contiguous reef and 3 on patch reefs. Each site on contiguous reef was situated on the slope of the fringing reef and measured 30 m x 30 m (area 900 m^2). Each of the patch reef sites consisted of 6 reefs, ranging in size from 40 m^2 to 306 m^2 (mean 114 m^2). Total area of reef at each of the patch reef sites ranged from 506 m^2 to 960 m^2. The fish studied were almost completely restricted to each site during the study (Chapter 3).

1. Dietary Composition

Over the course of a tagging study (see also Chapters 3 and 5) a total of 548 *Cephalopholis cyanostigma* and 311 *C. boenak* were captured underwater by baited hook and line at the 6 sites (see Table 1). Fish captured ranged in total length from 12.6 cm to 31.4 cm for *C. cyanostigma* and from 9.8 cm to 21.4 cm for *C. boenak*. Many of these fish regurgitated prey upon or soon after capture, providing gut content information. Any regurgitated material was collected in plastic zip-lock bags underwater or in specimen jars (containing a 10% buffered formalin solution) if regurgitation occurred while fish were being tagged in the boat. Collecting gut content information in this way allowed for repeated sampling of the same populations of fish without any effect on their abundance.

a) Validation of dietary analysis using regurgitated prey

To validate the accuracy of the regurgitated gut content samples I also dissected fish from which regurgitated material had already been collected. In August 1996 (Winter) 26 *Cephalopholis cyanostigma* individuals were collected from areas adjacent to 4 of the main study sites (2 areas of patch reef and 2 areas of contiguous reef). Between February and April 1997 (Summer) 89 *C. cyanostigma* and 62 *C. boenak* individuals were also collected from the 6 study sites. Fish were captured and tagged as previously before being sacrificed in an ice / seawater slurry. Fish were then gut injected with a 10% buffered formalin solution and kept on ice for 2 to 4 hours before being dissected. The frequency of prey items dissected was compared to that regurgitated as were the relative proportions of fish and invertebrates in the samples. This was to determine if the regurgitated samples were biased.

b) Estimation of digestion rates

Information on digestion rates was already available for *Cephalopholis boenak* (Martin 1994) so this part of the study only involved *C. cyanostigma*. During February and March

1997, 12 individuals, ranging in size from 210 mm to 290 mm total length (TL), were captured in the field and then kept in 2000 litre outdoor aquaria for 2 days to acclimatise. Each individual was then fed one fish (Pomacentridae - either *Pomacentrus moluccensis* or *P. amboinensis*) and one crab (Xanthidae). Fish size ranged from 23 mm to 33 mm standard length (mean 28.25 mm) while crab size ranged from 13 mm to 16 mm carapace length (mean 14.88 mm). The volume of each fish and crab consumed was approximately equivalent (1 ml). This type and size of prey was typical of that taken in the field (see results). At each of 4 different time periods after fish were fed (1 hr, 4 hrs, 12 hrs and 24 hrs), 3 individuals were sacrificed in an ice / seawater slurry. Fish were then gut injected with a 10% buffered formalin solution and kept on ice for 2 to 4 hours before being dissected. Any prey remaining in the stomachs was assigned to one of 5 categories denoting the degree of digestion (see Table 2). This provided a typical time scale for each digestion category and determined if fish and crustaceans were digested at different rates.

c) Overall dietary composition

All regurgitated and dissected prey collected was examined under a binocular microscope and classified to the highest taxonomic level possible (usually to family). If possible each prey item was allocated to an individual fish (this was not always possible for regurgitated prey) and was also classified according to the digestion scale (Table 2). The importance of different families of prey in the diet of each species was examined in four different ways. Firstly, by percentage frequency (ie the number of times that family of prey was recorded as a percentage of the total number of identifiable prey items), secondly by percentage occurrence (ie the number of fish containing that family of prey as a percentage of the total number of fish containing identifiable prey) and thirdly by percentage volume (ie the total volume of that family of prey as a percentage of the total volume of all families of prey). Volume was measured by water displacement and was only assessed for prey belonging to digestion category 3 or above. The fourth measure, an index of relative importance (IRI) (Pinkas et al. 1971; Hyslop 1980), was a combination of the three previous measures, calculated by the following formula:

$$\mathbf{IRI = (\%F + \%V) \times \%O / 100}$$

where %F was the percentage frequency, %V was the percentage volume and %O was the percentage occurrence. Each measure of importance was calculated separately for fish and invertebrates.

d) Ontogenetic variation in dietary composition

Using both the regurgitated and dissected samples the relative percentages of fish and invertebrates consumed by different size-classes of rock-cods was examined to determine if the degree of piscivory changed with size. The standard length (SL) of each fish containing prey was also plotted against the SL of the prey it had consumed. This examined how prey size-selection varied with increasing fish size..

e) Seasonal and spatial variation in dietary composition

Using the regurgitated and dissected samples, seasonal variation in the degree of piscivory was examined when at least 10 individuals of each species had been captured at each site. Mean percentage of piscivory in each season (or at different times of the year for *Cephalopholis boenak*), using sites as replicates, was compared by one-way ANOVA. Data was arcsine transformed due to heterogenous variances (Cochrans C Test, $p < 0.05$). Seasonal and spatial variation in the percentage frequency of different families of prey was also examined. When sample size allowed, prey items were separated into those consumed on the two different reef types (patch and contiguous) in two different seasons (summer and winter). Sufficient sample size was deemed to be at least 10 prey items for each combination of season and reef type. Fish and invertebrates were analysed separately and data was pooled between years and across sites within the different reef types. The size composition of fish prey taken on each reef type and in each season was also examined and compared.

2. Prey selection

a) Field observations

The above data on temporal and spatial variation in dietary composition was then compared to the abundance of prey fish available at each place and time (using the prey surveys from

Chapter 3). In this case data was again pooled across sites within reef types but not between years. This enabled me to examine if some families of prey were consumed in greater or lesser proportion than would be expected from their availability. To quantify any prey selection occurring an electivity index (E*) (Vanderploeg & Scavia 1979) was calculated using the following formula:

$$\omega_i = \frac{\frac{r_i}{P_i}}{\Sigma_i \frac{r_i}{P_i}} \quad \text{and} \quad E* = \frac{[\omega_i - (\frac{1}{n})]}{[\omega_i + (\frac{1}{n})]}$$

Where r_i was the proportion of each family consumed and P_i was the proportion available. A positive value of E* indicates selection for a prey type while a negative value indicates selection against a prey type. This index would be biased if families of prey were rare in the environment (Lechowicz 1982) so selection was only examined for the most common families of prey on each reef type and in each season.

b) Laboratory experiment

The prey selection of *Cephalopholis boenak* was further investigated in a laboratory experiment conducted during February and March 1997. In large outdoor aquaria (2000 litre), small patch reefs (approx. 0.125 m^3) were built from live *Porites cylindrica,* with 1 *C. boenak* (approx. 150 mm TL) added to each of 6 treatment tanks while 6 identical control tanks were left free from predators. After 2 days acclimatisation 5 *Apogon fragilis*, 5 *Neopomacentrus azysron* and 5 *Pomacentrus moluccensis* (all between 10 and 20 mm TL) were released into each aquaria after first being floated in plastic bags for 5 minutes. The number of each species surviving was then monitored after 1 hour, 2 hours and then every 12 hours for a 7 day period. The number of each species surviving at the end of the experiment was compared by ANOVA with the single fixed factor being species. Tukey's honestly significant difference (HSD) method was used to examine differences between species (Day and Quinn 1989).

3. Feeding rates

a) Diel variation in feeding rates

Feeding rates were calculated by simply dividing the number of prey collected by the number of rock-cods captured. Diel variation in feeding rates was examined in two ways. Firstly, the number of fresh prey (ie digestion stage 1 or 2) regurgitated was divided by the number of fish captured in each of three different time periods of the day (morning 6am-10am, midday 10am-2pm and afternoon 2pm-6pm). Secondly, feeding rates were calculated for regurgitated prey of all digestion stages. This part of the study was based only on fish prey collected during summer, when all 3 time periods were sampled. Data was pooled across sites, reef types and years. Observations of fish behaviour at night (6pm-10pm) were also made on four different occasions.

b) Seasonal and spatial variation in feeding rates

Seasonal and spatial variation in feeding rates was examined when at least 10 individuals of each rock-cod species were captured at each site. Feeding rates (based on both frequency and volume) were calculated separately for the fish and invertebrates regurgitated at each site. Using sites as replicates, the mean feeding rate on each reef type at each sampling date was then determined. Differences between reef types and times were examined by two way ANOVA. The two fixed factors were season (or time of year for *Cephalopholis boenak*) and reef type. Data was square root transformed when variances were heterogeneous (Cochrans C Test, $p < 0.05$). Tukey's HSD method was used in post-hoc analysis to compare means. Feeding rates on the two reef types during summer 1997 were also examined by combining the data from both regurgitated and dissected prey. A one way ANOVA was performed on this data with the single fixed factor being reef type. Data was again square root transformed when necessary.

4. Impact of *Cephalopholis cyanostigma* and *C. boenak* on prey populations

The impact of *Cephalopholis cyanostigma* and *C. boe*nak on prey fish populations was calculated for the period between February and August 1996 and compared to the estimated loss of prey during the same time (see Chapter 3). Impact was calculated separately for each reef type using information on the density of each rock-cod species (see Chapter 3) and the mean of the summer and winter feeding rates. Rock-cod densities were adjusted according to the cryptic nature of each species (see Chapter 2) and feeding rates were converted to the number of prey consumed each day using information on the proportion of prey regurgitated and digestion rates.

Results:

1. Dietary composition

a) Validation of dietary analysis using regurgitated prey

In winter for *Cephalopholis cyanostigma* and for both species in summer, approximately 60% of the prey consumed was regurgitated (Table 3). The relative proportions of fish and invertebrates were very similar in both the regurgitated and dissected samples (Table 3).

b) Digestion rates

Digestion of fish prey was quite rapid in *Cephalopholis cyanostigma* (Fig 1a). After 4 hours substantial digestion of prey had occurred (digestion stage 3) and after 12 hours prey had completely disappeared. This suggests prey were digested in approximately 6 to 8 hours. Crustacean prey, on the other hand, were much slower to digest and even after 24 hours they were still relatively intact (digestion stage 2-3). Based on this comparison, crustaceans probably take at least four times longer than fish prey to be digested. Digestion of fish prey was similar for *C. boenak* (Fig 1b).

c) Overall dietary composition

Overall, fish made up 74.7% by frequency of the gut contents collected from *Cephalopholis cyanostigma* and 76.9% by volume. For *C. boenak* the respective figures were 65.38% by frequency and 74.4% by volume. Approximately 64% of fish prey and all of the invertebrate prey (except for Caridean shrimps) could be identified to family. Thirteen families of fish and 6 families (and 1 separate infraorder) of invertebrates were found in the diet of *C. cyanostigma* (Table 4). Using the index of relative importance, apogonids were by far the most important fish family consumed, followed by pomacentrids, caesionids and clupeids (Table 4). In terms of invertebrate prey, crustaceans belonging to the families (or infraorder) Squillidae (stomatopods), Caridea, Portunidae and Xanthidae were most highly represented. The only non-crustacean invertebrate prey was an octopus. Within the different families, 17 species of fish and 2 species of invertebrate could also be identified in the diet of *C. cyanostigma* (Table 5).

The diet of *Cephalopholis boenak* was similar to that of *C. cyanostigma*, but not quite as diverse. Approximately 59% of fish prey and all of the invertebrate prey (again except for Caridean shrimps) could be identified to family. Representatives of 7 families of fish were consumed and again apogonids dominated, followed by pomacentrids and clupeids (Table 6). Of the invertebrate prey, 6 families (and 1 separate infraorder) were identified, with caridean shrimps followed by stomatopods (Squillidae) and galatheid crabs being the most important. The only non-crustacean invertebrate prey was a polychaete worm (Eunicidae). Seven species of fish and 2 species of invertebrates were identified in the diet of *C. boenak* (Table 7).

d) Ontogenetic variation in dietary composition

Cephalopholis cyanostigma did not show any change in the degree of piscivory with increasing fish size (Fig. 2a), but larger *C. boenak* tended to eat proportionally more fish than smaller ones (Fig 2b). Small prey (10 mm SL) were consumed by fish of all sizes belonging to both species (Fig. 3). Maximum size of prey consumed, on the other hand, appeared to be limited to approximately one third of the body length of the predator (Fig. 3). The mean ratio of prey to predator size was 14.0% for *C. cyanostigma* and 15.6% for *C. boenak*.

e) Seasonal and spatial variation in dietary composition

There was little seasonal variation in the degree of piscivory exhibited by either species (Fig. 4, Table 8). At family level, on the other hand, there was considerable seasonal and spatial variation in dietary composition (Table 9 and 10). On contiguous reef in both summer and winter, *Cephalopholis cyanostigma* fed mainly on apogonids followed by pomacentrids and caesionids. On patch reefs in summer, on the other hand, *C. cyanostigma* fed equally on clupeids and apogonids, followed by pomacentrids. In winter, however, clupeids were absent from the diet on patch reefs, which was dominated by apogonids and pomacentrids. Feeding on invertebrates also varied (Table 9). On contiguous reef in summer, stomatopods and caridean shrimps were most important while in winter caridean shrimps followed by xanthid crabs were most commonly eaten. On patch reefs in summer caridean shrimps and galatheid crabs were the main prey, while in winter it was trapezid and galatheid crabs.

Due to insufficient samples, spatial variation in the diet of *Cephalopholis boenak* could only be examined in summer. Feeding by *C. boenak* on contiguous reef in summer was similar to that of *C. cyanostigma*, with the main prey being apogonids and pomacentrids, although no caesionids were taken (Table 10). On patch reefs in summer, *C. boenak* again followed a similar pattern to *C. cyanostigma*, feeding equally on clupeids and apogonids, followed by pomacentrids. Feeding on invertebrates by *C. boenak* in summer was quite similar on patch and contiguous reefs with caridean shrimps and galatheid crabs being the main prey. Stomatopods were also quite commonly taken on contiguous reef (Table 10).

In addition to variation in family composition, both species consumed a much higher proportion of small prey fish (< 25 mm SL) in summer than in winter (Fig 5). There were no real differences between the size composition of prey consumed on patch and contiguous reef, except that *Cephalopholis cyanostigma* tended to take slightly more large fish (> 50 mm SL) on contiguous reef (Fig. 6).

2. Prey selection

a) Field observations

Relating the above information on temporal and spatial variation in dietary composition to patterns of prey abundance revealed that prey selection also varied temporally and spatially (Fig. 7 and 8). In summer 1996 both *Cephalopholis cyanostigma* and *C. boenak* selected clupeids on patch reefs while apogonids were consumed less than would be expected from their abundance. On contiguous reef in summer 1996 clupeids were not present and both species selected apogonids. In winter 1996 clupeids were not present on either reef type and *C. cyanostigma* again selectively fed on apogonids. In summer 1997 apogonids were again selected for by both species on both reef types and *C. cyanostigma* also selected for caesionids on contiguous reef. In all cases both species ate lower proportions of pomacentrids than would be expected from their abundance.

b) Laboratory experiment

The laboratory experiment examining the feeding behaviour of *C. boenak* also showed selection of some prey species over others (Fig 9, Table 11). Initial mortality of *Apogon fragilis* was very high, closely followed by *Neopomacentrus azysron*, while only a few *Pomacentrus moluccensis* were taken throughout the experiment. After 7 days the number of *A. fragilis* and *N. azysron* surviving was very low and did not differ from one another, but a significantly higher number of *P. moluccensis* had survived (Fig. 9, Table 11). Only 1 *A. fragilis* died in the control aquaria.

3. Feeding rates

a) Diel variation in feeding rates

There was no obvious diel variation in either the frequency of fresh prey or all prey in the guts of either rock-cod species (Table 12). Together these results also indicated that prey eaten in the morning were evacuated during the day. Night-time observations revealed that both species were inactive during this period and were sheltering within the reef matrix.

b) Seasonal and spatial variation in feeding rates

Feeding rates of *Cephalopholis cyanostigma* could be calculated at all 6 sites in both summer and winter over the two years. Feeding rates of *C. boenak*, on the other hand, could only be calculated at 4 sites and not in winter 1995. Feeding rates of both species were often highly variable at site level but some general patterns did emerge. Firstly, the number of fish prey per predator was much higher in summer than winter for *C. cyanostigma* (Fig. 10, Table 13), and higher in one of the two summers for *C. boenak* (Fig. 11, Table 14). There was little seasonal variation (in terms of numbers or volume) in feeding on invertebrates (Fig 10 and 11). The volume of fish prey per predator was higher in one summer for *C. boenak* (Fig. 11, Table 14) but there were no differences for *C. cyanostigma* (Fig. 10, Table 13). This indicates that *C. cyanostigma* consumed fewer, but larger, prey during winter. There were no overall significant differences between feeding rates on the two different reef types (Fig. 12 and 13, Tables 13 and 14). In winter 1996 a greater number and volume of prey was consumed on patch reefs by *C. cyanostigma* but in summer 1997 a greater volume of prey was consumed on contiguous reef (Fig. 12). *C. boenak* consumed a greater number of fish prey on patch reefs during winter 1996 but in summer 1997 the pattern was reversed with more fish consumed on contiguous reef (Fig 13). The combined regurgitated and dissected samples indicated that in summer 1997 a greater volume of fish was consumed by *C. cyanostigma* on contiguous reef but there were no other differences (Table 14).

4. Impact of *Cephalopholis cyanostigma* and *C. boenak* on prey populations

From visual censuses the density of *Cephalopholis cyanostigma* on patch reefs in February 1996 was estimated to be 5.7 per 100 m^2 (Chapter 3). Given that only 55% are seen in visual censuses (Chapter 2) the real density was estimated to be 10.3 per 100 m^2. Taking an average of the summer and winter feeding rates and assuming these represent half of the fish taken per day (given a digestion time of 6 hours) and that only 60 % of prey are regurgitated, the mean feeding rate was calculated to be 1.1 fish per day. When combined these two figures estimate that on patch reefs between February and August 1996, *C. cyanostigma* consumed 2075 fish per 100 m^2. On contiguous reef the actual density of *C. cyanostigma* was calculated to be 3.6 per 100 m^2 and using a feeding rate of 0.8 fish per day gave a consumption rate of 533 fish per 100 m^2. The actual density of *C. boenak* was calculated to be 10.0 per 100 m^2 on patch reefs and 1.5 per 100 m^2 on contiguous reef. Using feeding rates calculated to be 1.3 fish per day on patch reefs and 1.0 per day on contiguous reefs, *C. boenak* was estimated to have consumed 2300 and 260 fish per 100 m^2 respectively. The two species combined are therefore estimated to have accounted for 4375 fish per 100 m^2 on patch reefs and 793 fish per 100 m^2 on contiguous reefs. The observed decline over the same time period was 1548 fish per 100 m^2 on patch reefs and 231 fish per 100 m^2 on contiguous reef (Chapter 3). Therefore, the two rock-cod species are estimated to have accounted for approximately 3 times the observed prey loss.

Discussion:

The use of regurgitated gut contents in this study was a highly successful way of obtaining samples from the same population of fish over time. The fact that regurgitated samples accounted for the majority of prey consumed and were unbiased in their composition is testimony to this. The application of this method may be limited to fish caught underwater, however, as regurgitation often occurred soon after capture. Other studies (Randall & Brock 1960, Randall 1967, St John 1995) have found that predatory fish caught by line fishing from boats are of limited use for examining diet as guts are often empty or only contain bait. I would postulate that most of these fish had already regurgitated their gut contents before they were brought into the boat. The other alternative is that line fishing predominantly catches hungry fish with empty stomachs. Given the generally high feeding rates I observed in this study, however, this did not seem to be the case. Indeed some individual fish caught with bait regurgitated as many as 7 prey items while others contained very large prey. Feeding rates in this study were actually higher than those observed in another study on the same species (Martin 1994), which used spearing and quinaldine (anaesthetic) to capture fish. If line fishing was biased towards hungry fish, this makes the feeding estimates from this study even more conservative. Either way, the main purpose of this study was to compare diet between different times and places, so an absolute estimate of feeding rate was not necessary.

The observation that stomachs of the two rock-cod species contained approximately 75% fish and 25% crustaceans is similar to that recorded for many other serranid species (Parrish, 1987) although it is somewhat different from the 50:50 ratio observed for the same species by Martin (1994). Determination of digestion rates, however, revealed that simply examining the frequency of crustaceans grossly overestimated their importance. This study showed that crustaceans probably take about 4 times longer than fish to be digested. With that being the case fish would actually make up about 92 % of prey items consumed and crustaceans only 8 %. Differential digestion rates have caused errors in the estimation of dietary importance in other studies (Hyslop 1980), but few researchers have addressed the problem. Another factor which may effect digestion rate is water temperature (Reshetnikov et al. 1972; Hyslop 1980; Elliot 1991). A similar study to this one (St John 1995), however, found seasonal variation in water temperature on the northern Great Barrier Reef had little effect on digestion rates of coral trout. The digestion rates measured in summer in this study are therefore likely to be maintained throughout the year. Further factors which may influence digestion rate include meal size, prey species and predator size (Reshetnikov et al. 1972). For example, tropical lutjanids were found to digest clupeids twice as fast as sardines (Reshetnikov et al. 1972). I tried to account for meal size, prey species and predator size by using typical meal sizes and species and a range of predator sizes. The speed of digestion observed in this study can therefore only be seen as an estimate of the average rate. All the same, digestion in the two rock-cod species appears to much more rapid than that observed for other tropical piscivores such as coral trout, (24 hours, St John 1995) and several lutjanid species (24-33 hours, Reshetnikov et al. 1972).

Like many other serranids, the two rock-cod species fed on a wide variety of prey families and species (Parrish 1987, St John 1995). Such patterns of feeding are probably a consequence of the diversity of coral reef fish communities (Sale, 1977) and the variable nature of prey recruitment (Doherty and Williams, 1988). Also in common with the few other detailed studies of the diet of coral reef piscivores (Kingsford 1992, St John 1995) several families of prey fish dominated the gut contents of both rock-cod species. These two other studies (both involving coral trout, *Plectropomus leopardus* on the Great Barrier Reef) also found Apogonidae, Pomacentridae, Clupeidae and Caesionidae to be among the main families of prey fish consumed. *P. leopardus* also concentrated on Scaridae, Labridae and Blennidae, however, which were absent from the diet of the rock-cods. These differences in diet could be the result of local variation in the availability of prey or differences between the species in terms of feeding behaviour. For example *P. leopardus* often feeds in mid-water (Kingsford 1992) while the rock-cods generally make their predatory strikes close to the shelter of the substrate (Martin 1994; pers. obs.). In addition, *P. leopardus* reaches a much larger maximum size (75 cm) than either of the rock-cod species (24 to 35 cm), (Randall et al. 1990). Species of fish belonging to the Labridae and Scaridae families often reach much larger maximum sizes than pomacentrids, apogonids and clupeids (Randall et al. 1990) and therefore are less likely to be preyed upon by the relatively small rock-cods.

Differences between the maximum size of *Cephalopholis cyanostigma* (35 cm) and *C. boenak* (24 cm), (Randall et al. 1990) may also explain differences in their dietary composition. For example, caesionids, which reach maximum sizes of 15 to 30 cm (Randall et al. 1990), were quite important in the diet of *C. cyanostigma* but were absent from the diet of *C. boenak*. Large crabs (eg. Portunidae and Xanthidae), were also relatively important in the diet of *C. cyanostigma* while the main invertebrate prey of *C. boenak* was the smaller caridean shrimps and galatheid crabs. Stomatopods, on the other hand, which may attain large sizes, were common in the diet of both rock-cod species.

There was some evidence that *Cephalopholis boenak* became more piscivorous as it increased in size, but this pattern was not apparent for *C. cyanostigma*. It is quite likely, however, that this was due to the size of fish caught and not any lack of such a pattern. For example, relatively few *C. cyanostigma* individuals less than 150 mm TL, and none less than 100 mm TL were sampled. For *C. boenak* the trend may also have been more pronounced than was evident, as few fish smaller than 100 mm TL were sampled and none contained prey. Other researchers who have reported ontogenetic variation in the diet of serranids (Harmelin-Vivien & Bouchon 1976; Parrish 1987; St John 1995), examined a much wider size range of fish than in this study. The higher proportion of crustaceans found in the diet of *C. cyanostigma* and *C. boenak* by Martin (1994) probably reflects the generally smaller fish which were captured.

Patterns of prey size-selection in this study were particularly interesting. There have been conflicting results recently with regard to whether or not large predators on coral reefs consume recently settled juveniles (Kingsford 1992, St John 1995, Connell 1998a). This study showed that predators as large as 300 mm prey upon fish as small as 12 mm, which would be very recent arrivals on the reef (Wellington and Victor, 1989). Prey fish less than 25 mm SL (many of which would be new recruits) also dominated the diet of both species during summer. These rock-cods may therefore be contributing significantly to the high mortality rates often observed for newly recruited fish (Doherty & Sale 1985; Eckert 1987; Meekan 1988). Further support for this is that the consistent inclusion of small prey in the diet of piscivorous fish has been found to be almost universal in other ecosystems (Juanes, 1994). The maximum size of prey taken was probably limited by the depth of the prey and the gape size of the predator (Werner 1974; Schmitt & Holbrook 1984; St John 1995). In this study prey as large as 40% of the length of the predator were taken, but the mean ratio was 14 to 15%. This is somewhat smaller than ratios of 20 to 30 % which are more commonly reported for piscivorous fish (Juanes, 1994). The two rock-cod species may therefore need to feed at relatively high rates to make up for their tendency to select small prey.

The lack of any seasonal variation in the degree of piscivory exhibited by the rock-cods was surprising, given the much higher abundance of prey fish during summer (Chapter 3). Patterns of seasonal variation in the abundance of crustacean prey, however, were not known. Other research has shown that species such as *Epinephelus merra* (Randall & Brock 1960) and *Lutjanus kasmira* (Oda & Parrish 1981) which normally eat crustaceans, switch to a much more piscivorous diet during the summer months. In contrast, *Plectropomus leopardus* remains almost entirely piscivorous throughout the year (Kingsford 1992; St John 1995).

Seasonal and spatial variation in dietary composition at family level, on the other hand, did appear to be effected by prey availability, along with the interacting effect of prey selection. The general pattern exhibited by both species of rock-cod was to target the two most abundant families of fish (Pomacentridae and Apogonidae) but to select apogonids over pomacentrids. This pattern was only disrupted by the presence of schooling prey, particularly clupeids and to a lesser extent caesionids. *Plectropomus leopardus* is also known to focus on pelagic schooling fish (such as clupeids and caesionids) when they are available (Kingsford 1992; St John 1995). At One Tree Island on the southern Great Barrier Reef this caused pelagic prey to dominate the diet during summer months (Kingsford 1992), (as in this study), while on the central Great Barrier Reef clupeids appeared in the diet of *P. leopardus* sporadically throughout the year (St John 1995). In contrast to this study on rock-cods and Kingsford (1992), St John (1995) also found almost no seasonal variation in feeding upon other families of prey fish. In addition to variation in predation on different families of fish I also observed variation in feeding on invertebrates. I did not measure the availability of invertebrates but there is some evidence that caridean shrimps and portunid crabs are the most abundant decapod crustaceans available at Lizard Island (Keable 1995). With that being the case the two rock-cod species appeared to show selection for some other invertebrate groups such as stomatopods and xanthid and galatheid crabs. Overall, the selective feeding behaviour displayed by the two rock-cod species is in sharp contrast to the perception that coral reef piscivores are generalist, opportunistic feeders.

Selection for certain types of prey by predators is governed by vulnerability to capture, handling time and nutritional value (Begon et al. 1986, Scharf et al. 1998). The selection of pelagic schooling prey by both the rock-cod species and *P. leopardus* suggests that they may be easier to capture than prey which are more closely associated with the substrate. Apogonids, which tend to hover above the reef (Randall et al. 1990), provide an example of intermediate habitat association, and they were selected for in the absence of pelagic prey. Pomacentrids, which are generally (but not always) closely associated with the reef (Randall et al. 1990) appeared to be at the least risk of predation by the rock-cods. Use of habitat as a refuge from predation is emerging as common practice among various species of coral reef fish (Hixon & Beets 1989, 1993; Caley & St John 1996; Beukers & Jones 1997). The patterns of prey selection observed in this study also matched patterns of prey loss at the study sites (Chapter 3). This indicates that either similar patterns of prey selection were common to many of the piscivores present or that the two rock-cod species were responsible for much of the observed loss of prey.

The laboratory experiment also indicated that prey behaviour, rather than taxonomy, was probably the most important factor influencing the risk of predation. *Neopomacentrus azysron*, which is unusual as a mid-water, schooling pomacentrid, suffered similar mortality to the apogonid, *Apogon fragilis*. Several other studies, (Eckert 1987; Connell & Gillanders 1997) have found higher mortality among schooling prey species than among solitary prey species of the same family. Species level variation in mortality rates has also been described for a range of species from different families (Sale & Ferrell 1988). Prey selection by predatory fish would appear to be the mechanism responsible for such variation in prey fish mortality. Piscivorous fish therefore have the potential to disrupt patterns of prey fish abundance established at settlement and to influence community structure (Carr & Hixon 1995).

In contrast to other studies (Parrish 1987; Shpigel & Fishelson 1989; Martin 1994) the rock-cods exhibited little diel variation in feeding rates. In particular, feeding activity in other species of serranids has often been observed to peak at dawn and dusk (Parrish 1987). Martin (1994), using remote video surveillance of *Cephalopholis boenak*, also observed a proportionally higher number of predatory strikes at dawn than either midday or dusk. In this study similar numbers of fresh prey were observed in the guts of both species throughout the day. If there was a peak in feeding activity at dusk, however, it may not have been recorded as I was rarely able to collect fish later than 30 minutes before sunset. *C. cyanostigma* and *C. boenak* also appear to only feed during the day, unlike some other serranid species such as *Cephalopholis argus* and *Epinephelus merra* (Harmelin-Vivien & Bouchon 1976).

Although the proportion of fish in the diet of the rock-cods did not vary seasonally, both species consumed many more fish in summer than in winter. This result is in contrast to that for *P. leopardus*, which fed at higher rates during winter (St John 1995). In this study, the higher feeding rates in summer appeared to be in response to increased prey availability due to an influx of new recruits (Chapter 3). The dominance of small prey fish in the diet of both species in summer further reflects this pattern. The possible influence of seasonal variation in temperature (approximately 5° C - Lizard Island Research Station) on the metabolism of the fish, and therefore feeding rates, however, can not be disregarded. Temperature is known to be one of the key factors influencing the rate of feeding in fish (Weatherley and Gill 1987). Despite the higher feeding rates, *C. cyanostigma* consumed larger prey in winter than in summer, so the net result was that fish consumed approximately the same volume of prey in both seasons. The size of fish consumed by *C. boenak*, on the other hand, was more similar in the two seasons, so the volume of fish eaten was greater in at least one summer. Seasonal variation in growth may therefore be more pronounced in *C. boenak* than *C. cyanostigma*.

It was initially surprising that there were no consistent differences between the feeding rates of the rock-cods on the two reef types. Analysis of home range and prey density data in February 1997 (Chapter 3) had suggested that on average each *C. cyanostigma* individual had 1.5 times more prey available on patch reefs than on contiguous reef and each *C. boenak* had 4 times as much prey available. Real differences were expected to be even greater as due to smaller home ranges on patch reefs (Chapter 3) the rock-cods would have to travel less distance in search of prey. There are several possible explanations for the observed patterns of feeding. Firstly, there may have been an abundant supply of prey available to the rock-cods on both reef types, resulting in both populations of fish feeding at maximum rates. Seasonal variation in feeding rates suggests that this was not the case and that the rock-cods were limited by the abundance of prey, at least during winter. This observation, however, is confounded by the effect of variation in temperature on metabolic rate. Another possible explanation for the observed patterns could be that rock-cods on contiguous reef primarily inhabit high density patches of prey which are surrounded by areas of low prey density. Such a pattern of prey distribution could still result in an overall lower abundance of prey on contiguous reef. Rock-cod densities were much lower on contiguous reef (Chapter 3), also making a patchy distribution of predators quite possible. Under this scenario each rock-cod on the two reef types could still have access to similar quantities of prey. Unfortunately, I did not attempt to quantify prey density within home ranges of individual fish, so this explanation remains speculative.

Comparison between the two reef types is also confounded by several other factors which may have influenced feeding rates such as habitat type and the density of competitors and predators (Werner et al. 1983a,b; Holbrook & Schmitt 1988). For example densities of both competitors and predators of the rock-cods themselves (eg. *Plectropomus leopardus* (St John 1995)) were considerably higher on patch reefs than on contiguous reef (Chapter 3). Finally, due to the high variability of the observed feeding rates, the data may also have only been sensitive to larger differences than were actually present. The question of whether or not feeding by the rock-cods was limited by the abundance of prey therefore remains unresolved.

Taken together, all of the previous results indicate that the two rock-cod species were having a considerable impact on populations of their prey. Indeed, my calculations suggest that between February and August 1996 the rock-cods accounted for almost 3 times the observed decline in prey density. It must be remembered that these calculations involved multiplying together many estimates with associated errors, but the rock-cods undoubtedly consumed a large number of prey fish. The feeding rates estimated in this study (approximately 1 prey fish per day) are actually less than those gained from direct observation of another piscivore at Lizard Island, (*Synodus variegatus*, 1.8 prey fish per day - Sweatman 1984). Even taking a more conservative approach and assuming a prey evacuation rate of 12 hours (the longest possible), the rock-cods still appear to have accounted for more than the observed decline.

Although *Cephalopholis cyanostigma* and *C. boenak* were among the most common piscivores at the study sites (Chapter 3), they still only made up approximately one third of all piscivores present. It is therefore difficult to picture how these prey populations were able to support such high densities of piscivores. One explanation could be that I underestimated the density of prey fish in February 1996. This would have been possible on patch reefs as the prey populations were often made up of large, mobile schools of fish which were very difficult to count. Due to the lower density of prey on contiguous reef I was much more confident in the accuracy of those counts. In either case, if I was systematically underestimating the abundance of prey it should have occurred in both the February and August censuses. This would still have resulted in relatively accurate measures of prey loss.

The other alternative is that additional prey moved into the study sites during the year. Little recruitment of fish is thought to occur between February and August on the Great Barrier Reef (Russell et al. 1977; Doherty 1991), so this input would have to have mainly been in the form of immigrants. Several families of prey fish (eg. Clupeidae and Caesionidae) are quite mobile (Randall et al. 1990) and therefore may have moved into or through the study sites during the 6 month period. It is therefore difficult to quantify the exact impact the rock-cods had on their prey populations, although it would appear to have been considerable. Mortality rates of over 90% within the first reef-associated year have been detected for some species of coral reef fish (Eckert 1987; Beukers & Jones 1997). Such patterns of mortality may largely be due to the influence of predation.

In summary, this study has demonstrated the usefulness of collecting regurgitated gut contents and the importance of accounting for differential digestion when examining diet. Significant temporal and spatial variation in the dietary composition and feeding rates of the two species of rock-cod, *Cephalopholis cyanostigma* and *C. boenak* was observed. This study is also the first to demonstrate prey selection by piscivorous species of coral reef fish. Such selection may be the mechanism responsible for the species level variation in mortality rates observed in other studies. In particular, both rock-cod species showed a preference for mid-water schooling prey over those more closely associated with the reef. The combination of high densities, high feeding rates and selection for certain sizes and types of fish indicated that the two rock-cod species were having a considerable impact on their prey. This impact appeared to effect both the abundance and family composition of their prey communities. Removal of large numbers of piscivorous coral reef fish (such as occurs with overfishing) may have significant effects which flow on to entire coral reef communities.

Table 1. Summary of the number of fish from which regurgitated gut contents were collected (S=Summer, W=Winter, Sp=Spring).

a) *Cephalopholis cyanostigma*

Reef Type	**Site**	**S95**	**W95**	**Sp95**	**S96**	**W96**	**Sp96**	**S97**	**Total**
Patch	1	47	11	27	12	16	14	18	145
	2	*	26	*	13	25	7	12	83
	3	*	*	*	13	20	5	11	49
Contiguous	1	*	*	23	11	15	5	12	66
	2	*	21	*	17	25	9	18	90
	3	*	26	10	15	30	7	27	115
Total		**47**	**84**	**60**	**81**	**131**	**47**	**98**	**548**

b) *Cephalopholis boenak*

Reef Type	**Site**	**S95**	**W95**	**Sp95**	**S96**	**W96**	**Sp96**	**S97**	**Total**
Patch	1	10	2	16	12	10	7	10	67
	2	*	*	*	35	19	7	22	83
Contiguous	1	*	17	*	26	24	12	18	97
	2	*	6	13	13	15	5	12	64
Total		**10**	**25**	**29**	**86**	**68**	**31**	**62**	**311**

Table 2. Digestion scale (Modified from Martin 1994)

a) Fish prey

1. Fresh	Little or no digestion.
2. Minor digestion	Some digestion of superficial surfaces.
3. Moderate digestion	Superficial surfaces fully digested. Head and tail partly digested. Measurement of length and volume still possible.
4. Major digestion	Body broken down into large pieces of flesh and bone.
5. Advanced digestion	Small fragments of flesh and bone remaining.
6. Complete digestion	Stomach empty

b) Invertebrate prey

1. Fresh	Little or no digestion.
2. Minor digestion	Some appendages missing or partially digested.
3. Moderate digestion	All appendages and body partially digested. Measurement of length and volume still possible.
4. Major digestion	Body broken down into large pieces.
5. Advanced digestion	Small fragments of flesh, carapace or appendages remaining.
6. Complete digestion	Stomach empty

Table 3. Validation of the use of regurgitated gut contents by comparison of the frequency of prey items collected by regurgitation and dissection. (Prey Reg. = proportion of prey regurgitated, Fish Reg. = proportion of fish in regurgitated sample, Fish Diss. = proportion of fish in dissected sample).

a) *Cephalopholis cyanostigma*

Season	**Prey Reg.**	**Fish Reg.**	**Fish Diss.**
Winter 96	57.14 %	62.50 %	66.66 %
Summer 97	60.53 %	78.26 %	70.00 %

b) *Cephalopholis boenak*

Season	**Prey Reg.**	**Fish Reg.**	**Fish Diss.**
Summer 97	62.50 %	60.00 %	57.14 %

Table 4. Summary of the overall dietary composition of *Cephalopholis cyanostigma* (Freq. = Frequency, Vol. = Volume, Occ. = Occurence, IRI = Index of Relative Importance).

a) Identified fish

Family	**Freq.**	**% F**	**Vol.**	**% V**	**Occ.**	**% O**	**IRI**
Apogonidae	51	46.79	34.40	25.78	36	46.15	33.49
Pomacentridae	19	17.43	25.40	19.03	18	23.08	8.41
Caesionidae	8	7.34	35.20	26.38	8	10.26	3.46
Clupeidae	19	17.43	6.80	5.10	10	12.82	2.89
Lutjanidae	1	0.92	17.00	12.74	1	1.28	0.18
Gobiidae	3	2.75	1.25	0.94	3	3.85	0.14
Synodontidae	2	1.83	3.30	2.47	2	2.56	0.11
Holocentridae	1	0.92	4.20	3.15	1	1.28	0.05
Lethrinidae	1	0.92	3.00	2.25	1	1.28	0.04
Atherinidae	1	0.92	1.00	0.75	1	1.28	0.02
Serranidae	1	0.92	1.00	0.75	1	1.28	0.02
Pseudochromidae	1	0.92	0.60	0.45	1	1.28	0.02
Siganidae	1	0.92	0.30	0.22	1	1.28	0.01
	109		**133**		**84**		

b) Identified invertebrates

Infraorder / Family	**Freq.**	**% F**	**Vol.**	**% V**	**Occ.**	**% O**	**IRI**
Squillidae	10	17.24	15.12	32.63	10	18.87	9.41
Caridea	16	27.59	4.50	9.72	13	24.53	9.15
Portunidae	8	13.79	15.70	33.89	8	15.09	7.20
Xanthidae	9	15.52	3.70	7.99	9	16.98	3.99
Trapeziidae	6	10.34	4.80	10.36	6	11.32	2.34
Galatheidae	8	13.79	0.80	1.73	6	11.32	1.76
Octopodidae	1	1.72	1.70	3.67	1	1.89	0.10
	58		**46**		**53**		

Table 5. Species of prey identified in the diet of *Cephalopholis cyanostigma*

a) Fish		b) Invertebrates	
Apogonidae	**24**	**Stenopodidea**	**1**
Apogon fragilis	16	*Stenopus hispidus*	1
Apogon doederleini	4	**Trapeziidae**	**1**
Apogon cyanosoma	2	*Trapezia septata*	1
Apogon fraenatus	1		
Cheilodipterus quinqelineatus	1		
Pomacentridae	**11**		
Pomacentrus moluccensis	5		
Pomacentrus nagasakiensis	2		
Neopomacentrus azysron	2		
Chromis viridis	1		
Dascyllus reticulatus	1		
Caesionidae	**6**		
Pterocaesio tile	3		
Pterocaesio trilineata	2		
Caesio cuning	1		
Gobiidae	**1**		
Amblygobius rainfordi	1		
Pseudochromidae	**1**		
Pseudochromis flammicauda	1		
Synodontidae	**1**		
Synodus dermatogenys	1		
Holocentridae	**1**		
Sargocentron diadema	1		

Table 6. Summary of the overall dietary composition of *Cephalopholis boenak* (Freq. = Frequency, Vol. = Volume, Occ. = Occurence, IRI = Index of Relative Importance).

a) Identified fish

Family	**Freq.**	**% F**	**Vol.**	**% V**	**Occ.**	**% O**	**IRI**
Apogonidae	30	50.00	16.00	47.55	22	50.00	48.77
Pomacentridae	9	15.00	9.65	28.68	8	18.18	7.94
Clupeidae	12	20.00	2.15	6.39	7	15.91	4.20
Gobiidae	3	5.00	0.55	1.63	3	6.82	0.45
Pseudochromidae	2	3.33	1.50	4.46	2	4.55	0.35
Serranidae	1	1.67	3.00	8.92	1	2.27	0.24
Atherinidae	3	5.00	0.80	2.38	1	2.27	0.17
	60		**34**		**44**		

b) Identified invertebrates

Infraorder / Family	**Freq.**	**% F**	**Vol.**	**% V**	**Occ.**	**% O**	**IRI**
Caridea	19	35.19	2.60	18.25	12	30.77	16.44
Squillidae	8	14.81	6.80	47.72	8	20.51	12.83
Galatheidae	15	27.78	1.20	8.42	12	30.77	11.14
Xanthidae	6	11.11	0.65	4.56	6	15.38	2.41
Trapeziidae	3	5.56	0.60	4.21	3	7.69	0.75
Portunidae	2	3.70	1.50	10.53	2	5.13	0.73
Eunicidae	1	1.85	0.90	6.32	1	2.56	0.21
	54		**14**		**44**		

Table 7. Species of prey identified in the diet of *Cephalopholis boenak*

a) Fish

Apogonidae	**9**
Apogon fragilis	7
Apogon doederleini	1
Cheilodipterus quinquelineatus	1
Pomacentridae	**6**
Neopomacentrus azysron	4
Pomacentrus moluccensis	2
Pseudochromidae	**1**
Pseudochromis flammicauda	1
Gobiidae	**1**
Fusigobius neophytus	1

b) Invertebrates

Galatheidae	**1**
Galathea sp.	1
Xanthidae	**1**
Liomera sp.	1

Table 8. Results of ANOVA examining the influence of season on piscivory (the proportion of fish in the diet).

a) *Cephalopholis cyanostigma*

SOURCE	SS	DF	MS	F	Sig of F
Season	0.01	1	0.01	0.25	0.624
Within + Residual	1.00	20	0.05		

b) *Cephalopholis boenak*

SOURCE	SS	DF	MS	F	Sig of F
Time	0.04	2	0.02	0.70	0.521
Within + Residual	0.24	9	0.03		

Table 9. Seasonal and spatial variation in the dietary composition of *Cephalopholis cyanostigma*, (Sum = Summer, Win = Winter, % F = Percentage frequency).

a) Identified fish

Family	**Contiguous Reef**				**Patch Reef**			
	Sum	**% F**	**Win**	**% F**	**Sum**	**% F**	**Win**	**% F**
Apogonidae	13	52.00	5	38.46	19	38.78	10	71.43
Clupeidae	0	0.00	0	0.00	19	38.78	0	0.00
Pomacentridae	5	20.00	3	23.08	5	10.20	3	21.43
Caesionidae	5	20.00	2	15.38	1	2.04	0	0.00
Gobiidae	0	0.00	0	0.00	2	4.08	1	7.14
Synodontidae	1	4.00	0	0.00	0	0.00	0	0.00
Atherinidae	0	0.00	1	7.69	0	0.00	0	0.00
Holocentridae	1	4.00	0	0.00	0	0.00	0	0.00
Lethrinidae	0	0.00	0	0.00	1	2.04	0	0.00
Lutjanidae	0	0.00	1	7.69	0	0.00	0	0.00
Pseudochromidae	0	0.00	0	0.00	1	2.04	0	0.00
Serranidae	0	0.00	1	7.69	0	0.00	0	0.00
Siganidae	0	0.00	0	0.00	1	2.04	0	0.00
Total	**25**		**13**		**49**		**14**	

b) Identified invertebrates

Infraorder / Family	**Contiguous Reef**				**Patch Reef**			
	Sum	**% F**	**Win**	**% F**	**Sum**	**% F**	**Win**	**% F**
Caridea	4	28.57	4	36.36	5	35.71	0	0.00
Squillidae	5	35.71	1	9.09	2	14.29	1	10.00
Galatheidae	1	7.14	1	9.09	4	28.57	3	30.00
Portunidae	2	14.29	1	9.09	2	14.29	1	10.00
Xanthidae	0	0.00	3	27.27	0	0.00	1	10.00
Trapeziidae	1	7.14	1	9.09	1	7.14	3	30.00
Octopodidae	1	7.14	0	0.00	0	0.00	0	0.00
Total	**14**		**11**		**14**		**10**	

Table 10. Spatial variation in the dietary composition of *Cephalopholis boenak* in summer (Sum = Summer, % F = Percentage frequency).

a) Identified fish

Family	**Contiguous Reef**		**Patch Reef**	
	Sum	**% F**	**Sum**	**% F**
Apogonidae	13	72.22	10	37.04
Clupeidae	0	0.00	12	44.44
Pomacentridae	4	22.22	3	11.11
Atherinidae	0	0.00	0	0.00
Gobiidae	0	0.00	1	3.70
Pseudochromidae	1	5.56	1	3.70
Serranidae	0	0.00	0	0.00
Total	**18**		**27**	

b) Identified invertebrates

Infraorder / Family	**Contiguous Reef**		**Patch Reef**	
	Sum	**% F**	**Sum**	**% F**
Caridea	4	23.53	9	50.00
Galatheidae	3	17.65	5	27.78
Squillidae	3	17.65	2	11.11
Xanthidae	2	11.76	2	11.11
Trapeziidae	2	11.76	0	0.00
Portunidae	2	11.76	0	0.00
Eunicidae	1	5.88	0	0.00
Total	**17**		**18**	

Table 11. Results of the laboratory experiment examining prey selection by *Cephalopholis boenak*.

a) Results of ANOVA comparing the number of different species of prey fish surviving at the end of the experiment (* indicates significant result).

SOURCE	SS	DF	MS	F	Sig of F
Species	36.33	2	18.17	15.00	< 0.000*
Within + Residual	18.17	15	1.21		

b) Results of Tukey's test (HSD method) comparing the number of different prey fish species surviving at the end of the experiment.

Pomacentrus moluccensis > *Neopomacentrus azysron* = *Apogon fragilis*

Table 12. Diel patterns of feeding on fish prey by *Cephalopholis cyanostigma* and *C. boenak* in summer.

a) *C. cyanostigma* - fresh prey only (digestion stages 1 and 2)

Time of Day	**Morning**	**Midday**	**Afternoon**
No. predators	119	39	68
No. prey	29	8	18
Feeding rate	**0.24**	**0.21**	**0.26**

b) *C. cyanostigma* - all fish prey

Time of Day	**Morning**	**Midday**	**Afternoon**
No. predators	119	39	68
No. prey	49	16	28
Feeding rate	**0.41**	**0.41**	**0.41**

c) *C. boenak* - fresh prey only (digestion stages 1 and 2)

Time of Day	**Morning**	**Midday**	**Afternoon**
No. predators	85	37	36
No. prey	17	7	7
Feeding rate	**0.20**	**0.19**	**0.19**

d) *C. boenak* - all fish prey

Time of Day	**Morning**	**Midday**	**Afternoon**
No. predators	85	37	36
No. prey	33	13	14
Feeding rate	**0.39**	**0.35**	**0.39**

Table 13. The influence of reef type and season on the feeding rate of *Cephalopholis cyanostigma.*

a) Results of ANOVA examining the influence of reef type and season on the number of prey fish per predator. Data was square root transformed (* indicates significant result).

SOURCE	SS	DF	MS	F	Sig of F
Reef	0.02	1	0.02	1.32	0.265
Season	0.17	1	0.17	10.47	0.005*
Reef by Season	0.00	1	0.00	0.12	0.735
Within + Residual	0.29	18	0.02		

b) Results of ANOVA examining the influence of reef type and season on the volume of prey fish per predator. Data was square root transformed (* indicates significant result).

SOURCE	SS	DF	MS	F	Sig of F
Reef	0.00	1	0.00	0.00	0.952
Season	0.02	1	0.02	1.06	0.317
Reef by Season	0.07	1	0.07	2.93	0.104
Within + Residual	0.41	18	0.02		

Table 14. The influence of reef type and time of year on the feeding rate of *Cephalopholis boenak.*

a) Results of ANOVA examining the influence of reef type and time of year on the number of prey fish per predator. Data was square root transformed (* indicates significant result).

SOURCE	SS	DF	MS	F	Sig. of F
Reef	0.003	1	0.003	0.963	0.364
Time	0.039	2	0.020	5.624	0.042*
Reef by Time	0.009	2	0.005	1.326	0.333
Within + Residual	0.021	6	0.004		

b) Results of Tukey's test (HSD method) comparing the number of prey fish per predator at different times of the year

Summer 1996 > Winter 1996 = Summer 1997

c) Results of ANOVA examining the influence of reef type and time of year on the volume of prey fish per predator. Data was square root transformed (* indicates significant result).

SOURCE	SS	DF	MS	F	Sig. of F
Reef	0.001	1	0.001	0.212	0.661
Time	0.050	2	0.025	5.942	0.038*
Reef by Time	0.008	2	0.004	1.037	0.410
Within + Residual	0.025	6	0.004		

d) Results of Tukey's test (HSD method) comparing the volume of prey fish per predator at different times of the year

Summer 1996 > Winter 1996 = Summer 1997

Table 15. The influence of reef type on the feeding rate of *Cephalopholis cyanostigma* and *C. boenak* in summer 1997 (regurgitated and dissected samples combined).

a) Results of ANOVA examining the effect of reef type on the number of prey fish per predator (*C. cyanostigma*).

SOURCE	SS	DF	MS	F	Sig of F
Reef Type	0.054	1	0.054	0.297	0.615
Within + Residual	0.733	4	0.183		

b) Results of ANOVA examining the effect of reef type on the volume of prey fish per predator (*C. cyanostigma*). Data was square root transformed. (* indicates significant result).

SOURCE	SS	DF	MS	F	Sig of F
Reef Type	0.212	1	0.212	8.056	0.047*
Within + Residual	0.105	4	0.026		

c) Results of ANOVA examining the effect of reef type on the number of prey fish per predator (*C. boenak*). Data was square root transformed.

SOURCE	SS	DF	MS	F	Sig of F
Reef Type	0.016	1	0.016	4.698	0.163
Within + Residual	0.007	2	0.003		

d) Results of ANOVA examining the effect of reef type on the volume of prey fish per predator (*C. boenak*).

SOURCE	SS	DF	MS	F	Sig of F
Reef Type	0.001	1	0.001	0.945	0.434
Within + Residual	0.001	2	0.001		

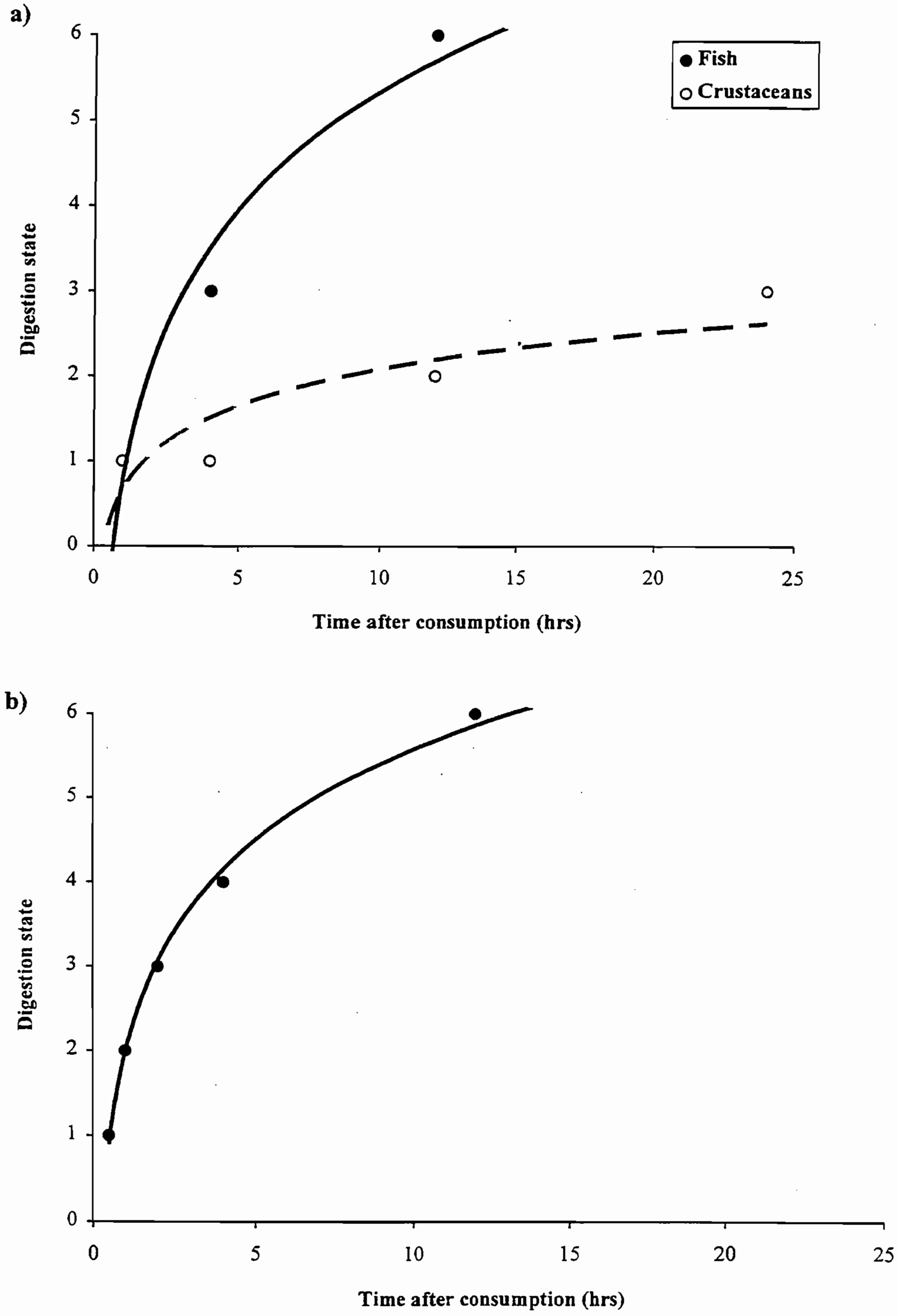
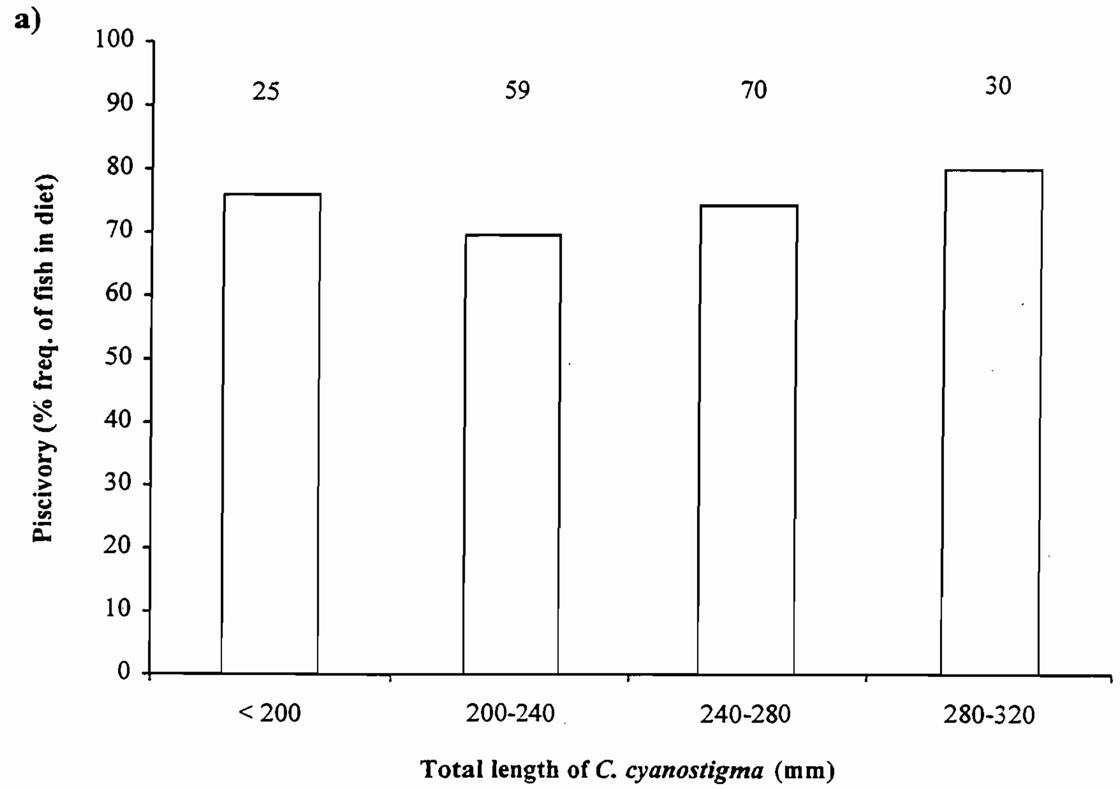


Figure 1. Rates of digestion for **a)** fish and crustaceans by *Cephalopholis cyanostigma* this study) and **b)** fish by *C. boenak* (Martin 1994), (n=3 per time period). See table 2 for description of digestive states.



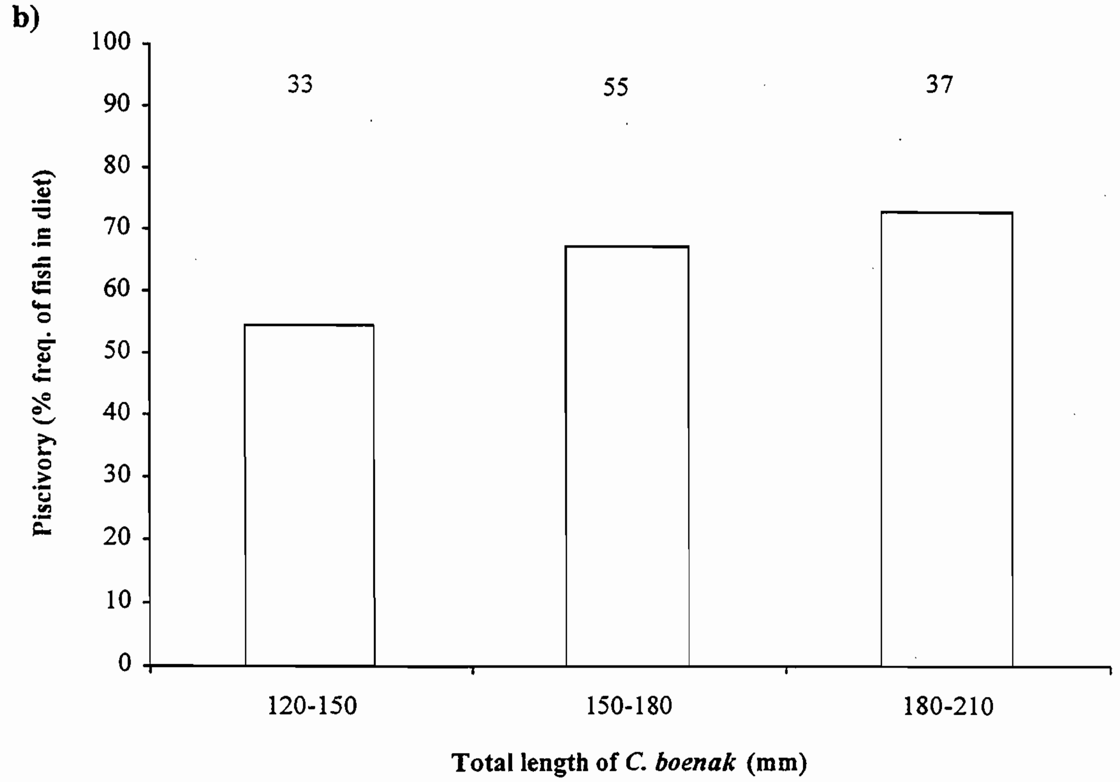
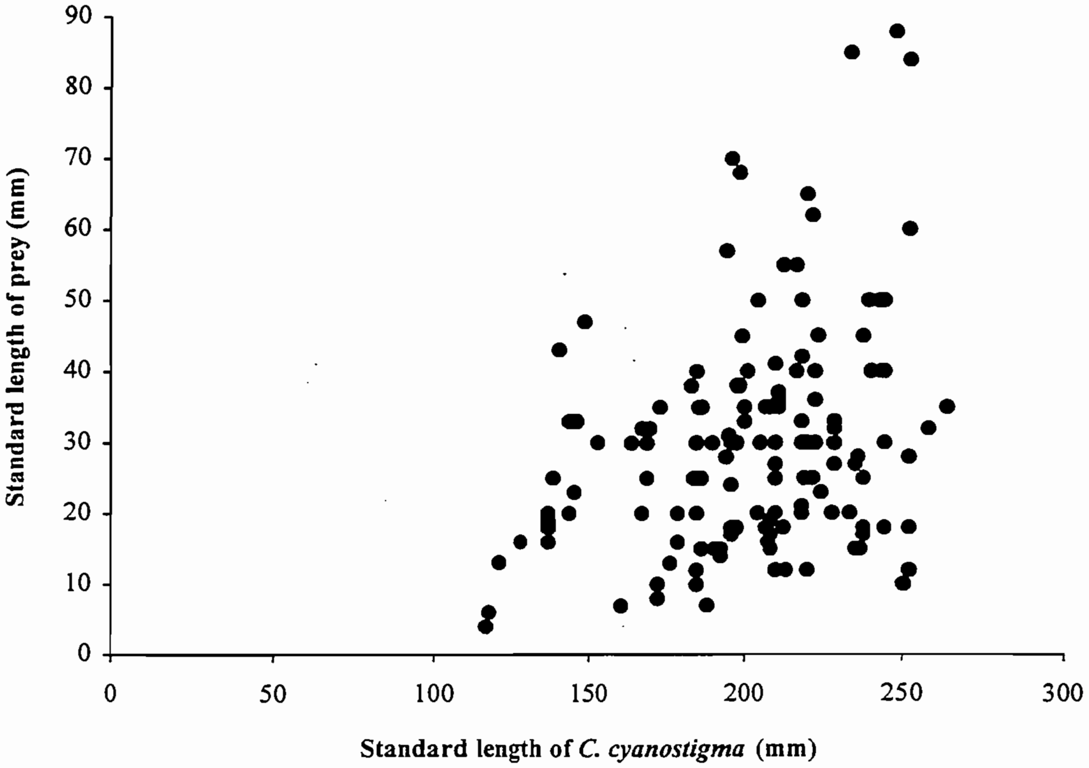


Figure 2. Ontogenetic variation in piscivory (percentage frequency of fish in the diet) by **a)** *Cephalopholis cyanostigma* and **b)** *C. boenak*. Numbers above columns represent the number of fish sampled.



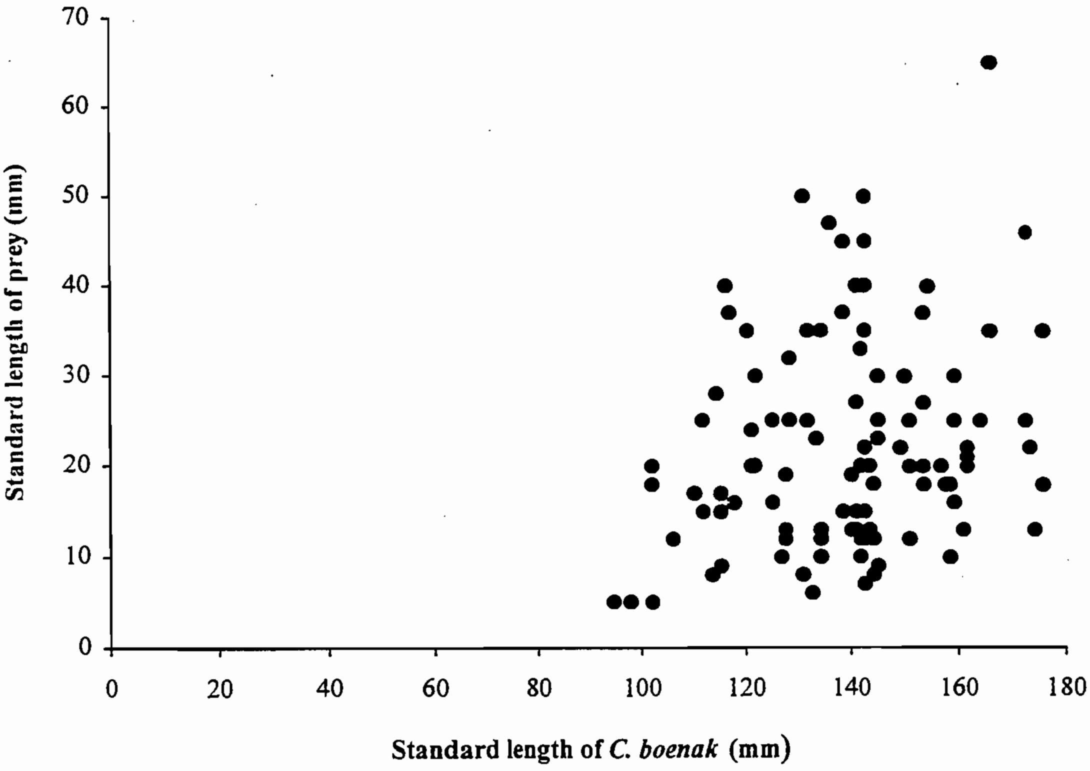


Figure 3. The relationship between predator length and prey length for **a)** *Cephalopholis cyanostigma* (n=165) and **b)** *C. boenak* (n=119)

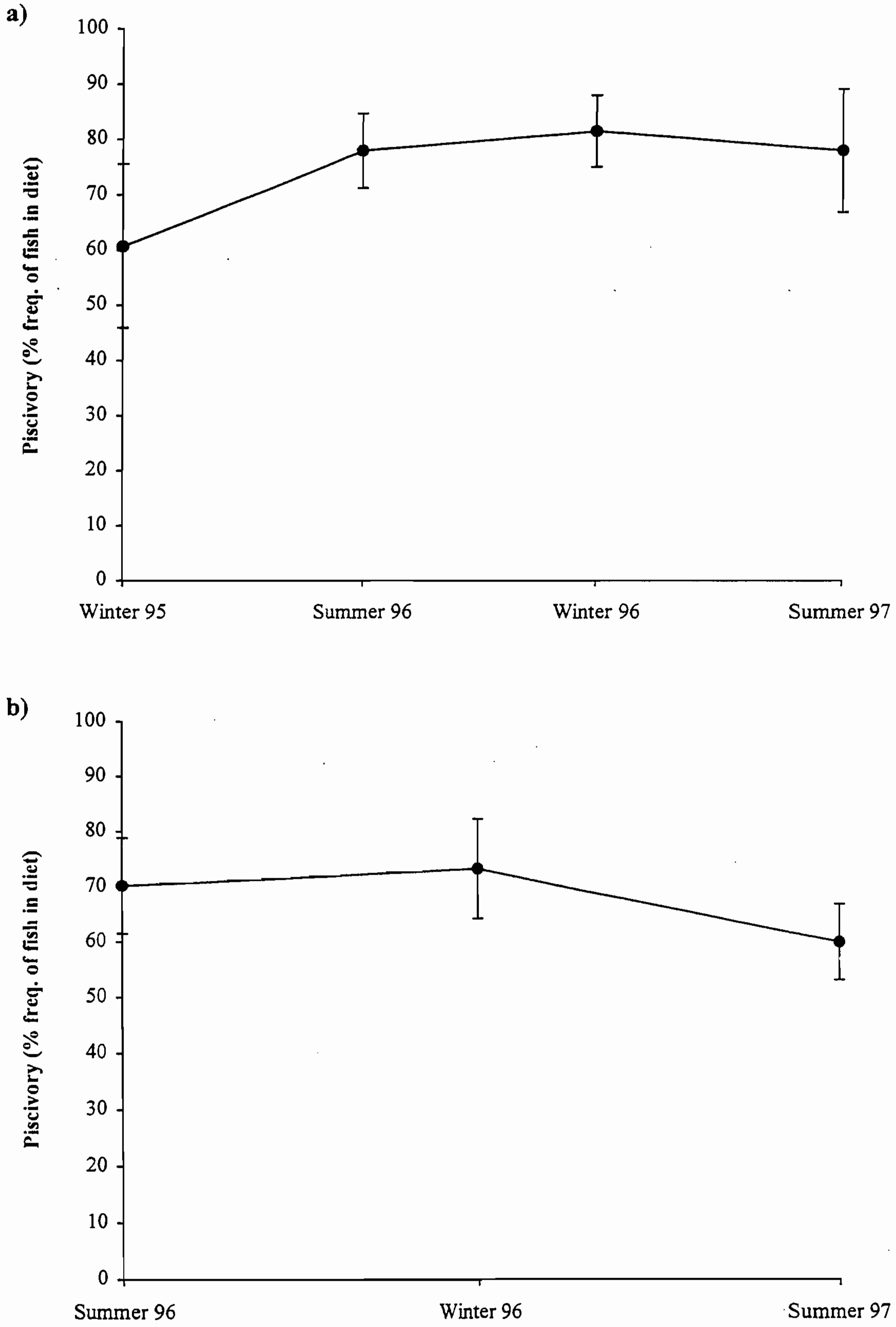


Figure 4. Seasonal variation in piscivory (mean percentage frequency of fish in the diet +/-SE) by **a)** *Cephalopholis cyanostigma* (n=6 sites) and **b)** *C. boenak* (n=4 sites)

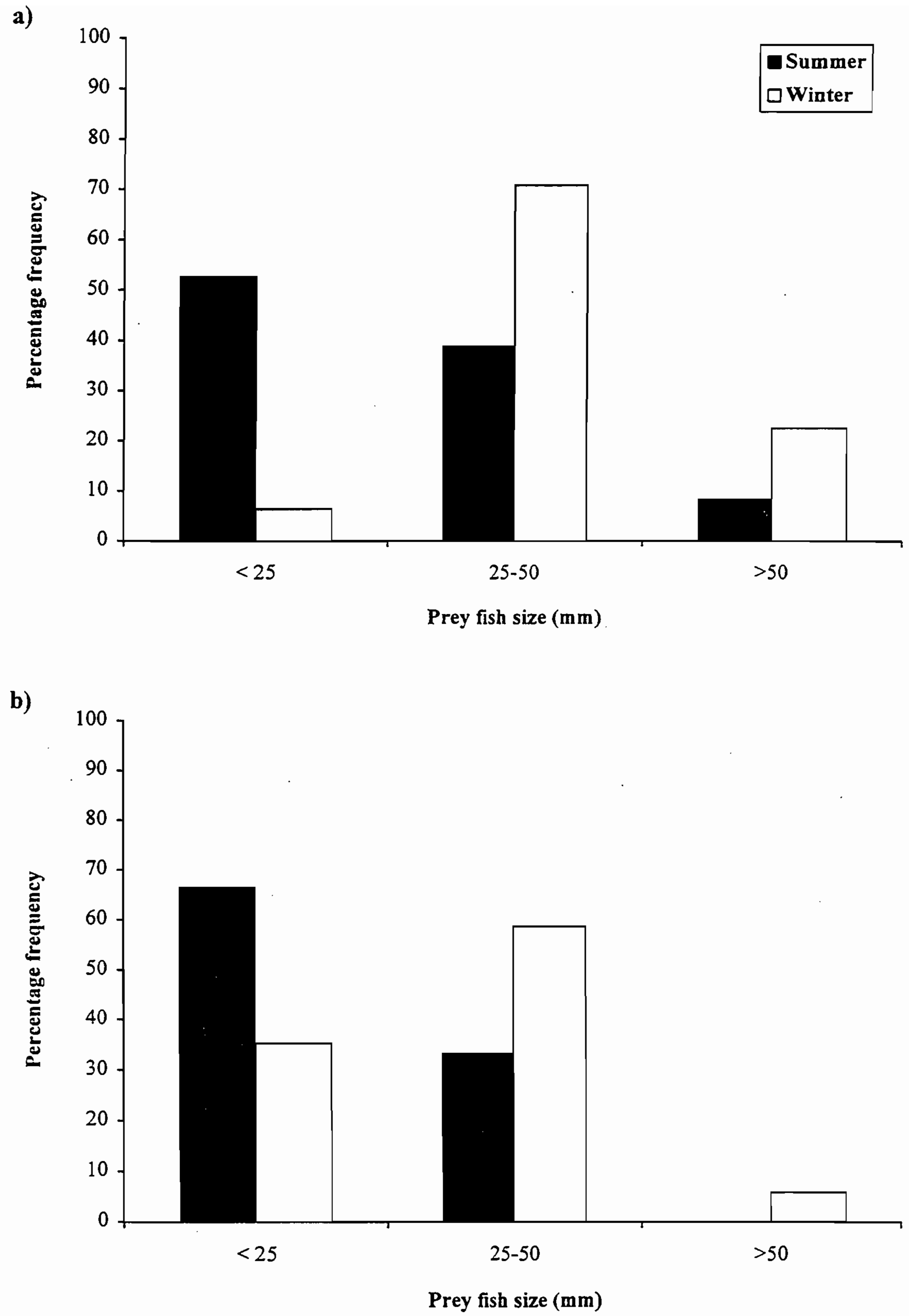


Figure 5. Seasonal variation in the size composition of fish prey consumed by **a)** *Cephalopholis cyanostigma* (n=108 in summer and 31 in winter) and **b)** *C. boenak* (n=69 in summer and 17 in winter).

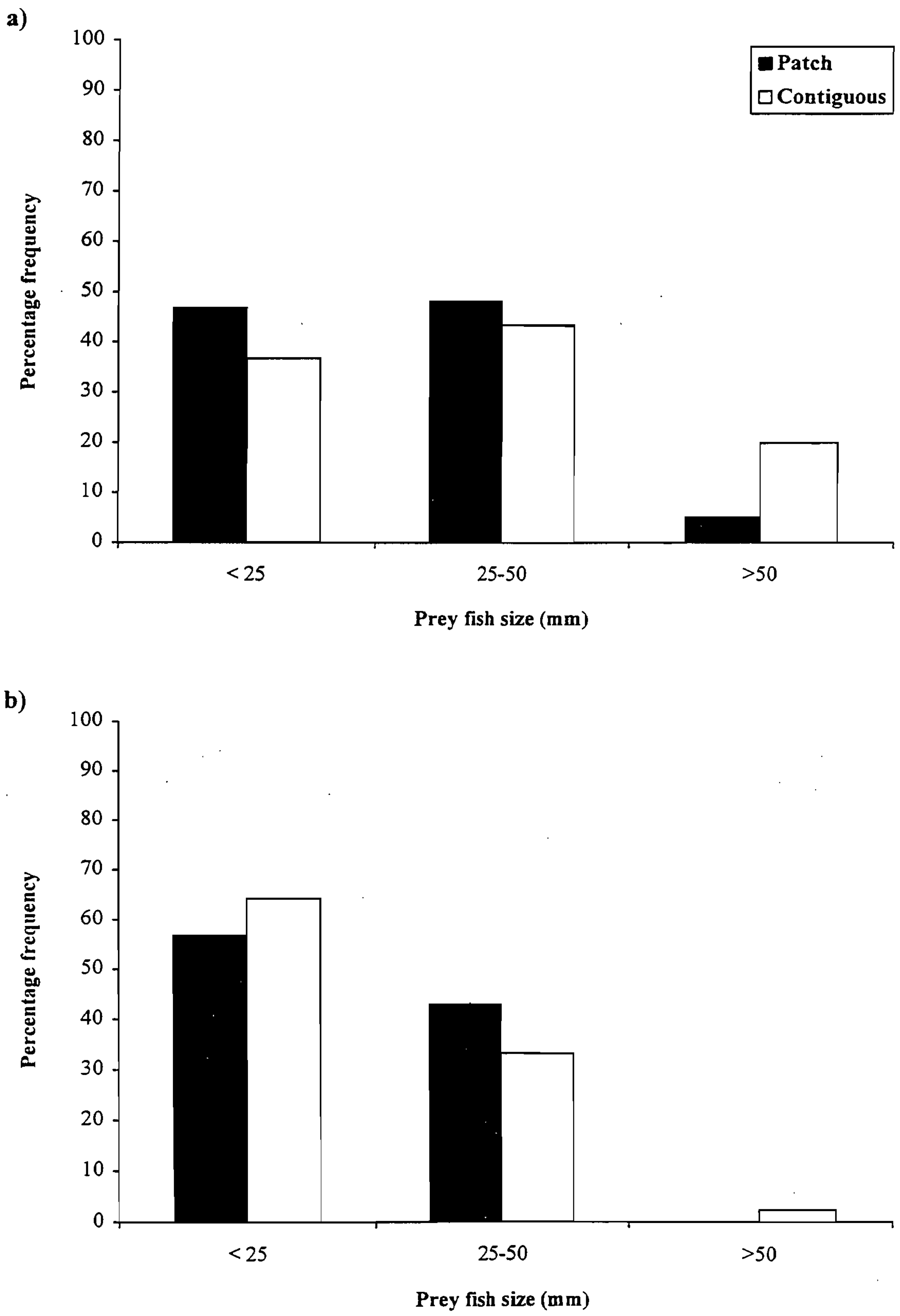


Figure 6. Spatial variation in the size composition of fish prey consumed by **a)** *Cephalopholis cyanostigma* (n=79 on patch and 60 on contiguous reef) and **b)** *C. boenak* (n=44 on patch and 42 on contiguous reef).

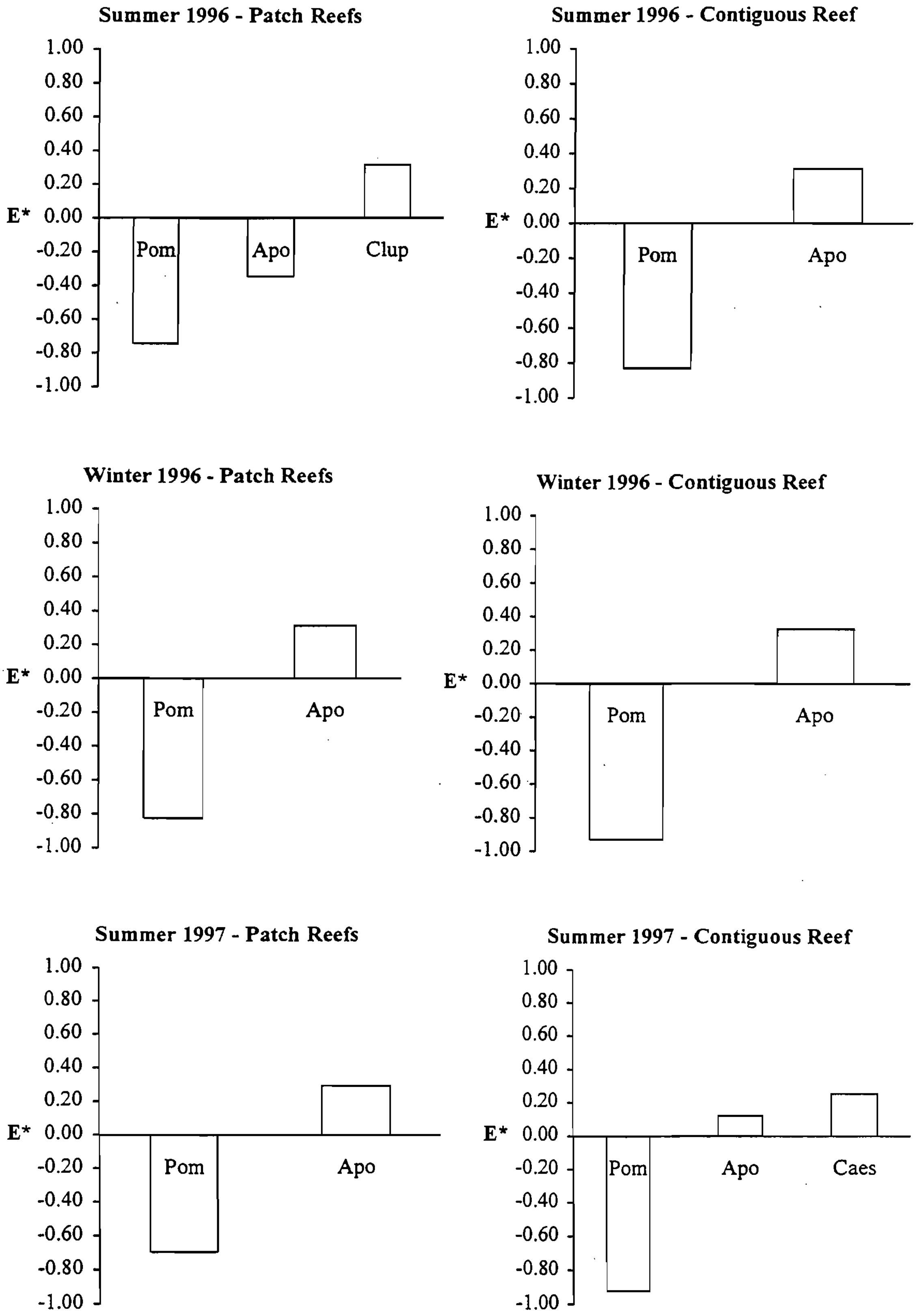
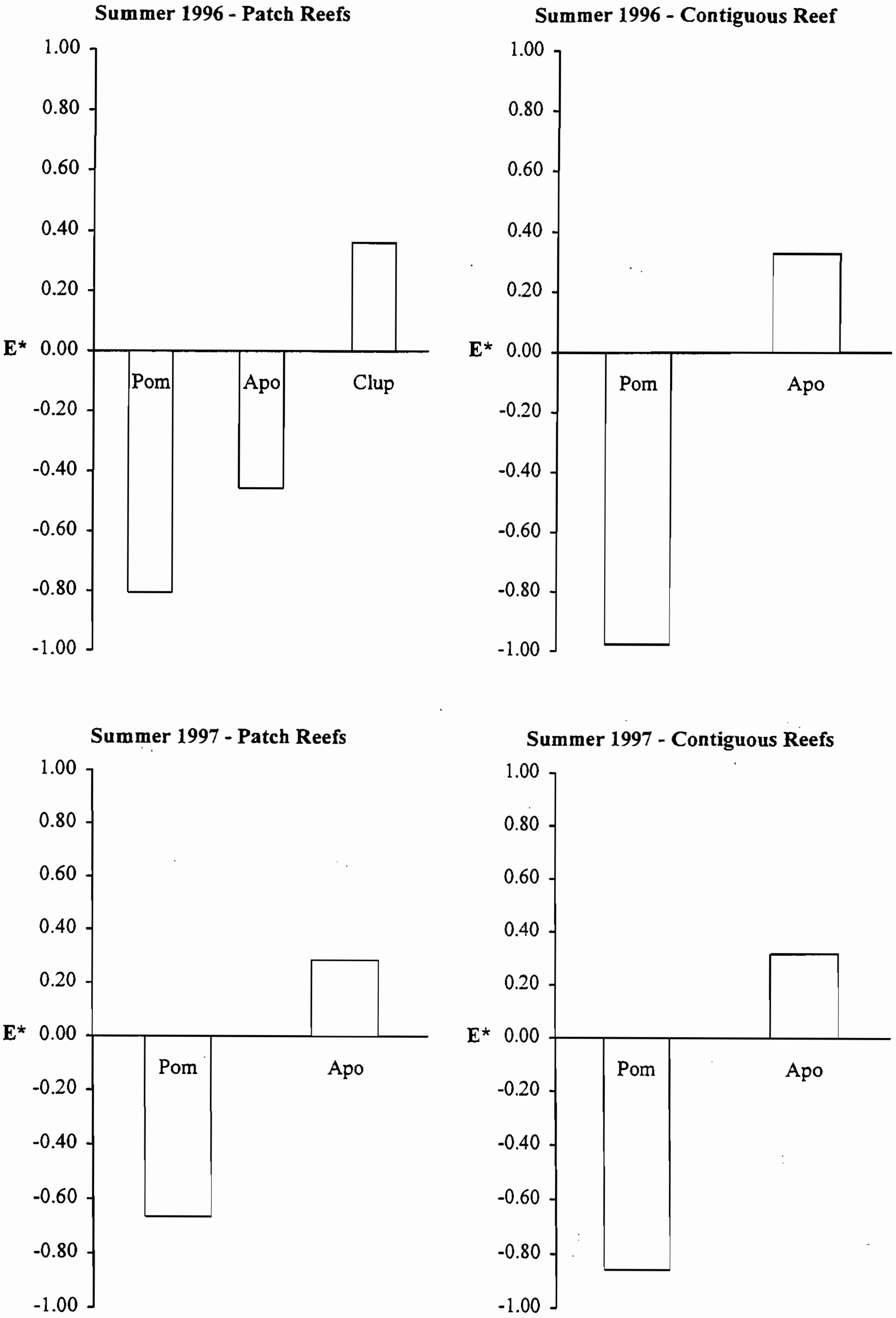


Figure 7. Temporal and spatial variation in prey selection by *Cephalopholis cyanostigma* (E* = Electivity index, Pom = Pomacentridae, Apo = Apogonidae, Clup = Clupeidae, Caes = Caesionidae).


Summer 1996 - Patch Reefs

Summer 1996 - Contiguous Reef

Summer 1997 - Patch Reefs

Summer 1997 - Contiguous Reefs

Figure 8. Temporal and spatial variation in prey selection by *Cephalopholis boenak* (E* = Electivity index, Pom = Pomacentridae, Apo = Apogonidae, Clup = Clupeidae).

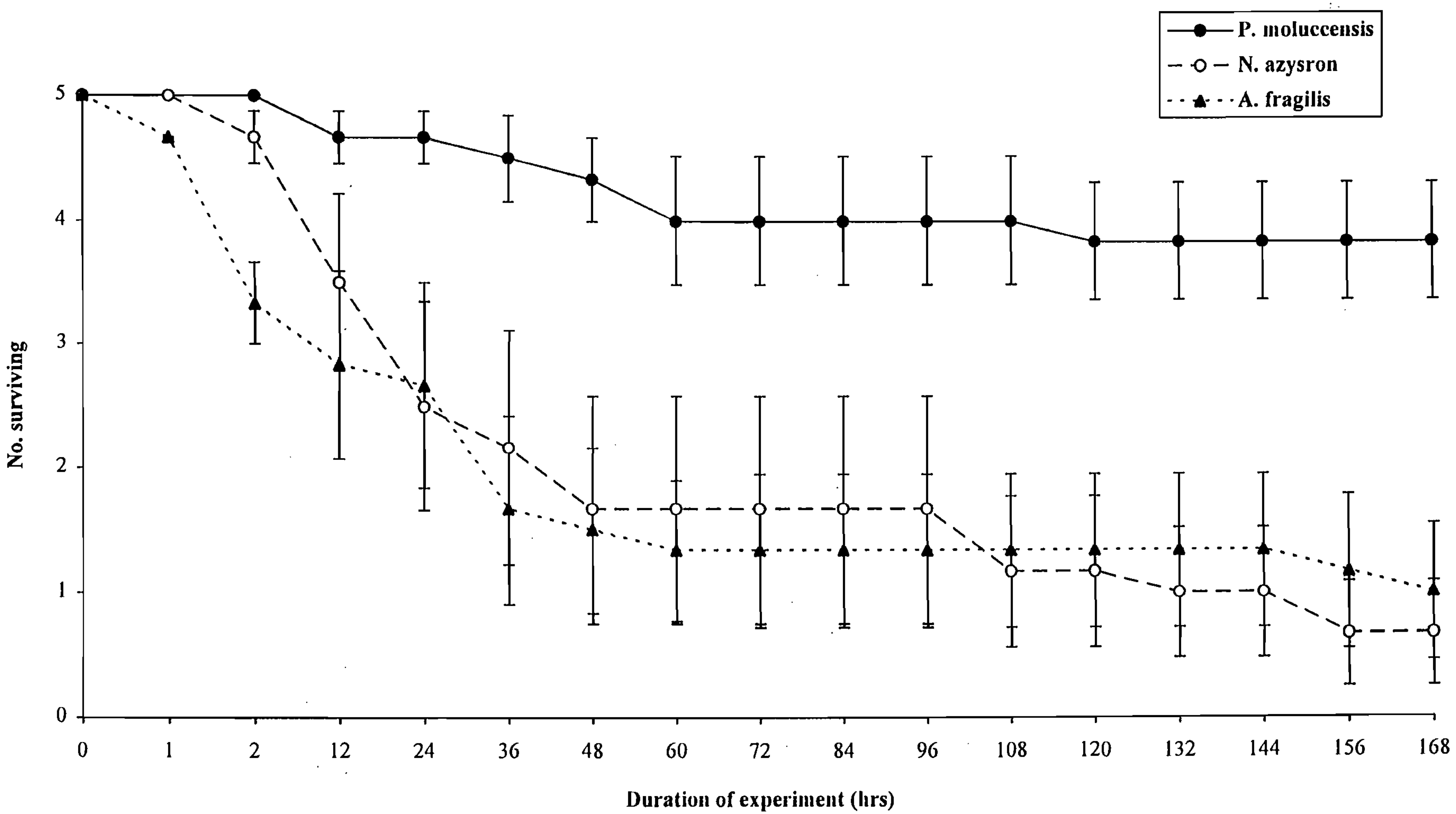


Figure 9. Survival of three different species of prey fish (*Pomacentrus moluccensis*, *Neopomacentrus azysron* and *Apogon fragilis)* exposed to predation by *C. boenak* in the laboratory. Note changing time scale.

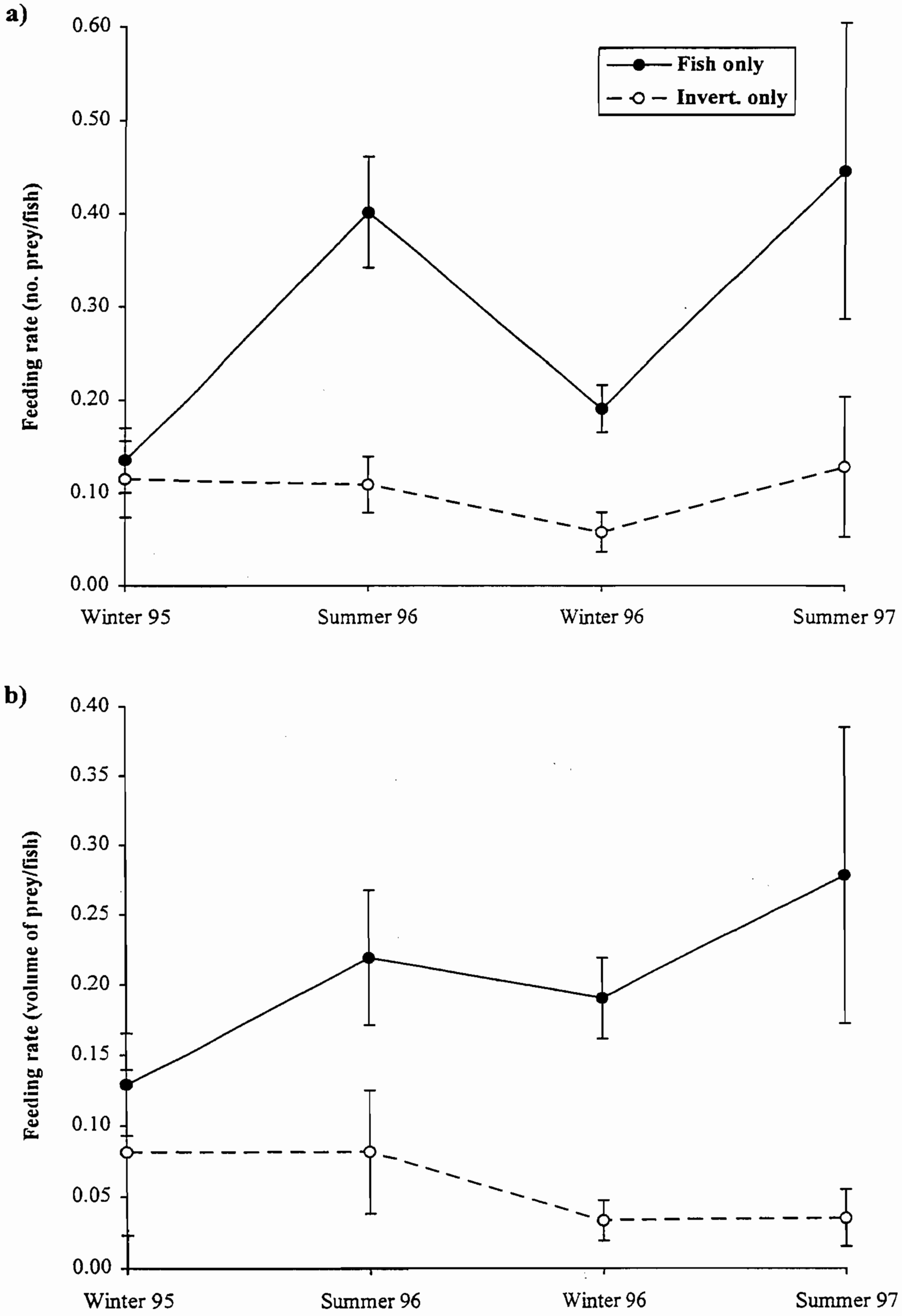


Figure 10. Temporal variation in **a)** the number of prey per fish (mean +/-SE) and **b)** the volume (ml) of prey per fish (mean +/-SE), regurgitated by *Cephalopholis cyanostigma* (n=6 sites).

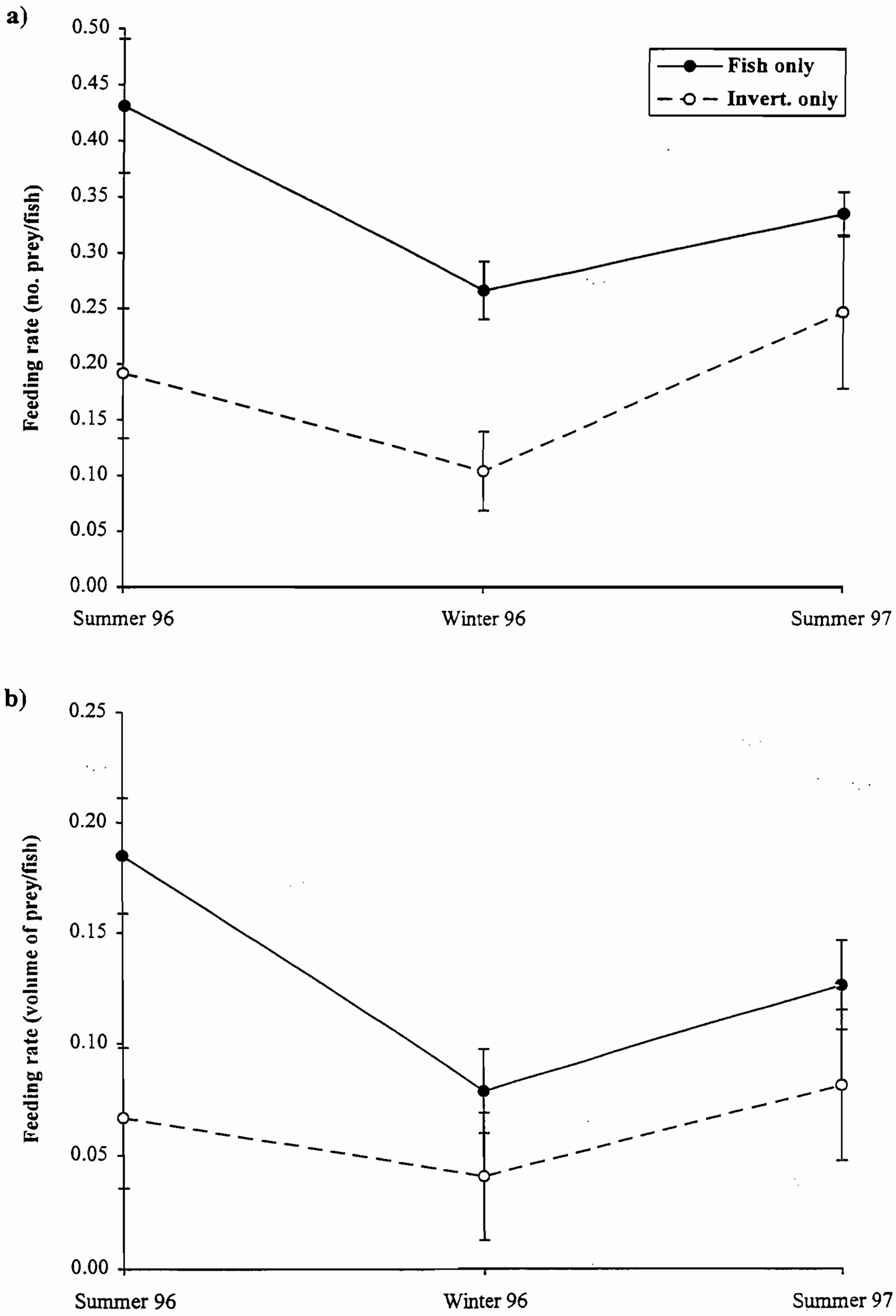


Figure 11. Temporal variation in **a)** the number of prey per fish (mean +/-SE) and **b)** the volume (ml) of prey per fish (mean +/-SE), regurgitated by *Cephalopholis boenak* (n=4 sites).

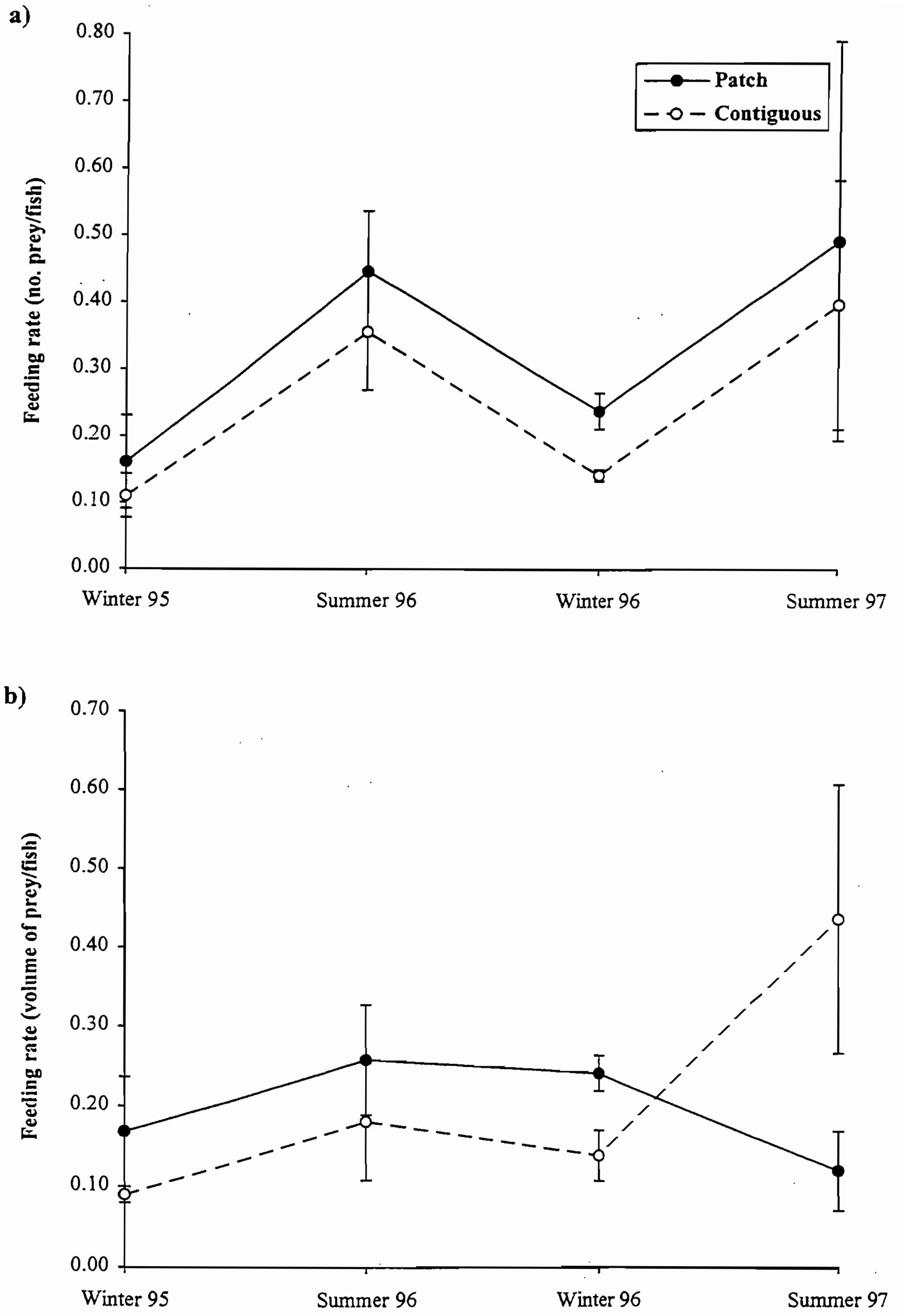


Figure 12. Temporal variation in **a)** the number of fish prey per fish (mean +/-SE) and **b)** the volume (ml) of fish prey per fish (mean +/-SE), regurgitated by *Cephalopholis cyanostigma* on patch and contiguous reef (n=3 sites per reef type)

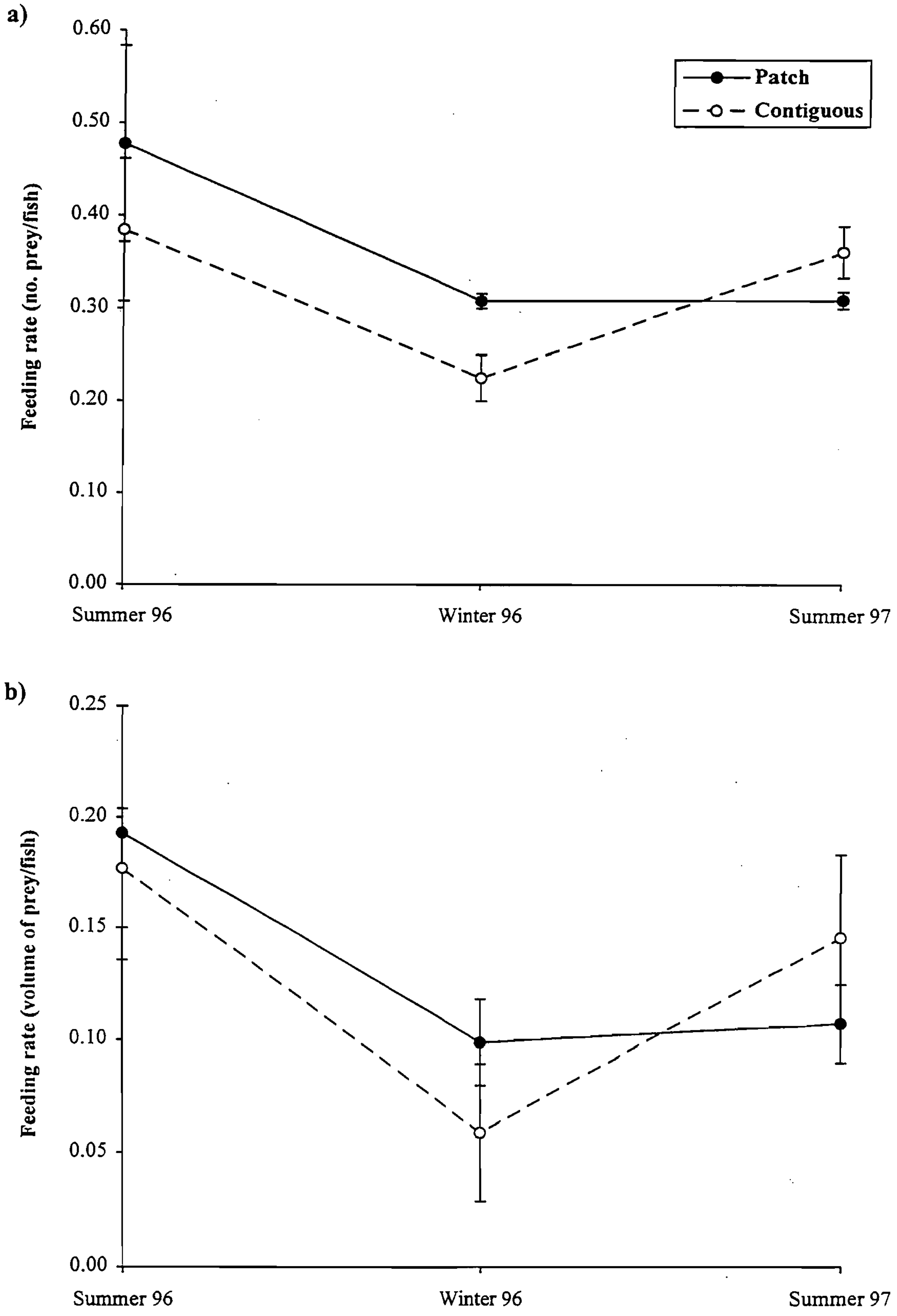


Figure 13. Temporal variation in **a)** the number of fish prey per fish (mean +/-SE) and **b)** the volume (ml) of fish prey per fish (mean +/-SE), regurgitated by *Cephalopholis boenak* on patch and contiguous reef (n=2 sites per reef type).

Chapter 5

Spatial and temporal variation in the life history characteristics and population structure of two piscivorous coral reef fishes

Abstract:

Spatial and temporal variation in the life history characteristics and population structure of piscivorous coral reef fish has rarely been investigated. Understanding the extent of this variation and its causes, is essential for assessing the impact of piscivores on their prey and for effectively managing fisheries for piscivorous species. This study examined the life history characteristics and size, age and sex structures of two piscivorous species of rock-cod, *Cephalopholis cyanostigma* and *C. boenak* (Serranidae) in two different habitats (patch and contiguous reef) at Lizard Island on the northern Great Barrier Reef, Australia. Validation of age estimates from otoliths showed that size-at-age, and age and size-at-maturity of both species were all very similar on the two reef types. Growth of tagged fish showed no difference between reef types for *C. cyanostigma* but was slightly higher on patch reefs than on contiguous reef for *C. boenak*. *C. cyanostigma* also grew faster in the summer than spring. Size, age and sex structures and mortality estimates were similar in the two habitats for *C. cyanostigma* but there were more smaller / younger *C. boenak* on patch reefs than on contiguous reef. Based on age structures, mortality of *C. boenak* was higher on contiguous reef than on patch reefs, but based on longevity there was no difference between reef types. There was also a higher ratio of female to male *C. boenak* on contiguous reef than on patch reefs. The minimal variation in life history characteristics and population structure, particularly for *C. cyanostigma*, could be due to either the conservative nature of these parameters or similar profitabilities of the two habitats. Differences in the growth and population structure of *C. boenak* among habitats may be explained by greater food availability on patch reefs and / or ontogenetic movement toward contiguous reef. Overall, the two rock-cod species could be described as slow growing and long lived (32 years for *C. cyanostigma* and 16 years for *C. boenak*). These characteristics, along with low

rates of natural mortality and recruitment would make them susceptible to overfishing, should they be targeted in the future.

Introduction:

Variation in the life history characteristics and population structure of piscivorous coral reef fishes has rarely been examined (eg. Newman et al. 1996; Russ et al. 1996). Most studies on coral reef fish have concentrated on small planktivorous and herbivorous species (Doherty & Williams 1988; Jones 1991). Knowledge of variation in life history and population structure can provide indirect evidence for different processes limiting fish populations and the mechanisms that determine these effects (Jones 1991). An understanding of the extent of such variation and its causes is also essential for assessing the impact of piscivores on prey and for effectively managing fisheries for piscivorous species.

Recent validation of annual increments in otoliths of coral reef fish (Fowler 1990, 1995; Ferreira & Russ 1992, 1994; Choat & Axe 1996; Choat et al. 1996) has provided a tool for examining growth rates, longevity and age structures of populations. Growth rates can also be estimated from tag-recapture studies (eg. Russ & St John 1988). Most directly, growth has effects on the size structure and biomass of populations. Variation in growth rate may also have effects on a species mortality, size and age-at-maturity and fecundity. For example, growth rate may be an important factor affecting survival, especially of young fish, as it controls the amount of time spent in the small size classes most vulnerable to predation (Smith 1985, Sogard 1997). If the onset of maturity is controlled by size then a faster growing individual will also mature at a younger age. In addition to higher survivorship and earlier maturation, fast growing individuals are also likely to reach maximum size more quickly. As fecundity is generally proportional to body size in reef fishes (Jones 1991), the combination of all of these factors could lead to greater reproductive output over the life time of an individual.

Some authors have suggested that age structures can provide a record of the history of recruitment to a population (eg. Doherty & Fowler 1994; Newman et al. 1996; Russ et al

1996). In particular, strong pulses of recruitment are thought to be maintained in age structures over time. If this is the case age structures could be used to predict the future size of adult populations. The influence of recruitment on a population may depend on longevity, however. It has been argued patterns of recruitment will have less influence on longer-lived species, as their populations will be predominantly structured by patterns of adult mortality and movement (Warner & Hughes 1988; Jones 1991). For example, there is mounting evidence that recruitment patterns can be substantially modified by post-settlement mortality (Jones 1991; Forrester 1995; Hixon & Carr 1997). Longevity can also be used to estimate mortality rates in a population (Hoenig 1984). Alternatively, mortality estimates can also be calculated from age structures using catch-curve-analysis (Pauly 1984). Analysis of age structures may therefore improve our understanding of the factors effecting fish population dynamics.

Movement of fish can be one of the most difficult parameters to assess as it is often unpredictable and can occur instantaneously (Jones 1991). Age and size structures of a population can provide indirect evidence of movement, particularly ontogenetic shifts in habitat use. For example, a preponderance of small / young fish in one habitat type and the presence of mainly larger / older fish in another would suggest their distribution has changed over time (eg. Eggleston 1995; Light & Jones 1997). There is increasing evidence that patterns of movement may have a large influence on the distribution and abundance of coral reef fishes (Lewis 1997; Ault & Johnson 1998), although detailed studies on individual species are rare (Samoilys 1986, Davies 1995; Zeller 1997a).

For species of fish which maintain haremic social systems, sex ratios may provide a good approximation of the size of social groups (Shapiro 1991; Shpigel & Fishelson 1991; Mackie 1993). The reproductive success of male fish, in particular, may largely depend upon the number of females it can successfully defend (Warner 1984). Variation in sex ratios may therefore have ramifications for the reproductive output of a population.

Variation in the life history and population structure of piscivorous coral reef fish may also have implications for predator / prey interactions (Kingsford 1992). Many predatory coral reef fish become increasingly piscivorous as they increase in size and age (Harmelin-Vivien & Bouchon 1976; Parrish 1987; St John 1995). Larger fish also generally consume more prey than smaller ones (Weatherly & Gill 1987). A greater proportion of large piscivores in the community is therefore likely to have a greater impact on prey fish populations and communities.

In addition, piscivorous coral reef fish are disproportionately targeted by recreational and commercial fishers (Russ 1991). Knowledge of their life history characteristics and population structure, and how and why they vary, is therefore essential if fisheries for these species are to be effectively managed.

The initial aim of this study was to examine variation in life history characteristics and population structure of two piscivorous species of rock-cod, *Cephalopholis cyanostigma* and *C. boenak* (Serranidae) at Lizard Island on the northern Great Barrier Reef, Australia. The study was conducted in two different habitats (patch and contiguous reef) and over a 2 year period so both temporal and spatial variation could be examined. A preliminary investigation on the central Great Barrier Reef (Mamauag 1993), indicated that both species were relatively slow growing and long lived, but age estimates were unvalidated and sample size was quite limited. There is no information on spatial or temporal variation in their life histories or population structures. Species of the genus *Cephalopholis* can be characterised as protogynous hermaphrodites which maintain social groups consisting of one male and up to 12 females (Shpigel & Fishelson 1991, Mackie 1993). Descriptive observations (Shpigel & Fishelson 1991, Mackie 1993) suggested that the structure of habitat available may effect the size of social groups but this idea was not been investigated in detail. Females of both *C. cyanostigma* and *C. boenak* maintain relatively exclusive territories, while the territories of males overlap those of the females within their social group (Mackie 1993, Chapter 3). These territories are stable in the short term (Mackie 1993), but may change over a period of years (Chapter 3).

This study was part of a larger investigation examining how variation in prey abundance effects various aspects of the ecology of the two rock-cod species (see Chapters 3 and 4).

Over the 2 years of the study prey abundance at Lizard Island remained significantly higher on patch reefs than on contiguous reef (Chapter 3). Food availability is known to be one of the main factors affecting fish growth (Weatherley & Gill 1987), including species on coral reefs (Jones 1986; Forrester 1990; Clifton 1995; Hart & Russ 1996). The second aim of this chapter was therefore to investigate if and how this difference in prey abundance affected the growth of *Cephalopholis cyanostigma* and *C. boenak*. Both species of rock-cod have already been shown to partly compensate for the differences in prey abundance by maintaining larger territories on contiguous reef, however, the number of prey available to each rock-cod was still higher on patch reefs. Despite this, feeding rates on fish prey were not significantly different on the two reef types (Chapter 4). Data on feeding rates was highly variable, however, so differences would have to have been very large to obtain a significant result. Examination of growth rates was expected to provide a more powerful test of the effect of prey abundance. Differences in growth rate would also represent a more significant, longer term response to variation in prey abundance. In addition, the small territories occupied by both species on patch reefs were expected to require less energy to maintain and little distance had to be covered in search of prey. It was therefore hypothesised that even if feeding rates were similar on the two reef types growth rates would still be faster on patch reef. Differences in growth rate were expected to translate into differences in various other aspects of each species life history.

The third aim of this chapter was to describe general patterns of age, growth, mortality and population structure for the two species, as validated estimates of such characteristics have not been produced previously. *C. cyanostigma*, in particular, is a common by-catch in the fishery for *Plectropomus leopardus* on the Great Barrier Reef (Williams and Russ 1994) and may be targeted in the future. Knowledge of life history characteristics of the rock-cods may therefore become important for their effective management.

Methods:

The study was conducted on the western (predominantly sheltered) side of Lizard Island ($14^0 40'$S; $145^0 28'$E) on the northern Great Barrier Reef, Australia. A small number of fish

(9 *Cephalopholis cyanostigma* and 13 *C. boenak*) were collected in October and December 1993. The majority of the study, however, was conducted on 3 patch and 3 contiguous reef sites (see Chapters 3 and 4) between February 1995 and April 1997. This included age validation, the tag-recapture program and the remaining otolith and gonad collection.

1. Age validation

A total of 271 *Cephalopholis cyanostigma* and 157 *C. boenak* were tagged with T-bar anchor tags and released at the 6 study sites over the period from February 1995 to November 1996 (see Chapters 2 and 3). Upon tagging a dosage of 50 mg of tetracycline per kg of fish (in a concentration of 50 mg per ml of sterile saline solution) was injected into the coelomic cavity of each fish. Each site was fished for approximately 2 days once every 3 months during the study period and any recaptured fish were reinjected with tetracycline. In April 1997, 34 tagged *C. cyanostigma* and 28 tagged *C. boenak* were collected for otolith dissection. Of these fish 29 *C. cyanostigma* and 24 *C. boenak* had been at liberty for approximately one year or more after the initial injection of tetracycline and therefore were suitable for age validation. Both sagittal otoliths were dissected from each of these fish and one of these was then embedded in epoxy resin and sectioned transversely with a Beuhler low speed Isomet saw. Sections were mounted on glass slides with Crystal Bond 509 adhesive and then ground and polished with wet and dry paper (ranging in grade from 800 to 1200). Examination of these otoliths under a combination of fluorescent and transmitted light at 40X magnification allowed for determination of the timing and periodicity of otolith increment formation in relation to the tetracycline marks.

2. Age, growth and mortality estimates from otoliths

Including the sample used for age validation, sagittal otoliths were dissected from a total of 139 *Cephalopholis cyanostigma* and 85 *C. boenak* captured at Lizard Island between October 1993 and April 1997. The majority of these fish (101 *C. cyanostigma* and 64 *C. boenak*) were collected underwater by baited hook and line between January and April 1997. Small specimens of *C. boenak* (< 100 mm total length) were captured using quinaldine (anaesthetic) and hand nets. All dissected otoliths were weighed to the nearest milligram and one from each pair was then sectioned as described above. Sections were viewed under transmitted light at 40X magnification and increments were counted to obtain age estimates. A sub-sample of 50 otoliths from each species was also re-examined (without reference to the previous count) to measure the repeatability of age estimates. Beamish and Fournier's (1981) method was used to calculate precision. To improve the accuracy of age estimates a birth date of the 1st of January (the middle of the spawning period, Mackie 1993) was assigned to each fish. Age was then calculated by adding the proportion of a year, elapsed between the 1st of January and the date the fish was captured, to the number of increments counted. In cases where fish were caught in October, November or December this was a negative proportion as increments were formed by the end of September (see results).

The relationship between otolith weight and age was examined for each species to determine whether or not otoliths continued to grow throughout the lives of fish. Logarithmic curves were then fitted to the relationships between age and fish length for each species on the two reef types to determine if growth differed. Curves were also fitted to the combined data to determine the overall growth parameters for each species at Lizard Island. Length frequency histograms were then produced to determine if the size range of fish sampled differed between the two reef types. The age composition of each species was used to estimate natural mortality rates on the two reef types (Pauly 1984). *Cephalopholis cyanostigma* and *C. boenak* less than 4 years old were not included in this analysis as they were not adequately sampled. Mortality estimates were also obtained for the overall population of each species. Mortality estimates from the age composition were then compared to estimates calculated using the following empirical formula based on longevity (Hoenig 1984).

$$\mathbf{\ln (Z) = 1.44 - 0.984 \ln (t_{max})}$$

Where Z = mortality and t_{max} = maximum age (longevity)

3. Growth of tagged fish

Given that fish may not have remained at each site throughout their lives (Chapter 3), and that conditions of prey abundance may have been different prior to the study, I also measured the growth of all fish tagged and released between February 1995 and November 1996. To gain growth estimates, the total length of each fish was measured upon tagging (to the nearest mm), and any fish recaptured during subsequent field trips was remeasured and released. The only exception was at end of the study (ie between January and April 1997) when all recaptured fish were retained for dissection.

a) Seasonal variation in growth

To determine if growth varied seasonally, I examined growth of tagged fish over six sequential 3 month periods between August 1995 and April 1997. Each of these periods corresponded to one of the four seasons and data was pooled across years. Growth measurements were taken from a range of different sized fish but I ensured that the average size of fish for each season was not significantly different (one way ANOVA). Examination of the effect of season on growth rate was then examined by one way ANOVA with the single fixed factor being season. When results were significant this was followed by a Tukey's test (honestly significant difference method) to compare the mean grow rates in each season.

b) Spatial variation in growth

Growth rates of fish tagged on patch and contiguous reefs were also compared. Due to the possible effect of seasonal variation in growth on the results, only fish which had been at liberty for between 9 and 15 months (ie approximately 1 year) were included in the analysis. For each reef type the relationship between fish length and growth rate was determined and these were compared between reef types using ANCOVA. The fixed factor was reef type and the covariate fish length. Data was Ln (x+1) transformed to improve heterogeneity and normality of variances (Underwood 1981)

4. Reproductive biology

Gonads were removed from all dissected fish and identified macroscopically as either immature, female or male. Identification was assisted by the fact that most fish were taken during the summer spawning season (and therefore mature gonads were ripe) and that at the onset of maturity *Cephalopholis cyanostigma* changes from a grey colour with yellow fins to a red / brown colour with blue spots (Randall et al. 1990). Using information from the above age estimates, age and size at maturity was calculated for the two species on each reef type and overall. The proportion of individuals of each sex in different age and size classes was also calculated and compared between reef types. In addition, sex ratios were calculated for each species on the two different reef types to provide an estimate of the size of social groups. Differences were examined by one way ANOVA with the fixed factor being reef type and the ratio of females to males being the dependent variable. Sites were used as replicates and data was arcsine transformed.

Results:

1. Age validation.

All fish injected with tetracycline showed clear fluorescent marks in their otoliths. Some fish had been recaptured (and hence re-injected) 2 or 3 times and therefore showed 2 or 3 marks. Comparison of the position of these marks with the position of otolith increments indicated that increments were formed annually from August to September. The age of fish from which validated estimates were obtained ranged from 4 to 26 years for *Cephalopholis cyanostigma* and 4 to 16 years for *C. boenak.*

2. Age, growth and mortality estimates from otoliths

Clear increments were present in almost all (98.6%) *Cephalopholis cyanostigma* otoliths and all *C. boenak* otoliths. Repeatability of these age estimates was very high (6.0 % error for *C. cyanostigma* and 5.5 % error for *C. boenak*). There was a strong relationship between otolith weight and age for both species (Fig 1), indicating otoliths continued to grow throughout the lives of the fish. Based on these age estimates both species appeared to grow at the same rate on patch and contiguous reef (Table 1, Fig. 2). *C. cyanostigma* and *C. boenak* grew at similar rapid rates for the first 2 to 3 years, while beyond that growth slowed substantially (Table 1, Fig. 3). During this period, however, growth of *C. cyanostigma* remained higher than that of *C. boenak* (Table 1, Fig. 3). Consequently, *C. cyanostigma* reached a larger size (approx. 30 cm total length (TL)) and maximum age (32 years) than *C. boenak* (approx. 21 cm TL and 16 years, respectively), (Table 1, Fig 3).

The length frequency distribution of fish collected was quite similar on patch and contiguous reef. The only real differences were a slightly higher proportion of *Cephalopholis cyanostigma* in the 251 - 275 mm size range on contiguous reef (Fig. 4) and a higher proportion of small *C. boenak* (< 100 mm) on patch reef (Fig. 4). Age structures of *C. cyanostigma*, and therefore mortality estimates, were also quite similar on patch and contiguous reef (Fig. 5 and 6). Overall, age structures of *C. cyanostigma* showed high numbers of fish 7 to 10 years old, particularly in the 8 year old age class, although fish between 11 and 21 years old were still well represented (Fig 7a). Based on this age structure the total mortality (Z=0.086) of *C. cyanostigma* was relatively low (Fig 7b). Age structures of *C. boenak* were quite different on the two reef types with both more young (< 1 year) and old (> 11 years) fish on patch reef than on contiguous reef (Fig 8). Mortality estimates were therefore lower on patch reef (Z=0.076) than on contiguous reef (Z=0.135), (Fig. 9). The overall age structure of *C. boenak* showed high numbers of fish from 3 to 12 years old, with much lower numbers of fish aged 13 to 16 (Fig 10a). Based on this age structure the total mortality (Z=0.163) of *C. boenak* was higher than that of *C. cyanostigma* (Fig 10b). All of these mortality estimates, however, were much lower than those derived using Hoenig's (1984) formula (Table 2) and in addition, Hoenig's method did not indicate any differences between reef types.

3. Growth of tagged fish

a) Seasonal variation in growth

Only *Cephalopholis cyanostigma* showed a significant effect of season on growth rate (Table 3). Tukey's test revealed that growth of *C. cyanostigma* was significantly higher in summer than in spring but there were no other significant differences. Both species, however, showed a trend for growth to be highest in summer and lower in the other seasons (Fig. 11). High variation in growth rate between individuals was responsible for these trends being non significant.

b) Spatial variation in growth

Of the fish recaptured, 81 *Cephalopholis cyanostigma* (42 on patch reefs and 39 on contiguous reef) and 38 *C. boenak* (22 on patch reefs and 16 on contiguous reef) fulfilled the growth criteria (ie had been at liberty for approximately one year). Growth rates of *C. cyanostigma* were not significantly different on patch and contiguous reef (Fig 12a, Table 4a), but *C. boenak* (particularly when less than 160 mm TL) grew slightly, but significantly, faster on patch reefs (Fig 12b, Table 4b). There was again high variation in individual growth rates.

4. Reproductive biology

Sex determination showed that both species were protogynous hermaphrodites. *Cephalopholis cyanostigma* reached sexual maturity (> 50% mature) as a female at 130 - 140 mm total length (TL) corresponding to an age of 3 years (Fig. 13). Transition to the male phase did not generally occur until fish were greater than 250 mm TL and older than 10 years (Fig. 13). The majority of fish greater than 275 mm TL and older than 20 years were male (Fig. 13). These patterns were very similar on patch and contiguous reef. Females made up 77.36 % of the mature population, indicating an average social group consisted of 3 or 4 females to every male. These patterns were almost identical on patch and contiguous reef (Table 5a)

In some respects, the reproductive biology of *Cephalopholis boenak* was quite similar to that of *C. cyanostigma* (Fig 14). *C. boenak* became sexually mature females at 120 - 130 mm total length (TL) corresponding to an age of 4 years (Fig. 14). Males were uncommon until fish were greater than 150 mm in length and 7 years old (Fig. 14). The majority of fish larger than 175 mm TL and older than 10 years were males (Fig 14). These patterns were again similar on patch and contiguous reef. Overall, females made up 66.10 % of the mature population, indicating an average social group consisted of 1 male and 2 or 3 females. These patterns were significantly different on patch and contiguous reefs, however (Table 5b). On patch reefs fish were generally monogamous (1.18 females to every male) while on contiguous reef larger social groups were evident (3.63 females to every male).

Discussion:

Many aspects of the life history and population structure of the two rock-cod species were very similar on patch and contiguous reef over the course of the study, despite apparent differences between the habitat types and different seasons of the year. This was particularly the case for *Cephalopholis cyanostigma*, with the only exception being seasonal variation in growth of tagged fish. For *C. boenak*, size-at-age and age and size at maturity was also consistent across reef types, although there was some variation in growth of tagged fish, and size, age and sex structures. The similarities between the populations on the two reef types could be due to the conservative nature of the traits measured and that they are relatively unaffected by environmental variables. This explanation would appear unlikely, however, as growth of fish, in particular, is known to be very sensitive to variation in factors such as food availability and water temperature (Weatherley & Gill 1987). Instead, it would appear that the profitability of living in the two different habitats (patch and contiguous reef) was reasonably similar, particularly for the *C. cyanostigma*. Differences between the biology of *C. cyanostigma* and *C. boenak* may account for the fact that *C. boenak* was more affected by differences between the two habitat types.

The lack of any differences between the size-at-age curves of each species on patch and contiguous reef was particularly surprisingly, given the substantial differences between the two reef types in terms of prey abundance (Chapter 3). The tagging study confirmed this result for *Cephalopholis cyanostigma* but for *C. boenak* growth was slightly, but significantly, faster on patch reefs. This result may have been due to differences in prey availability. For example, in February 1997, each *C. boenak* had 4 times more prey available to it on patch reefs than on contiguous reef (Chapter 3). For *C. cyanostigma* the difference was only 1.5 times. This situation arose because unlike for *C. cyanostigma*, home range sizes of *C. boenak* were only marginally (1.5 times) larger on contiguous reefs than on patch reefs, despite the fact that prey abundance was much lower (Chapter 3). It was therefore more likely that growth of *C. boenak*, rather than *C. cyanostigma* would have been limited by the lower density of prey on contiguous reef. Although data on feeding rates did not suggest that *C. boenak* would have grown faster on patch reefs, this data may not have been sensitive enough to pick up the small differences in feeding rate which may have been responsible for the small increase in growth rate.

The fact that size-at-age curves of *Cephalopholis boenak* were similar on the two reef types, despite differences in growth rate, could be explained by some degree of mixing or movement between the two populations. Tagging data (Chapter 3) indicated that such movements did occur, although they appeared to be uncommon. Given the average age of the *C. boenak* studied (approximately 7 years), however, some degree of movement over this time period would not be unexpected. Age and size structures of *C. boenak* provided additional evidence of movement between the reef types. Reasonable numbers of small and young *C. boenak* on patch reefs, compared to their scarceness on contiguous reef, suggests they may undergo an ontogenetic shift from patch to contiguous reef (see Jones 1991).

Despite this evidence of the effect of prey abundance on the growth of *Cephalopholis boenak*, it was still not immediately obvious why differences in growth rate were only small and why there was no difference for *C. cyanostigma*. In addition to the large differences between the two habitats in terms of prey abundance, it was expected that the smaller distances fish were travelling on patch reefs would also provide an energetic advantage.

There are a number of possible explanations for the results. Firstly, it is possible that prey abundance was not limiting and that all fish were growing at, or near to, maximum rates. Traditional ecological theory (Hairston et al. 1960; Menge and Sutherland 1987), however, would suggest that this would be unlikely for predators high in the food chain. Alternatively, energy gains on patch reefs may have been funnelled into reproductive, rather than somatic growth. Unfortunately I did not investigate this possibility.

Perhaps the most plausible explanation is that other factors such as competition and predation were inhibiting the feeding rates (and consequently growth rates) of the rock-cods on patch reefs. Reduced growth in the presence of high numbers of competitors has been observed several times in coral reef fish populations (Jones 1987, Forrester 1990, Booth 1995). The density of competitors (both conspecifics and other species) was significantly higher on patch reefs (Chapter 3). The two rock-cod species were territorial and were often aggressive towards potential competitors (Chapter 3; pers. obs.). If competitors had to be chased away more often on patch reefs this would certainly have represented a significant time and energy drain. Competitors may also have reduced the density of prey within the home ranges of rock-cods on patch reefs. The extent of this would depend on how effective the rock-cods were in keeping competitors from feeding within their territories. There was definitely some overlap between territories of neighbouring rock-cods (Chapter 3) and several other piscivorous species such as *Plectropomus leopardus*, *Lutjanus carponatatus*, *Carangoides fulvogattus* and *C. ferdau* were observed feeding within rock-cod territories. High densities of competitors would therefore be very likely to have effected growth rates.

The risk of predation is also known to inhibit feeding rates of fish (Milinski 1986). This phenomenon has often been observed in other environments such as freshwater lakes and streams (Milinski 1986), seagrasses (Tupper & Boutilier 1995) and temperate reefs (Holbrook & Schmitt 1988), and recently has also been demonstrated on coral reefs (Connell 1998b). A known predator of the two rock-cod species, *Plectropomus leopardus* (St John 1995), was much more common on patch reefs than on contiguous reef (Chapter 3). The presence of this large predator may therefore have also effected the feeding behaviour of the rock-cods.

Seasonal variation in growth rates also suggested that the rock-cods may have been limited by the prey available, at least during autumn, winter and spring. Both prey abundance (Chapter 3) and feeding rates (Chapter 4) were much lower in these seasons than in summer. Unfortunately, however, this evidence is inconclusive. Given that fish were only growing a small amount over the 3 month periods, and that measurement error was probably +/- 1 mm, it was difficult to accurately calculate growth. More important, though, was the confounding effect on temperature on the results. Temperature is one of the main factors known to effect fish growth (Weatherley & Gill 1987), and water temperature at Lizard Island was on average 5^0 C higher in summer than in winter (Lizard Island Research Station). Seasonal variation in growth may therefore have been the result of combined fluctuations in temperature and prey abundance.

Variation in the age compositions of both species of rock-cod suggested that their recruitment at Lizard Island may have been both temporally and spatially variable. For example, high numbers of 8 year old *Cephalopholis cyanostigma* on both reef types and high numbers of both young (< 1 year old) and 12 year old *C. boenak* on patch reefs, may have resulted from strong recruitment pulses (Doherty & Fowler 1994, Newman et al. 1996; Russ et al. 1996). On the other hand, the longevity of both *C. cyanostigma* (32 years) and *C. boenak* (16 years) raises the potential for their patterns of recruitment to be substantially modified by adult mortality and movement (Warner & Hughes 1988; Jones 1991). The contribution of recruitment to patterns of abundance would therefore be better estimated by detailed recruitment surveys (see Chapter 3).

Based on the age composition data, mortality estimates of both *Cephalopholis cyanostigma* and *C. boenak* were reasonably similar on patch and contiguous reef. The somewhat higher estimate of mortality for *C. boenak* on contiguous reef can not be given much weight as the method used to calculate mortality can be unreliable with small sample sizes. This became evident when the combined samples from patch and contiguous reef produced higher mortality estimates for both species. This method of calculating mortality also assumes constant recruitment, which is very unlikely in coral reef fish populations (Doherty 1991;

see above). Hoenig's (1984) method, based on longevity, was probably more appropriate for making comparisons between reef types. This method demonstrated no real differences between mortality rates on patch and contiguous reef. It also gave higher mortality estimates overall. This difference between methods can probably be attributed to fact that young fish of both species were not adequately sampled in this study. Hoenig's method therefore probably also gave the most accurate estimates of overall mortality. The higher mortality suffered by *C. boenak* in comparison to *C. cyanostigma* can probably be attributed to its slower growth rate and smaller maximum size (Smith 1985, Sogard 1997).

Due to similar size-at-age curves of both rock-cod species on patch and contiguous reef, age-at-maturity and transition from female to male was consistent across reef types. For *Cephalopholis boenak*, however, there were substantial differences between sex ratios on patch and contiguous reef. Sex ratios give a good approximation of the size and composition of social groups of Cephalopholids (Shpigel & Fishelson 1991, Mackie 1993) although in some cases male fish may only form associations with certain females during the mating season (Mackie 1993). The result that social groups of *C. boenak* appeared to be smaller on patch reefs was actually the reverse of what was expected. It was thought that the higher density of prey on patch reefs would lead to the formation of large social groups. This was because many rock-cods were able to live within close proximity of one another on patch reefs (Chapter 3) and the provision of one male to many females would be expected to maximise reproductive output (Warner 1984). It can only be assumed that the higher predation pressure on patch reefs lead to the reduced size of social groups of *C. boenak* (Shapiro 1991). The effect was presumably greater on the social structure of *C. boenak* as due to it's smaller size it was under increased risk of predation (Smith 1985, Sogard 1997).

Overall, despite some differences for *C. boenak*, the life history characteristics and population structures of the rock-cods could generally be described as reasonably similar on the two reef types. Therefore, variation in these traits would not appear to be a major factor in predator / prey interactions. Instead, differences between the densities of the rock-cods on the two reef types probably has a much greater influence on mortality patterns of their prey (see Chapter 3).

In general, the life history characteristics of *Cephalopholis cyanostigma* and *C. boenak* appear to be similar to those of many other tropical serranids (Manooch 1987). In fact, the estimates of age, growth, mortality and size and age-at-maturity obtained for the two rock-cod species in this study were almost identical to the unvalidated estimates obtained on the central Great Barrier Reef (Mamauag 1993). Tropical serranids tend to be characterised by several years of relatively rapid growth, followed by a prolonged period of slow growth (Manooch 1987, Ferreira & Russ 1992, Beets & Hixon 1994, Ferreira & Russ 1994). The longevity of the two species in this study (16 years for *C. boenak* and 32 years for *C. cyanostigma*), however, is among the greatest recorded for serranids. Natural mortality rates of the rock-cods were correspondingly low. Although neither species is commercially targeted at present, any future fishery for the rock-cods would have to be carefully managed. The combination of their slow growth, low mortality and low recruitment (Chapter 3) would make them very susceptible to overfishing.

In summary, over the course of the study, *Cephalopholis cyanostigma* and *C. boenak* appeared to live in a well balanced community at Lizard Island. Despite dramatic temporal and spatial variation in the abundance of prey, there was only minimal variation in the life histories and population structures of the rock-cods. *C. boenak* accounted for most of the variation, which suggested that patch reefs may be a more profitable habitat for young individuals, but that they shift from patch reefs to contiguous reef as they grow. In general, however, it appeared that the rock-cods, along with other piscivores, primarily responded to variation in prey abundance by aggregating in high density patches of prey (see Chapter 3). The resultant competition, possibly in conjunction with increased predation pressure, seemed to negate much of the energetic advantage they may otherwise have gained. The influence of prey abundance on the feeding and growth rates of coral reef piscivores requires further attention, however. This would provide us with a greater understanding of the importance of post-recruitment processes to the ecology of both piscivores and their prey.

Table 1. Comparison of size-at-age curves for *Cephalopholis cyanostigma* and *C. boenak* on patch and contiguous reef and both reef types combined. All relationships significant ($p < 0.05$).

a) *Cephalopholis cyanostigma*

Sample	n	Relationship	R^2
Patch Reefs	56	Age = 67.07 Ln (length) + 70.03	0.87
Contiguous Reefs	81	Age = 71.75 Ln (length) + 59.62	0.88
Combined	137	Age = 69.62 Ln (length) + 64.49	0.88

b) *Cephalopholis boenak*

Sample	n	Relationship	R^2
Patch Reefs	44	Age = 42.39 Ln (length) + 75.45	0.94
Contiguous Reefs	41	Age = 45.64 Ln (length) + 67.67	0.80
Combined	85	Age = 42.98 Ln (length) + 73.51	0.90

Table 2. Comparison of mortality estimates calculated using age structures and Hoenig's (1984) empirical method based on longevity.

a) *Cephalopholis cyanostigma*

Sample	Age Structure	Longevity
Patch Reefs	0.047	0.144
Contiguous Reef	0.068	0.139
Combined	0.086	0.144

a) *Cephalopholis boenak*

Sample	Age Structure	Longevity
Patch Reefs	0.076	0.276
Contiguous Reef	0.135	0.294
Combined	0.163	0.294

Table 3.

a) Results of ANOVA examining the influence of season on growth rates of tagged *Cephalopholis cyanostigma* (* indicates significant result).

SOURCE	SS	DF	MS	F	Sig of F
Season	0.01	3	< 0.00	4.59	0.005*
Within + Residual	0.04	72	< 0.00		

b) Results of Tukey's test (HSD) method comparing the growth rates of tagged *Cephalopholis cyanostigma* in different seasons

Summer > Spring
Summer = Autumn = Winter
Autumn = Winter = Spring

c) Results of ANOVA examining the influence of season on growth rates of tagged *Cephalopholis boenak*.

SOURCE	SS	DF	MS	F	Sig of F
Season	< 0.00	3	< 0.00	0.39	0.759
Within + Residual	0.02	50	< 0.00		

Table 4. Results of ANCOVA examining the effect of reef type on growth rates of tagged fish. Data was Ln (x+1) transformed (* indicates significant result).

a) *Cephalopholis cyanostigma*

SOURCE	SS	DF	MS	F	Sig of F
Reef Type	0.84	1	0.84	2.24	0.138
Regression	20.28	1	20.28	54.02	< 0.000*
(Model)	21.94	2	10.97	29.21	< 0.000*
Within + Residual	29.29	78	0.38		

R-Squared = 0.428

b) *Cephalopholis boenak*

SOURCE	SS	DF	MS	F	Sig of F
Reef Type	0.66	1	0.66	6.35	0.018*
Regression	7.55	1	7.55	72.48	< 0.000*
(Model)	7.56	2	3.78	36.32	< 0.000*
Within + Residual	2.91	28	0.10		

R-Squared = 0.722

Table 5. Results of ANOVA examining the influence of reef type on the ratio of female to male rock-cods. Data was arcsine transformed (* indicates significant result).

a) *Cephalopholis cyanostigma*

SOURCE	SS	DF	MS	F	Sig of F
Reef Type	< 0.000	1	< 0.000	0.010	0.927
Within + Residual	0.017	4	0.004		

b) *Cephalopholis boenak*

SOURCE	SS	DF	MS	F	Sig of F
Reef Type	0.108	1	0.108	93.21	0.011*
Within + Residual	0.002	2	0.001		

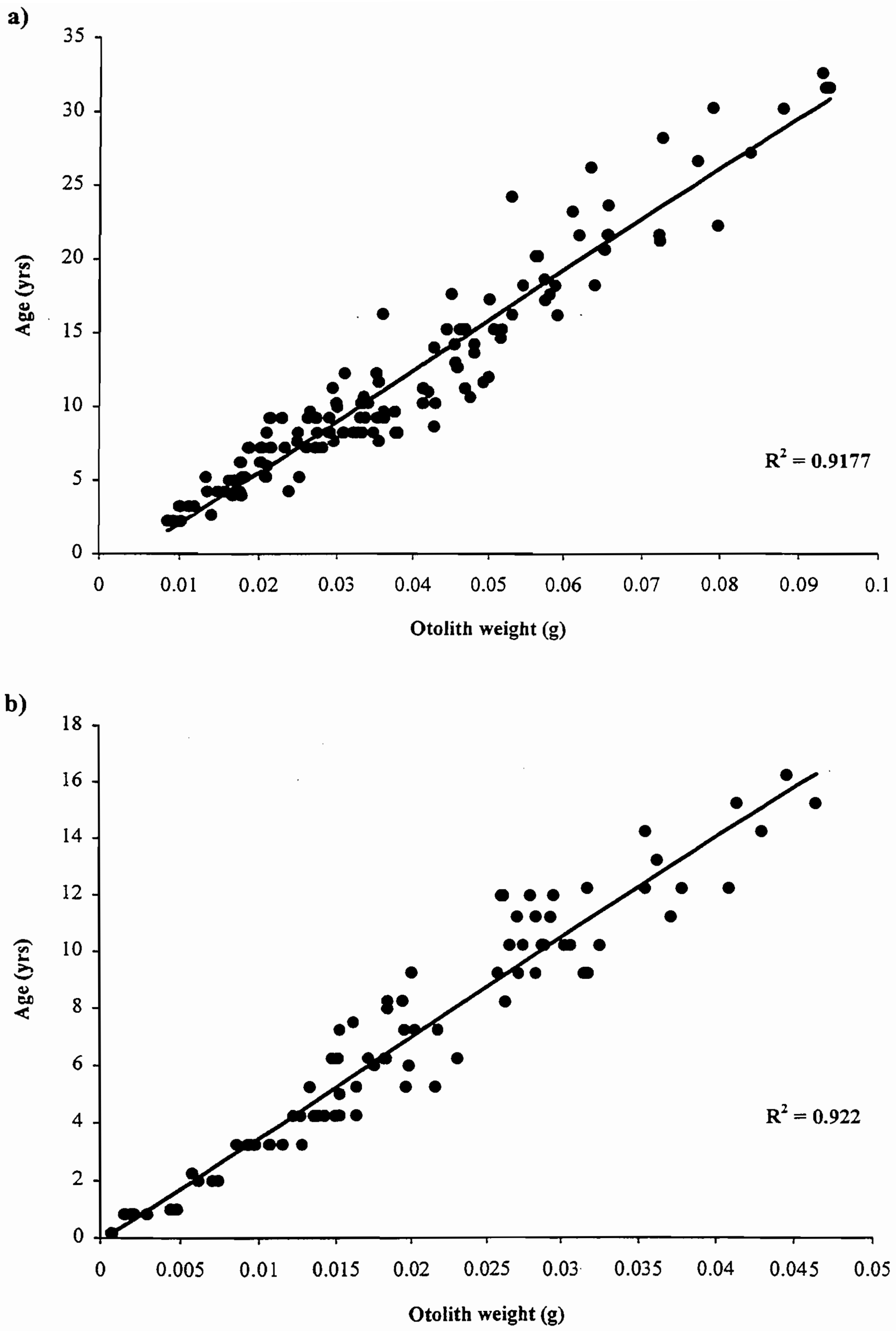


Figure 1. The relationship between otolith weight and age for **a)** *Cephalopholis cyanostigma* (n=131) and **b)** *C. boenak* (n=83)

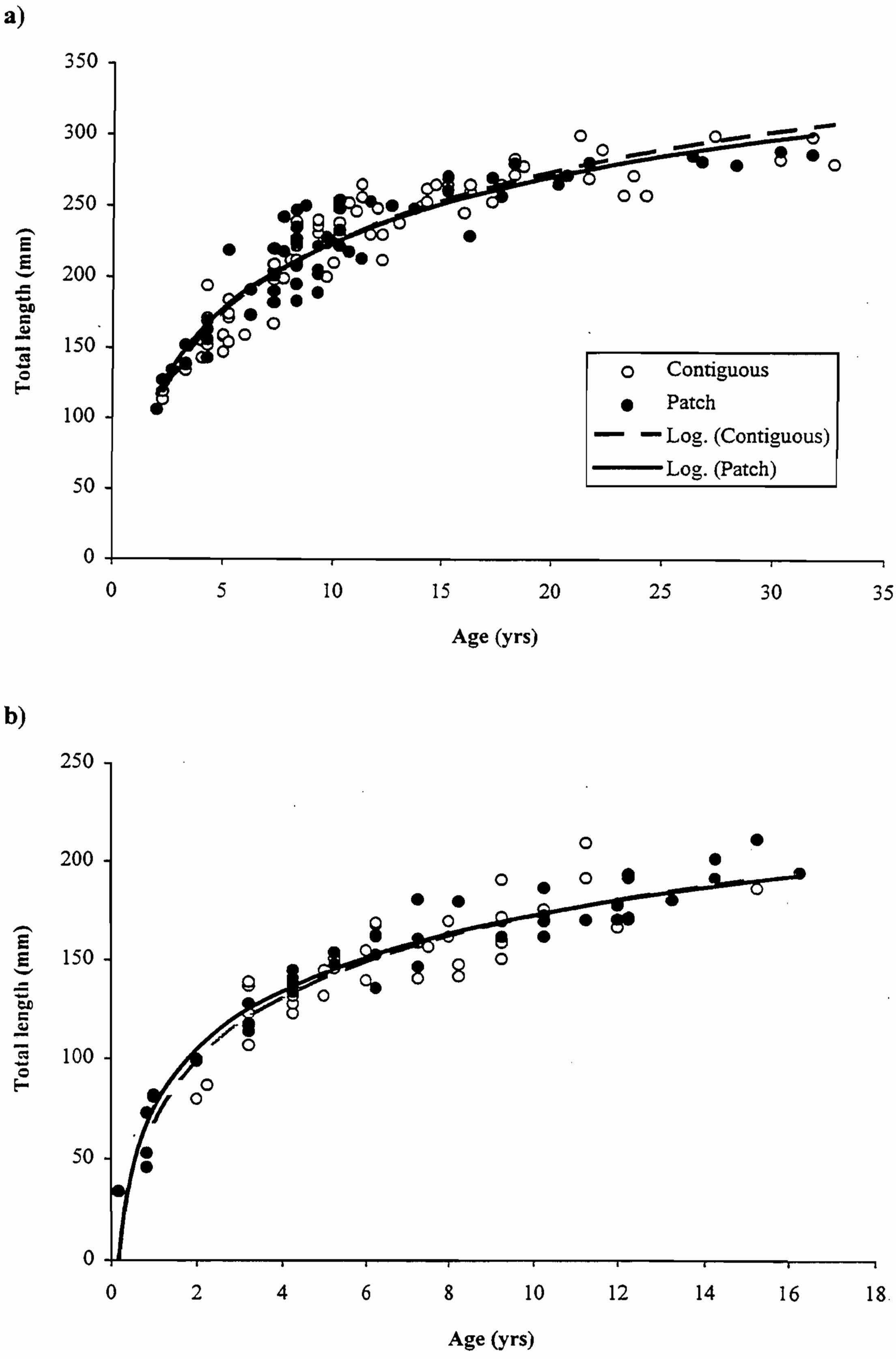


Figure 2. Comparison of size-at-age curves on patch and contiguous reef for **a)** *Cephalopholis cyanostigma* (n=56 and 81) and **b)** *C. boenak* (n=44 and 41).

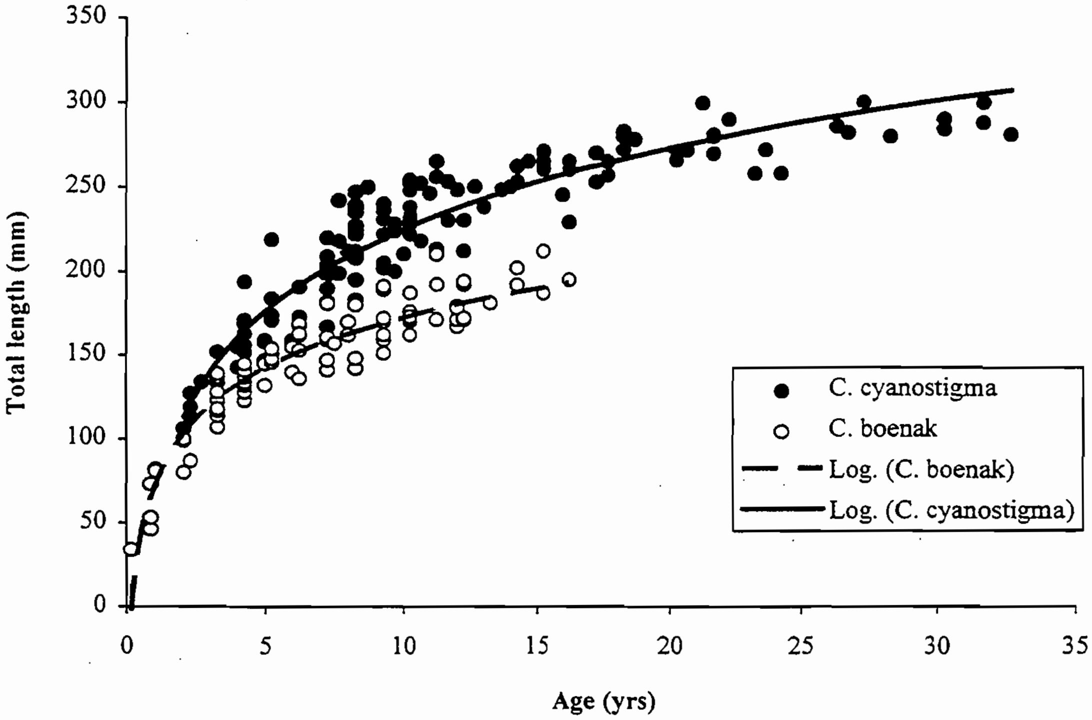


Figure 3. Overall size-at-age curves of *Cephalopholis cyanostigma* (n=137) and *C. boenak* (n=85) at Lizard Island.

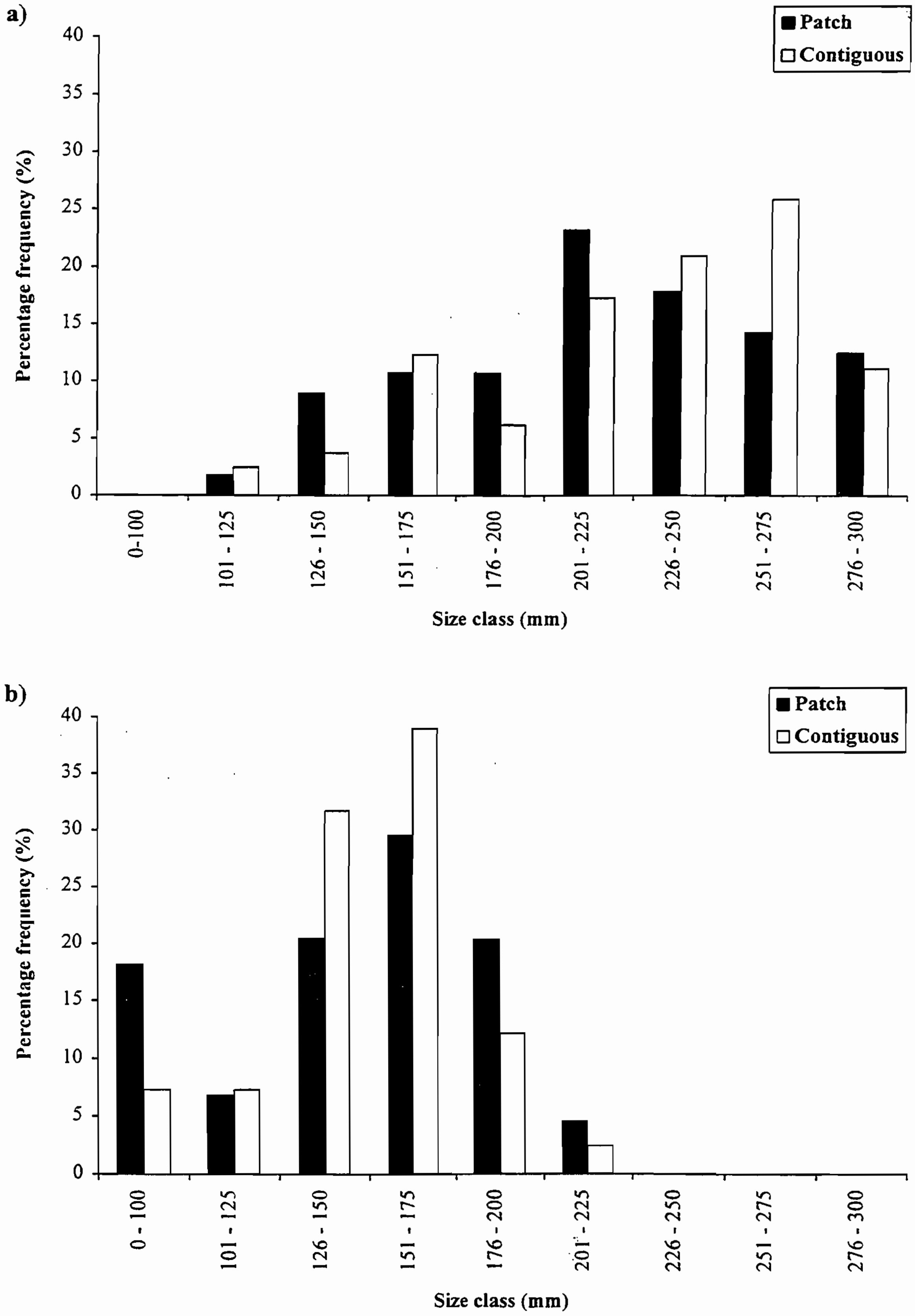
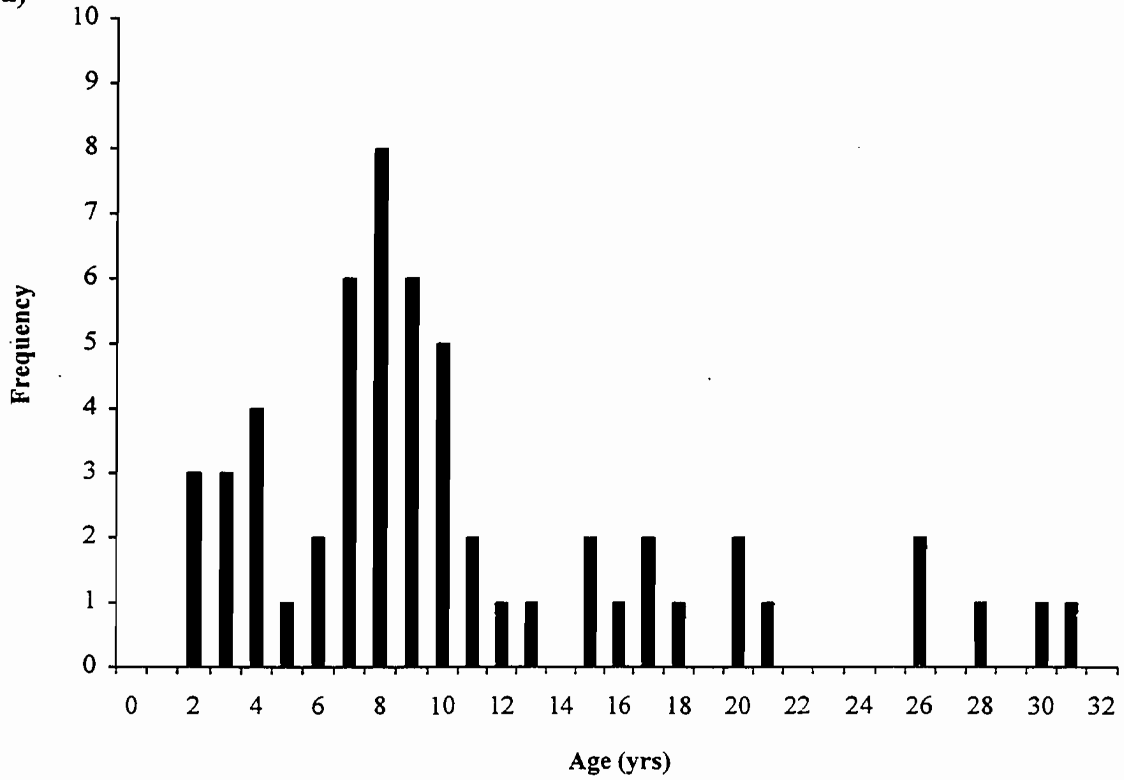


Figure 4. Size composition of the two rock-cod species on patch and contiguous reef, **a)** *Cephalopholis cyanostigma* (n=56 and n=81) and **b)** *C. boenak* (n=44 and n=41)

a)



b)

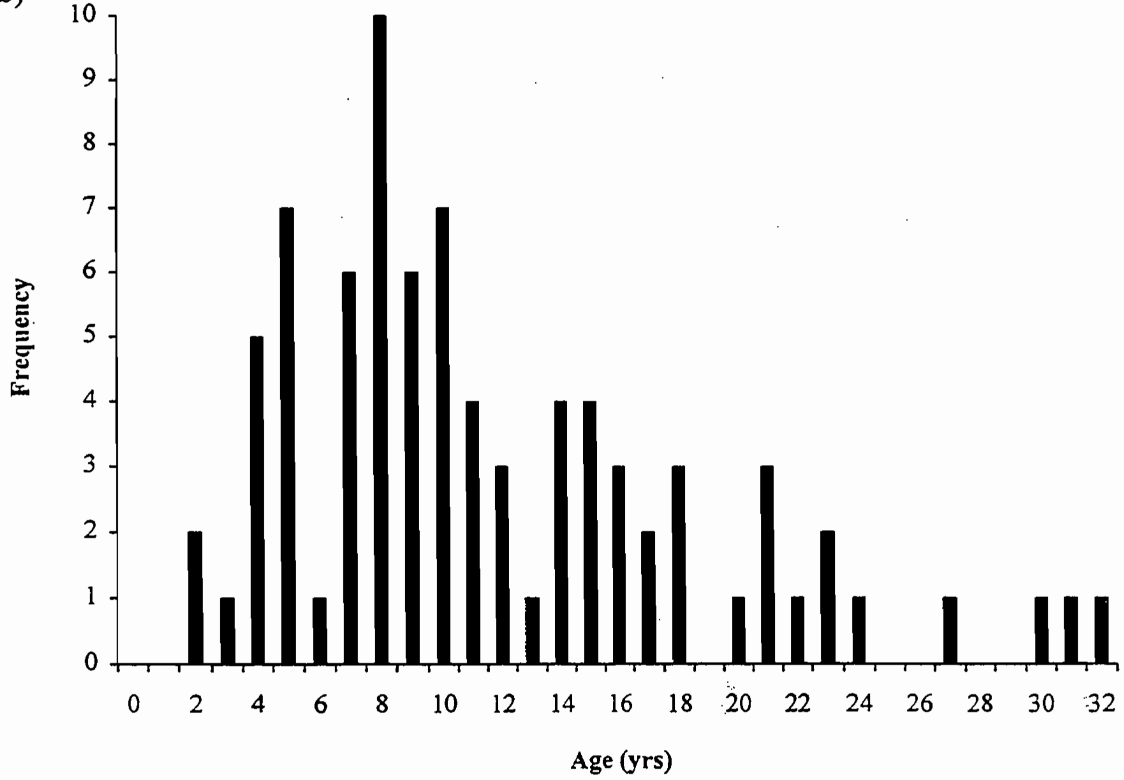
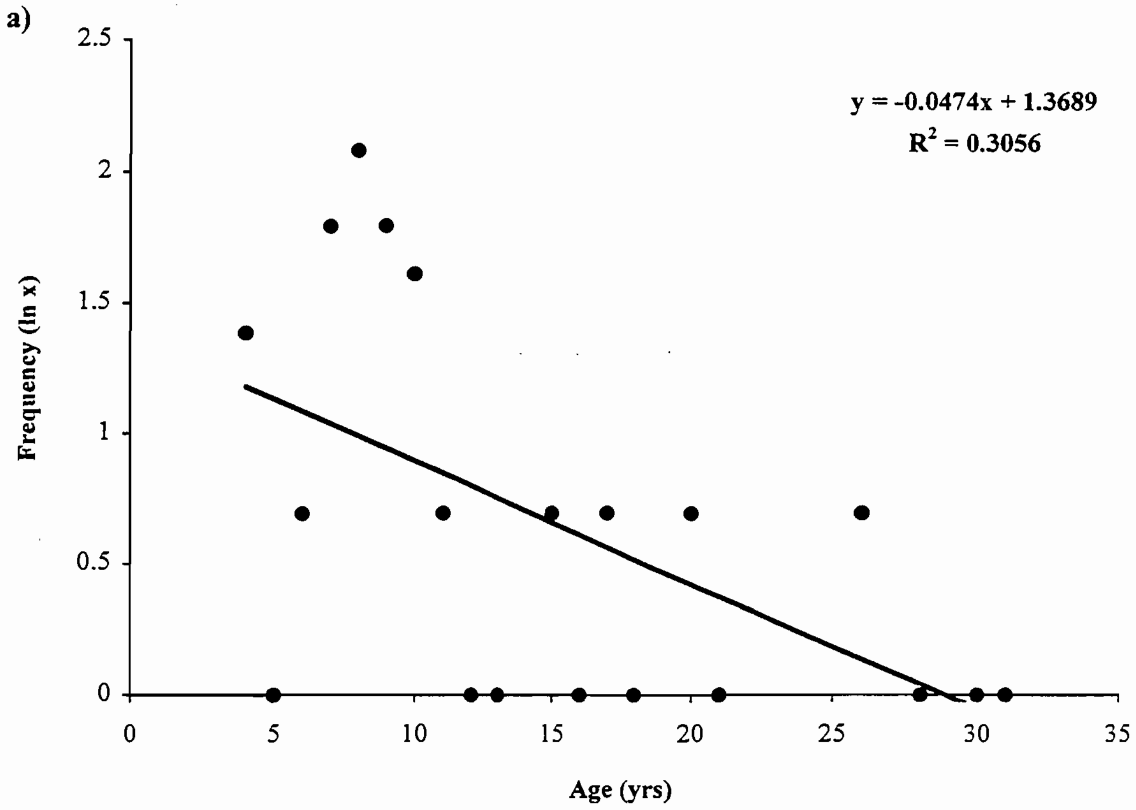


Figure 5. Age composition of *Cephalopholis cyanostigma* on **a)** patch reef (n=56) and **b)** contiguous reef (n=81)



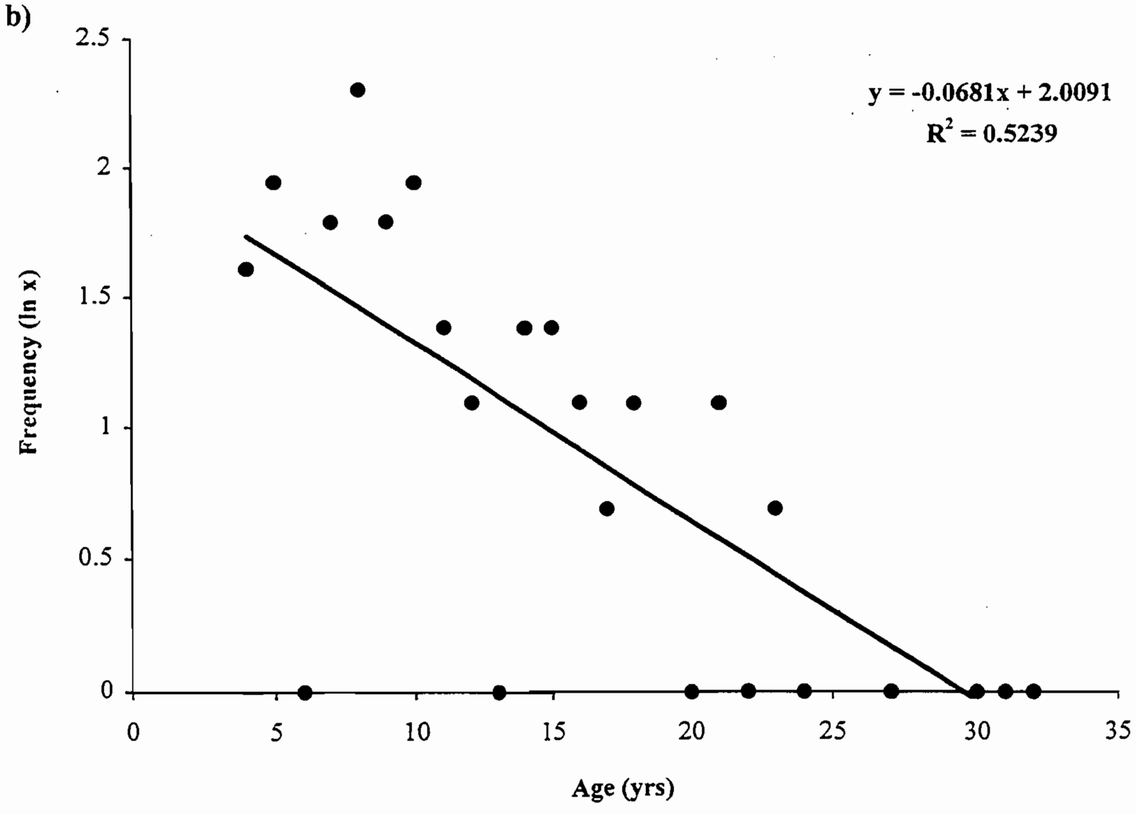
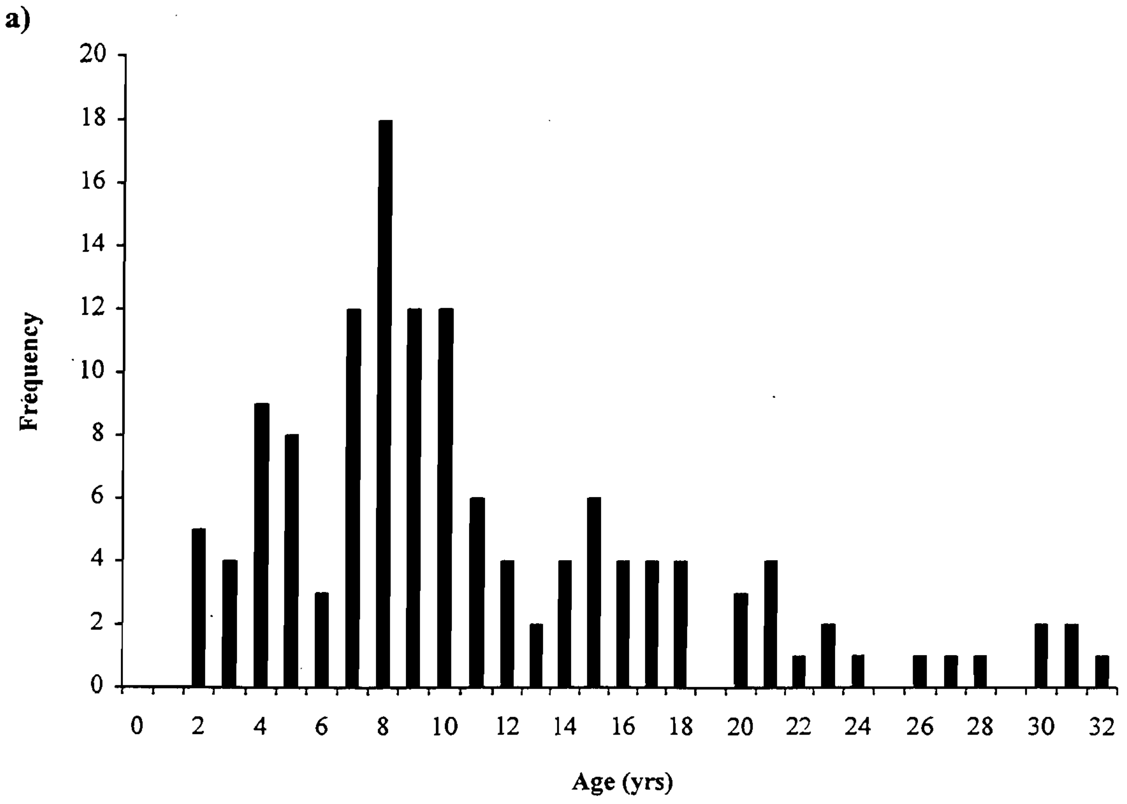


Figure 6. Mortality estimates (slope = Z) for *Cephalopholis cyanostigma* on **a)** patch reef (n=56) and **b)** contiguous reef (n=81)



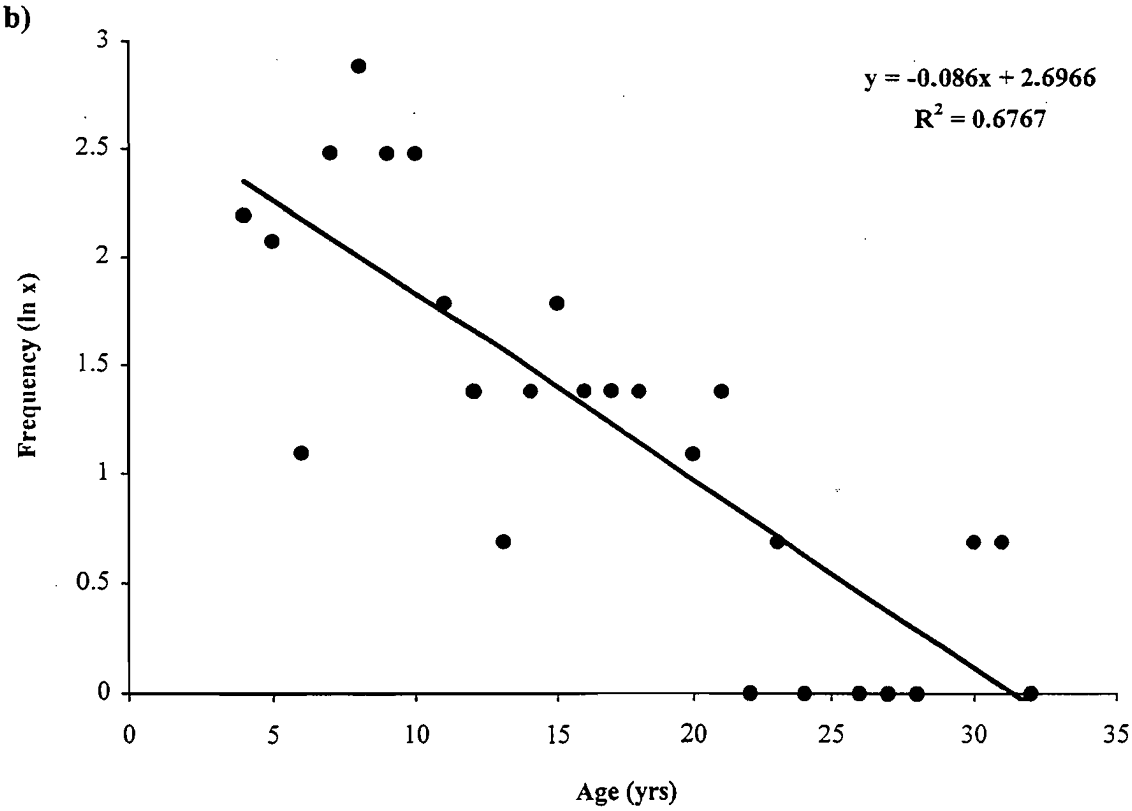


Figure 7. Overall **a)** age composition and **b)** mortality estimate (slope = Z) for *Cephalopholis cyanostigma* at Lizard Island (n = 137)

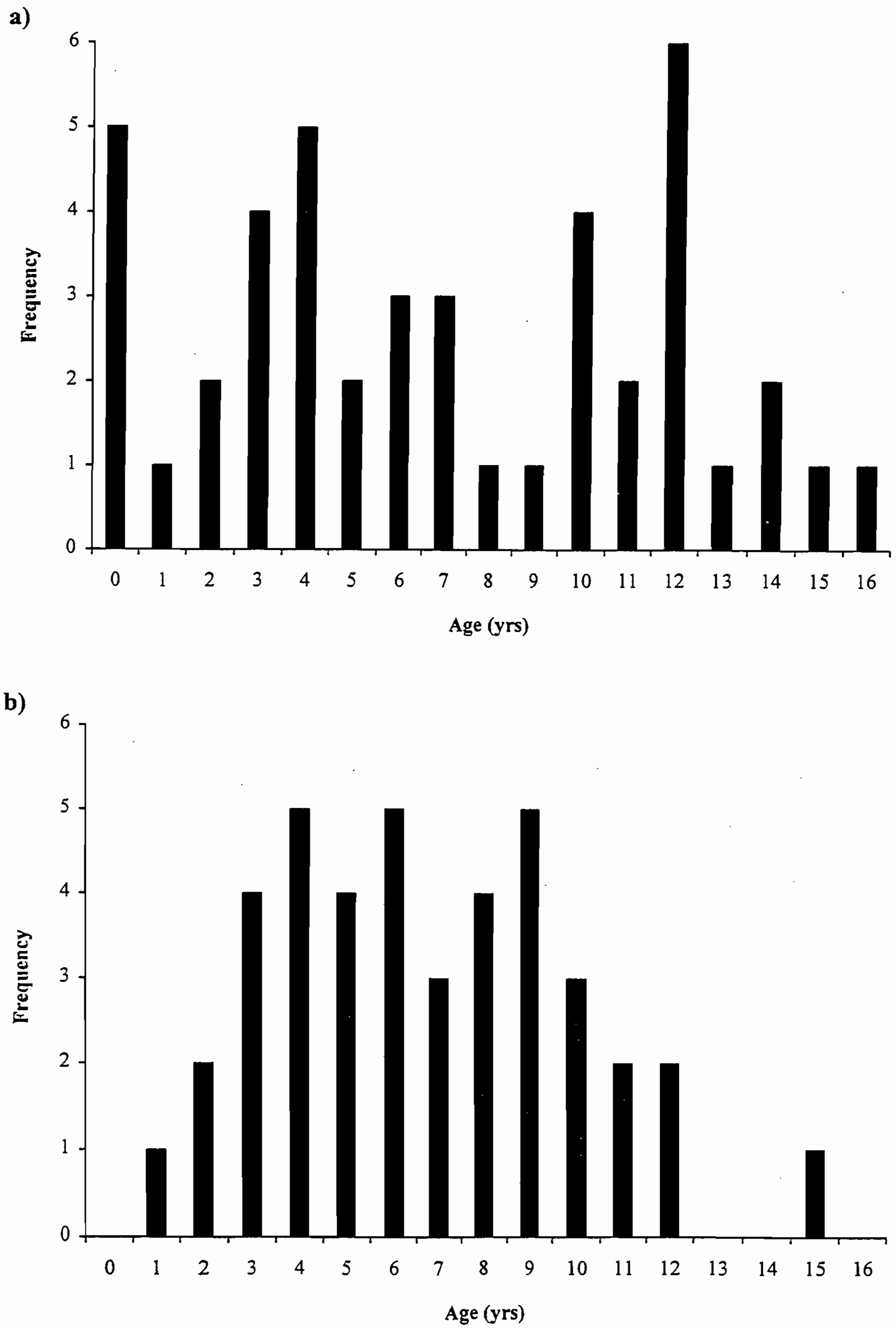


Figure 8. Age composition of *Cephalopholis boenak* on **a)** patch reef (n=43) and **b)** contiguous reef (n=41)

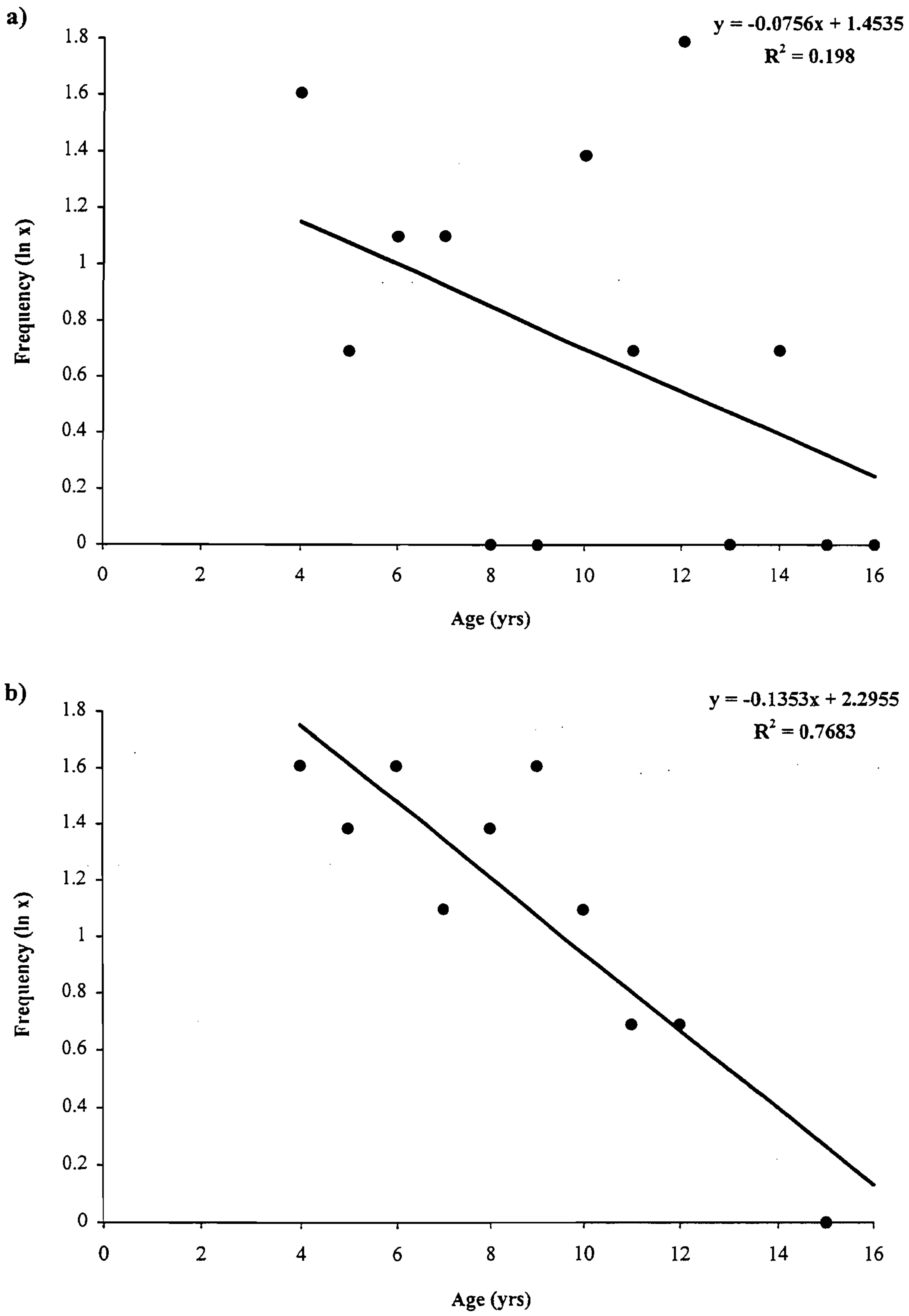
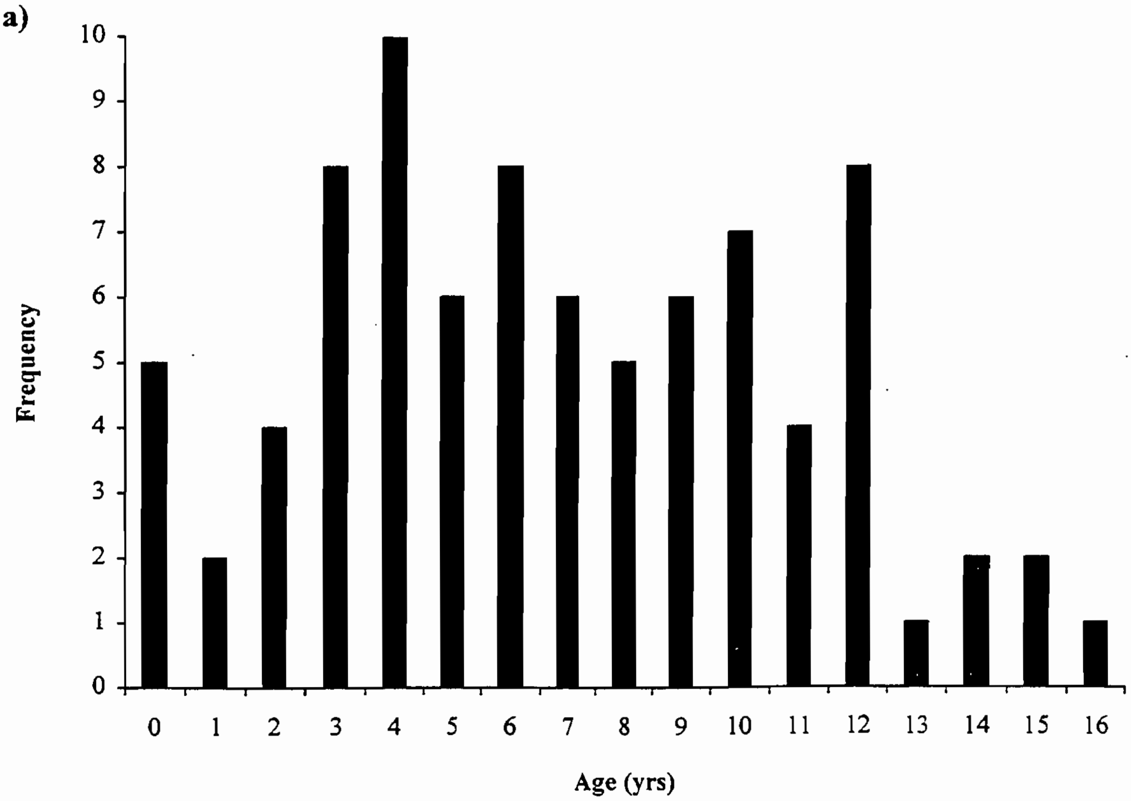


Figure 9. Mortality estimates (slope = Z) for *Cephalopholis boenak* on **a**) patch reef (n=43) and **b**) contiguous reef (n=41)

a)



b)

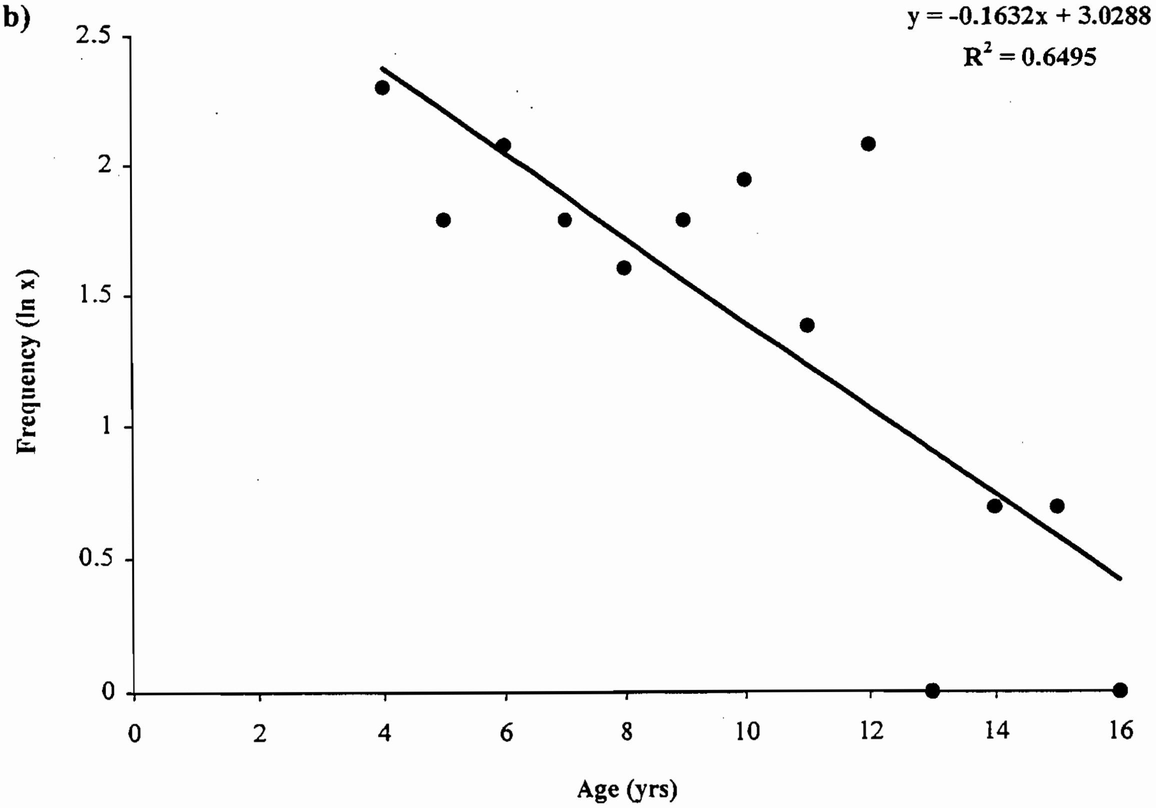


Figure 10. Overall **a)** age composition and **b)** mortality estimate (slope = Z) for *Cephalopholis boenak* at Lizard Island (n = 85)

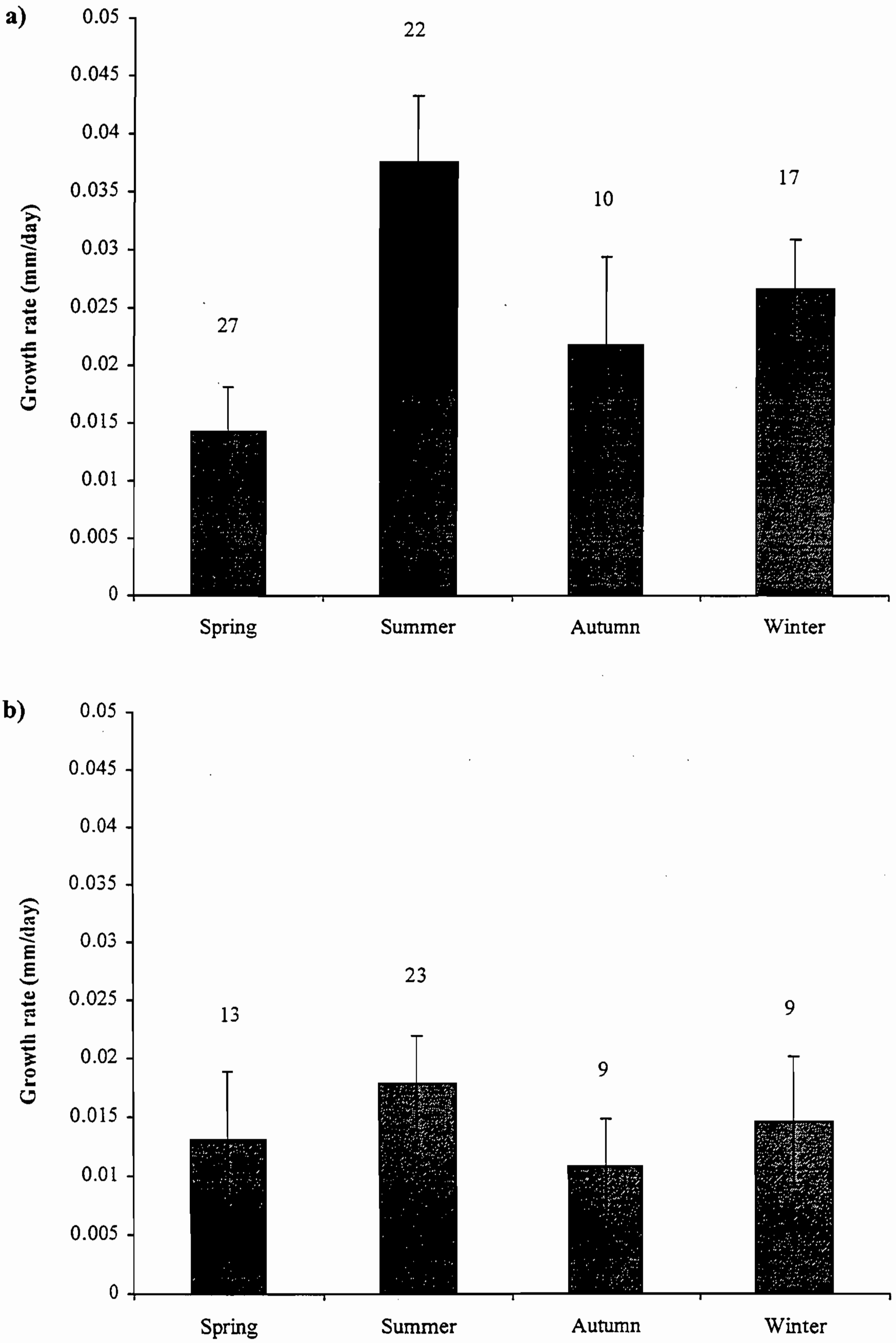
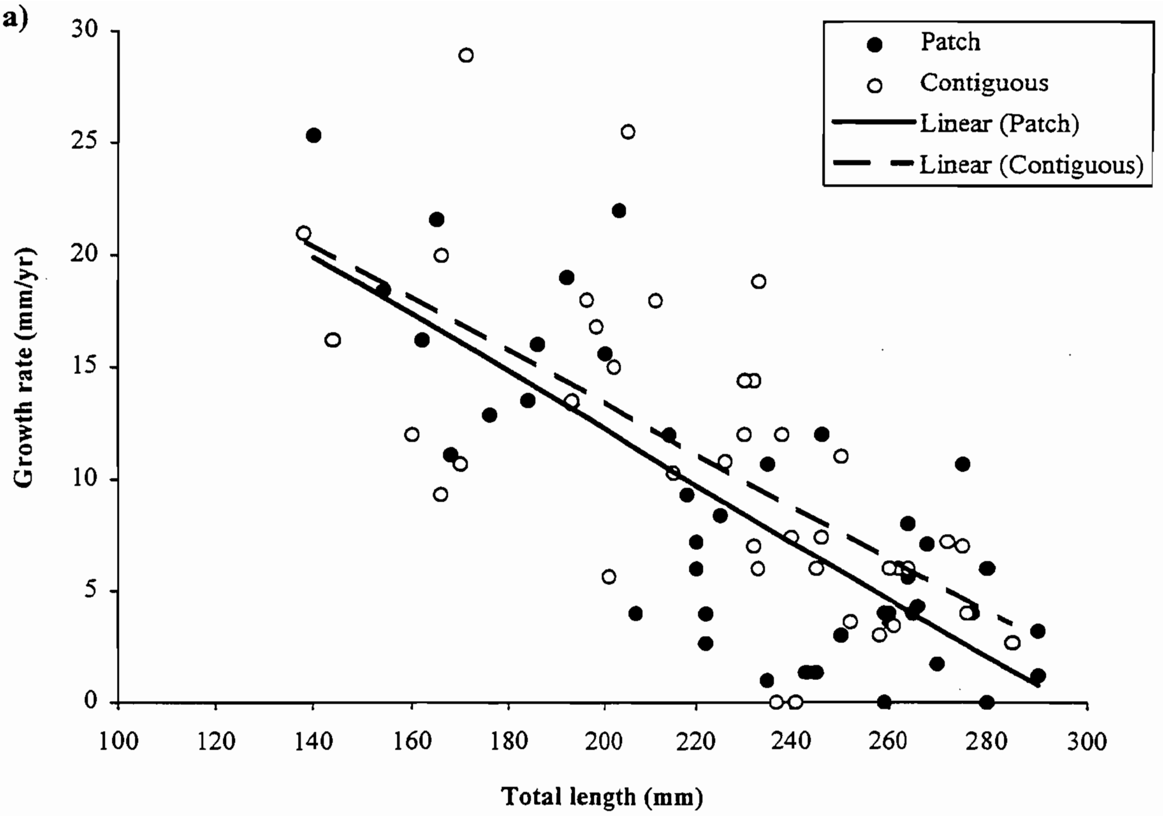


Figure 11. Seasonal growth rates (mean +/- SE) of tagged **a)** *Cephalopholis cyanostigma* and **b)** *C. boenak*. Numbers above columns indicate sample size.

a)



b)

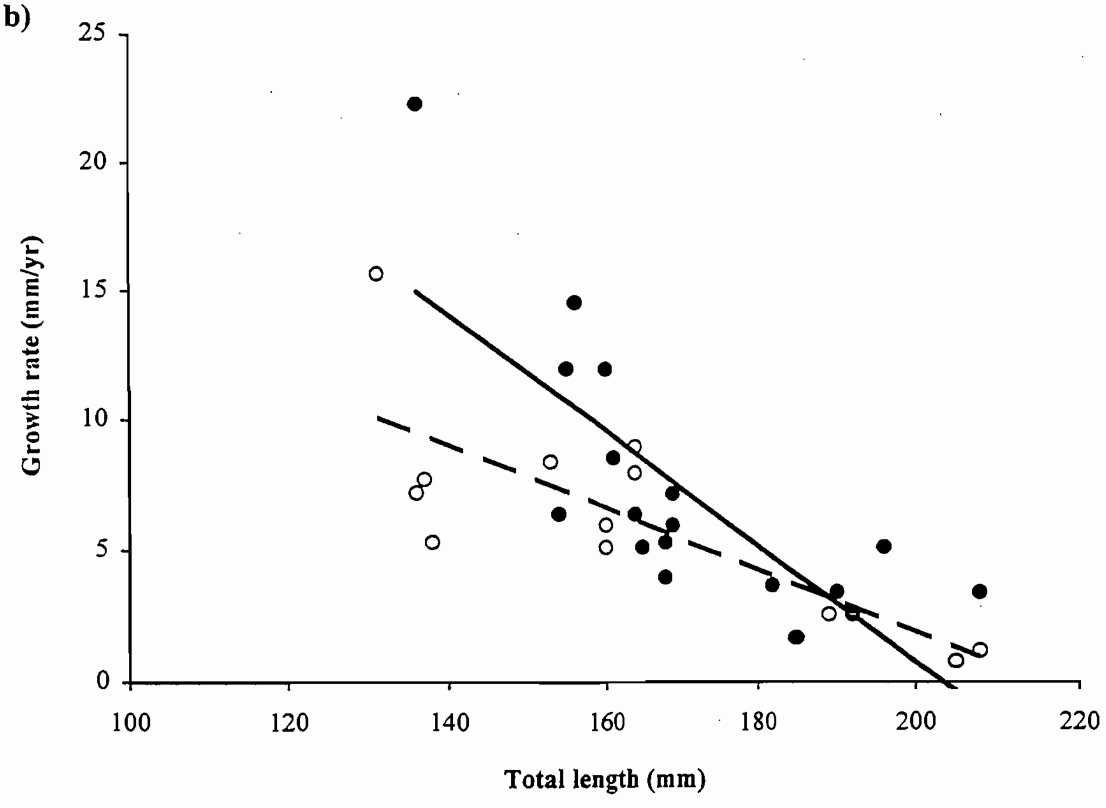


Figure 12. Comparison of growth of tagged fish on patch and contiguous reef for **a)** *Cephalopholis cyanostigma* (n=42 and 39) and **b)** *C. boenak* (n=18 and 13)

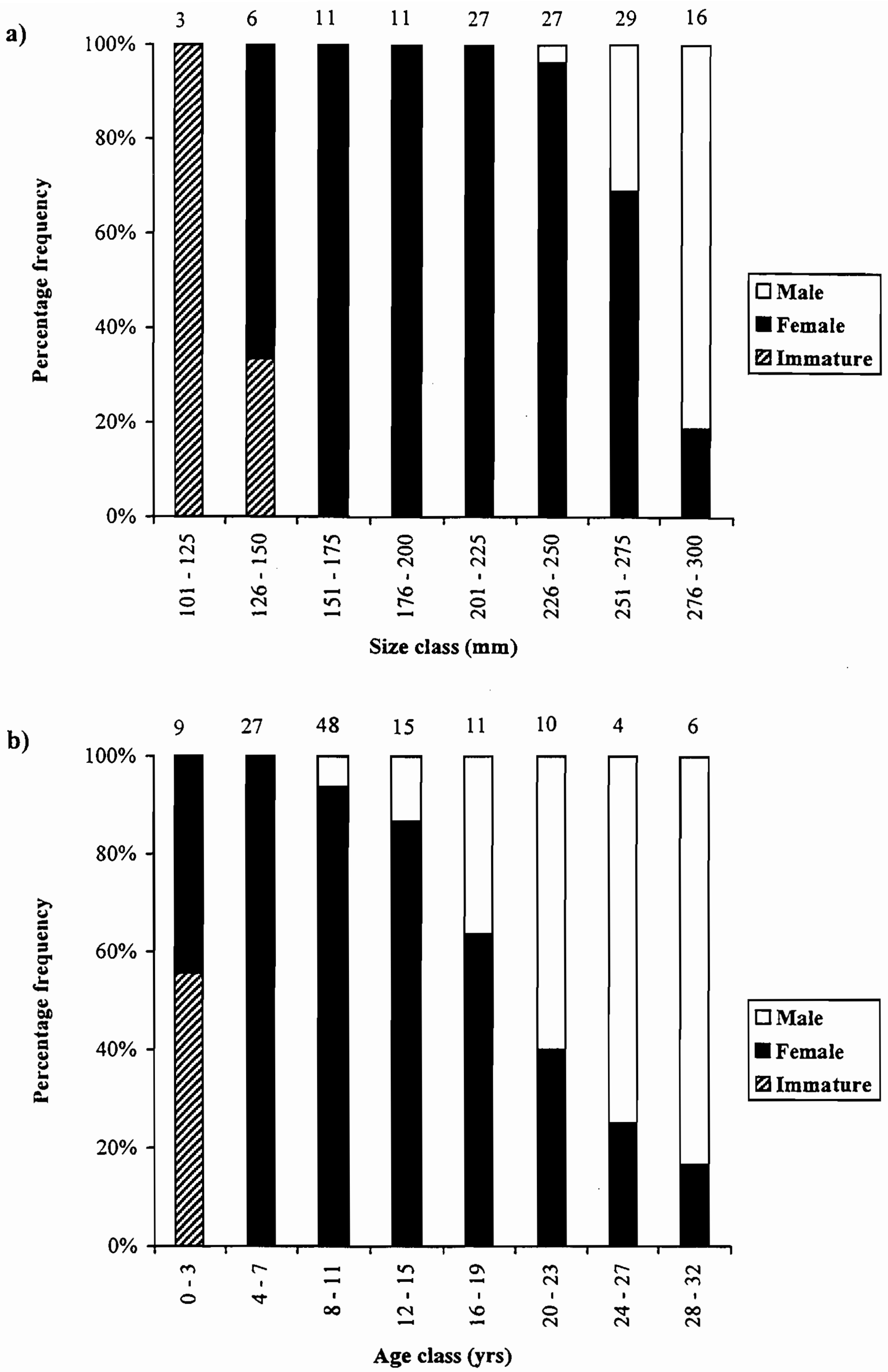


Figure 13. Sex composition of *Cephalopholis cyanostigma* by **a)** size class and **b)** age class. Numbers above columns indicate sample size.

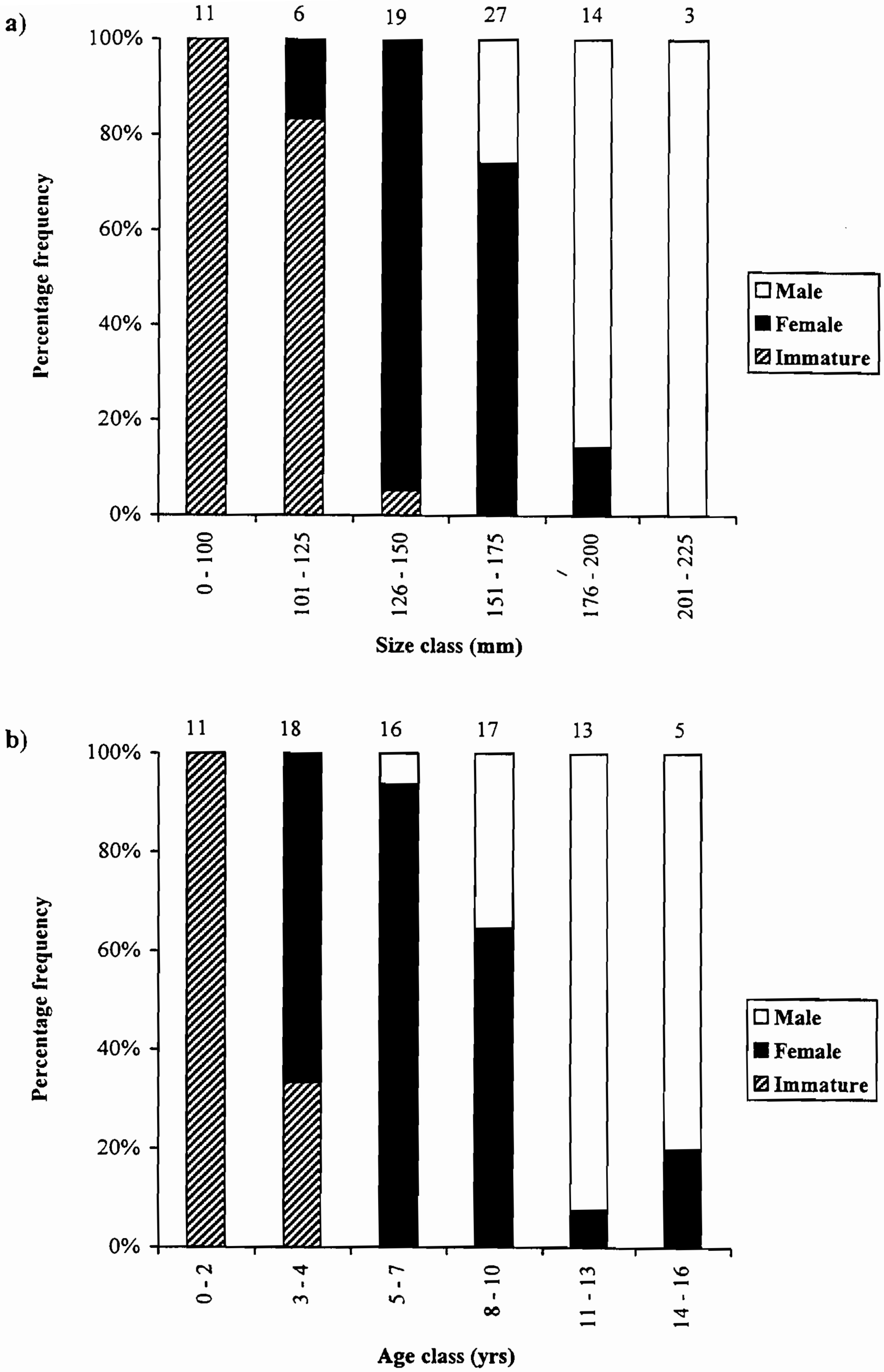


Figure 14. Sex composition of *Cephalopholis boenak* by a) size class and b) age class. Numbers above columns indicate sample size.

Chapter 6

Behavioural and developmental responses of a piscivorous coral reef fish to variation in prey abundance: an experimental approach

Abstract:

Predation appears to play an important role in structuring communities of coral reef fish. However, whether or not piscivorous coral reef fish are food-limited and how they respond to fluctuations in the abundance of their prey has rarely been investigated. This study describes an experiment which examined how the movement, diet and growth of a piscivorous rock-cod, *Cephalopholis boenak* (Serranidae) responded to variation in the abundance of its prey. Two hypotheses were tested which would be consistent with food-limitation of *C. boenak*, (1) that *C. boenak* would move from areas of low to high prey density (an aggregative response), and (2) that in these areas *C. boenak* would eat more (a functional response) and grow faster (a developmental response). Predator densities were manipulated on small, identical patch reefs that exhibited natural variation in prey abundance. Both behavioural (aggregative and functional) and developmental (growth rate) responses were observed. Thirty one percent of tagged individuals moved between patch reefs during the experiment, all from areas of low to high prey density. Feeding rates were also higher on patch reefs of higher prey to piscivore ratio. Due to few recaptures of tagged fish on low prey reefs, growth could not be compared within the experiment. Both feeding and growth rates on the experimental reefs, however, were much higher than those on natural patch reefs over the same time period. These patterns corresponded with much higher prey densities on the experimental patch reefs. Hence these results suggest that abundance and growth of *C. boenak* was food-limited on the patch reefs studied. The observed responses of *C. boenak* to fluctuations in prey abundance also provide a potential mechanism for recent observations of density-dependent mortality of coral reef fish.

Introduction:

Traditional ecological theory suggests that predators are limited by the availability of prey (Hairston et al. 1960, Menge & Sutherland 1987). With that being the case predators are expected to respond to variation in prey abundance either numerically (Solomon 1949), developmentally (Murdoch 1971) or behaviourally (Hassell 1978). Behavioural responses include aggregative responses, functional responses, or a combination of the two (Hassell 1978). Aggregative responses refer to movements of predators in response to patchiness in prey abundance and distribution (Fretwell & Lucas 1970; Hassell & May 1974). Functional responses, on the other hand, refer to the relationship between the number of prey a predator consumes and the density of prey available (Holling 1959, 1966, Murdoch 1973, Abrams 1982). When food is limited there is generally a positive relationship between prey density and the number of prey consumed, which eventually reaches a plateau due to the effect of handling time or satiation (Holling 1959). Thus aggregative and functional responses provide indirect evidence that predator populations are limited by the availability of prey.

Behavioural responses may lead to increases in the somatic and reproductive growth rates of predators (a developmental response - Murdoch 1971). For predatory fish, in particular, prey availability may be one of the most important factors effecting growth (Weatherley & Gill 1987). Increases in growth rate will have effects on the size structure and biomass of predatory fish populations. Variation in growth rate may also have effects on a species mortality, size and age-at-maturity and fecundity (Jones 1991).

Behavioural and developmental responses by predators have been well documented in terrestrial (eg. Goss-Custard 1970), freshwater (eg. Thompson 1975), intertidal (eg. Boulding & Hay 1984, Robles et al. 1995) and seagrass (Jenkins et al. 1993) environments. It is not known, however, if piscivorous fish on coral reefs are limited by prey abundance or how they respond to fluctuations in the abundance of their prey. There is increasing evidence that predation plays an important role in shaping populations and communities of coral reef fish (Hixon 1991, Hixon & Beets 1993, Beukers & Jones 1997, Hixon & Carr 1997), however, the predators responsible for this effect have been little studied (Jones 1991). There is some information emerging on general patterns of diet, growth and movement of coral reef piscivores (Kingsford 1992, Ferreira & Russ 1994, Zeller 1997) but these patterns have rarely been related to environmental variables such as prey abundance.

Recently, I conducted a series of studies on the response of piscivorous fish to variation in prey abundance in natural communities at Lizard Island on the Great Barrier Reef, Australia (Chapters 3 to 5). The studies were carried out on both patch reefs, which supported high numbers of prey and contiguous reef, which supported much lower numbers. Strong positive relationships between predator and prey abundance were maintained at these sites over an 18 month period and loss rates of prey were found to be density-dependent. The mechanisms responsible for these patterns, however, were not entirely evident. Tagging of two of the most abundant piscivores in the community, the rock-cods *Cephalopholis cyanostigma* and *C. boenak* (Serranidae), revealed that they rarely moved either between the two habitats or between individual patch reefs. Examination of their feeding and growth rates also showed few differences between the two reef types. However, there was some evidence of faster growth of *C. boenak* on patch reefs, where the ratio of prey to predator abundance was highest.

The failure to detect some of the expected responses could be the result of a number of confounding factors. The most obvious is the effect habitat type itself may have had on the results. For example, the isolation of the patch reef sites may have restricted the movement of fish to and from these areas. Habitat structure may also have differed in complexity on the two reef types, effecting the availability of prey to predators (Hixon & Beets 1993, Caley & St. John 1996, Beukers & Jones 1997). Densities of both competitors and predators of the two rock-cod species were also much higher on the patch reef sites (Chapter 3). Both of these factors are known to inhibit feeding rates of predators

(Hassell 1978, Milinski 1986). Transient predators also appeared to have a significant effect on the mortality of prey on patch reefs (Chapter 3), although this could not be quantified. Hence although predators appeared to have more prey available on patch reefs, the reality may have been quite different.

In this study I aimed to test two predictions that would be consistent with prey-limitation: (1) that predatory fish would move from low to high prey density areas (an aggregative response), and (2) that predators in high prey density areas would eat more (a functional response) and grow faster (a developmental response). Motivated by the difficulties of examining these responses in natural communities, I decided an experimental approach may be more appropriate.

Predator / prey ratios were manipulated on small patch reefs constructed to standard specifications. The movement, diet and growth of the piscivorous rock-cod, *Cephalopholis boenak*, was then monitored on these reefs over a 6 month period. Patch reefs were all of the same size, separated by the same distance and located in a small area. Predators of *C. boenak* would therefore have had similar access to all reefs. These patch reefs could be naturally divided into two groups, those supporting high numbers of prey and those supporting low numbers. Predator / prey ratios were manipulated by relocating *C. boenak* so that equal numbers were present on each reef. The two treatments were therefore equivalent in terms of habitat, isolation and competitor (*C. boenak*) and predator density with the only real difference being the density of prey. Feeding and growth rates of *C. boenak* on these experimental reefs were also compared to those on natural patch reefs in the same area.

Methods:

The study was conducted at Lizard Island ($14^0$40'S; $145^0$28'E) on the northern Great Barrier Reef, Australia. The experimental reefs were located in the lagoon between Lizard, South and Palfrey Islands while the natural patch reefs were located on the western side of Lizard Island (see Chapter 3). Both locations were sheltered from the prevailing wind conditions.

1. Description of experimental patch reefs

Twenty six small patch reefs of live *Porites cylindrica* (each approximately 1m X 3m) were built in the lagoon of Lizard Island in early 1994 for a previous experiment. Each reef was 20 to 30m apart from one another and the surrounding contiguous reef. Reefs were located on a sandy bottom at a depth of 5 to 10m. At the start of the original experiment different densities of newly recruited damselfish (*Pomacentrus amboinensis*) and predators (*Cephalopholis boenak* and *Pseudochromis fuscus*) were transplanted to each reef. Between then and the conclusion of this experiment, natural fish communities of fish were allowed to form on the reefs.

2. Experimental manipulation of the abundance of *Cephalopholis boenak*

In August 1996 I removed almost all *Cephalopholis boenak* from the experimental reefs using quinaldine (anaesthetic) and hand nets. Fish were then transported back to the laboratory where they were kept in several large outdoor aquaria for a period of up to 2 weeks. At the completion of this removal exercise 52 of the captured *C. boenak* were measured (to the nearest mm) and tagged in the dorsal musculature with 2 T-bar anchor tags. Two different colours were used and each tag was placed in one of three different positions on either side of the fish. This produced a large number of combinations which allowed each fish to be recognised underwater. Tagged fish ranged in total length from 103 mm to 217 mm.

Twenty six pairs of *Cephalopholis boenak* were then selected haphazardly from the tagged fish to be transplanted back onto each different reef. The aim of this was ensure that at the start of the experiment the density of *C. boenak* was consistent across reefs. This density of *C. boenak* was slightly lower than that originally observed on the reefs (2.73 - see results), although it was subsequently revealed that a few individuals had remained on the reefs. I ensured each of the two fish selected as a pair differed by at least 40 mm in length and that one was less than 150 mm in total length. This was expected to minimise aggressive interactions. Cephalopholids have a size based hierarchical social system with the largest individual in a group being male and maintaining a harem of smaller females (Shpigel & Fishelson 1991, Mackie 1993). Hence the experimental patch reefs were unlikely to support more than 1 male fish. By selecting 1 large and 1 one small fish (< 150 mm) I increased the chance that I had selected a fish of each sex. In natural populations males were rare until fish were greater than 150 mm total length (Chapter 5). In the absence of a male fish the largest female in a group may change sex to become a male (Mackie 1993).

3. Prey and piscivore abundance on experimental and natural patch reefs

In early September 1996, the day after the tagged *Cephalopholis boenak* had been released, all piscivores and prey on the experimental reefs were censused. Piscivores were identified on the basis of published dietary analysis (see Chapter 3) while prey were identified as fish less than 5cm standard length belonging to the families Apogonidae, Pomacentridae, Clupeidae, Caesionidae and Atherinidae. Fish of this type and size made up more than 90% of the prey consumed by *C. boenak* in natural communities at Lizard Island (Chapter 4). This initial census revealed that prey communities on half of the patch reefs were dominated by large schools of apogonids. Reefs supporting these schools were designated as high prey reefs while the others were designated as low prey reefs. Piscivore / prey censuses were repeated in November 1996 (spring) and February 1997 (summer).

Temporal and spatial variation in both prey and piscivore abundance and the ratio of prey to piscivores on experimental reefs was examined by ANOVA. The two fixed factors were census date and reef type (high or low prey density). Date was treated as a fixed factor to allow comparisons between times. Overall patterns of prey and piscivore abundance on these experimental patch reefs were then compared to those on natural patch reefs censused at the same times (see Chapter 3). In this case the two fixed factors were again census date and reef type (experimental or natural). Patterns of abundance of *Cephalopholis boenak* on experimental reefs were also examined separately - factors as above. When necessary (Cochran's C Test, $p < 0.05$), raw data was transformed to improve normality and heterogeneity (Underwood 1981). Post-hoc analysis was done using Tukey's honestly significant difference (HSD) method (Day & Quinn 1989).

4. Movement, diet and growth of *Cephalopholis boenak* on experimental and natural patch reefs

a) Movement

Any tagged *Cephalopholis boenak* seen during the piscivore / prey censuses on experimental reefs were identified and their location noted. This allowed for examination of how any movement between reefs related to levels of prey abundance. In early March 1997, immediately after the final census, all *C. boenak* on the reefs were again captured using quinaldine and sacrificed in an ice / seawater slurry. The location of any tagged fish recaptured was again noted and related to patterns of prey abundance.

b) Diet

Any prey items regurgitated during the final capture of *Cephalopholis boenak* were retained for analysis. Sacrificed fish were also gut injected with a buffered formalin solution and kept on ice. Within 4 hours the stomach contents were removed from these fish. The number and volume of prey per predator (based on the combined regurgitated and dissected samples) was then calculated for fish on high and low prey density reefs. These feeding rates were calculated simply by dividing the number (or volume) of prey collected by the number of *C. boenak* captured. Volume of prey was measured by water displacement and only included items of digestion stage 3 or above (see Chapter 4). The overall feeding rates on the experimental reefs were also compared to the feeding rates of *C. boenak* taken on natural patch reefs in February and March 1997 (Chapter 4).

c) Growth

Each fish captured in March 1997 was also measured (to the nearest mm). For tagged fish this allowed for growth, over the 6 months of the experiment, to be calculated. Growth rates were compared between high and low prey density reefs and overall growth rates on experimental reefs were compared to the growth, over the same period, of *C. boenak* tagged on natural patch reefs. Comparisons were made by ANCOVA with the fixed factor being reef type and the covariate initial total length. Data was again transformed when necessary.

Sagittal otoliths were also dissected from the *Cephalopholis boenak* collected from the experimental reefs. Increments in these otoliths have been validated as annual (Chapter 5), allowing for accurate age determination. Otoliths were prepared and sectioned for viewing as in Chapter 5. Size-at-age curves of fish sampled from the experimental and natural patch reefs were then compared.

Results:

1. Numerical changes in prey and piscivore abundance on experimental and natural patch reefs: the aggregative response

a) Numerical changes in prey and piscivore abundance

The density of prey on the reefs designated as high prey reefs remained higher than that on low prey reefs throughout the experiment (Fig. 1a, Table 1a). Prey density also varied significantly over time (Fig. 1a, Table 1a), with an increase due to recruitment between August and November 1996, followed by a decline between November 1996 and February 1997 (Fig. 1a). The density of piscivores was also significantly, although only slightly, higher on the high prey reefs throughout the experiment (Fig. 1b, Table 1b). There was little change in piscivore abundance between August and November 1996 but there was a large and significant increase between November 1996 and February 1997 (Fig. 1b, Table

1b). This increase was mostly due to the recruitment of schools of lutjanids (5 to 80 individuals) to many of the reefs. *Lutjanus quinquelineatus* was the most common species, but *L. gibbus* and *L. vitta* were also abundant. Corresponding to these patterns the ratio of prey to piscivores also remained higher on the high prey reefs throughout the experiment (Fig. 1c, Table 1c). This ratio converged between the two reef types over the course of the experiment, however (Fig. 1c). Overall, the ratio increased between August and November 1996, due to the recruitment of prey, but decreased between November 1996 and February 1997, due the recruitment of piscivores (Fig. 1c).

The overall prey and piscivore densities on the experimental reefs were much higher than those on the natural patch reefs (Fig. 2a and b, Table 2a and b). This was particularly evident after the recruitment of prey to the experimental reefs between August and November 1996 (Fig. 2a) and the recruitment of piscivores to the experimental reefs between November 1996 and February 1997 (Fig. 2b). Tukey's HSD tests showed that this temporal variation was responsible for the significant interactions between census date and reef type (Table 2a and b). Comparison of the ratio of prey to piscivores on experimental and natural patch reefs also showed an interaction between reef type and census date, but no significant difference between reef types (Fig. 2c, Table 2c). Tukey's HSD test revealed that the ratio was significantly higher on experimental reefs in August and November 1996, but was significantly higher on natural reefs in February 1997 (Fig. 2c). This switch in patterns was largely due to the recruitment of piscivores to experimental reefs between November 1996 and February 1997.

There was also a significant difference between the density of *Cephalopholis boenak* on high and low prey reefs during the experiment (Fig. 3, Table 3). Before the experiment started the density of *Cephalopholis boenak* was significantly higher on the high prey reefs than the low prey reefs (Fig. 3, Tukey's HSD test). After the manipulations at the start of the experiment, however, densities on the two reef types were exactly the same (Fig. 3). During the course of the experiment these densities diverged on the two reef types were again significantly higher on the high prey reefs by February 1997 (Fig. 3, Tukey's HSD test). Densities on the two reef types at the end of the experiment were similar to those prior to the start of the experiment (Fig. 3). Comparison of these densities with those of all piscivores (Fig. 1b) showed that *C. boenak* made up more than half of the piscivores on the experimental reefs in August and November 1996. In February 1997 this proportion was much reduced due to the recruitment of lutjanids (see above).

b) Movement of *Cephalopholis boenak*

In November 1996 a total of 23 tagged *Cephalopholis boenak* were resighted during the piscivore / prey census. Four (17 %) of these fish had moved between patch reefs. One fish had moved to the next reef, one across 2 reefs and 2 across 4 reefs (a distance of approximately 100m). In all cases movements were from low to high prey density reefs. In February / March 1997, 27 tagged *C. boenak* were either resighted or recaptured. Another 6 of these fish had moved between patch reefs, 3 to the next reef and 3 across 2 reefs. Again, all movements were from low to high prey reefs. Overall, 32 different tagged *C. boenak* were resighted or recaptured over the course of the experiment (62 % of the number originally tagged). Of these fish, 10 individuals (31 %) moved between patch reefs. By comparison only 6 % of the *C. boenak* individuals tagged on natural patch reefs moved between reefs over a 2 year period (see Chapter 3).

2. Diet, feeding rates and growth of *Cephalopholis boenak* on experimental and natural patch reefs: the functional and developmental response

a) Diet

In March 1997 a total of 46 *Cephalopholis boenak* (22 tagged) were captured on the experimental reefs. A total of 60 prey items were collected from these fish (25 regurgitated and 35 dissected) of which 40 (66.67%) were fish and 20 (33.33%) were crustaceans. Of the fish prey identified, apogonids dominated, making up 71 % of items. Shrimps of the family Rhynchocinetidae (45%) and galatheid crabs (25%) were the most commonly identified crustacean prey.

b) Feeding rates

Of the *Cephalopholis boenak* collected, 32 were from high prey reefs and 14 from low prey reefs. Although the nature of the data did not allow for statistical tests, feeding rates on fish prey appeared to be higher on the high prey reefs (1 fish per predator) than on the low prey reefs (0.5 fish per predator). The pattern for volume of prey was similar, 0.35 ml of fish prey per predator on high prey reefs compared to 0.17 ml of fish prey per predator on low prey reefs.

Overall, feeding rates also appeared to be higher on the experimental patch reefs than on natural patch reefs at the same time. Feeding rates on all prey (fish and crustaceans) were 1.30 prey per predator on experimental reefs compared to 0.84 prey per predator on natural patch reefs. In terms of volume the comparison was 0.53 ml of prey per predator on experimental reefs to 0.21 ml of prey per predator on natural reefs. Feeding rates on fish prey only were 0.85 fish per predator on experimental reefs compared to 0.50 fish per predator on natural reefs. The pattern was again similar for volume, 0.29 ml of fish prey per predator on experimental reefs compared to 0.16 ml of fish prey per predator on natural reefs.

c) Growth

Although 22 tagged *Cephalopholis boenak* were recaptured in March 1997, only 4 of these fish were from low prey reefs. It was therefore not possible to make meaningful comparisons between the growth of fish on high and low prey reefs. Calculation of the growth rates of all *C. boenak* captured on the experimental reefs, however, showed that growth rates were much higher on experimental reefs than on natural patch reefs over the same time period (Fig. 4a, Table 4). Comparison of size-at-age curves on experimental and natural reefs also showed that size-at-age was generally greater on the experimental reefs (Fig. 4b).

Discussion:

Cephalopholis boenak exhibited both behavioural (aggregative and functional) and developmental (growth rate) responses to variation in prey abundance. The propensity to move among experimental patch reefs was always from low to high prey density reefs. This suggests that movement in the experiment was largely in response to differences among reefs in prey to predator ratios, caused by the manipulation of *C. boenak* densities at the start of the experiment. This movement appeared to cause densities of *C. boenak* on high and low prey reefs to diverge during the experiment until they were identical to the densities prior to manipulation. This movement of *C. boenak* may also have contributed to the convergence of prey to predator ratios on the two reef types over the course of the experiment. The large number of lutjanid recruits in March 1997, however, would also have had a strong influence on these patterns.

Some other studies (Hixon & Beets 1993, Beets & Hixon 1994) have shown that another serranid, *Epinephelus striatus*, has a strong homing tendency when displaced from it's original reef. Such behaviour is unlikely to have explained the movement in this experiment, however. *Cephalopholis boenak* individuals were selected haphazardly for deployment on reefs, therefore it would have been unlikely that they were placed within 1 or 2 reefs of where they were originally captured. This was the normal range of movement recorded. If homing was occurring, some movement from high to low prey reefs would also have been expected, but this was never observed.

Comparison of feeding rates of *Cephalopholis boenak* both within the experiment and between experimental and natural patch reefs, indicated that a functional response was also occurring. On experimental reefs feeding rates were twice as high on reefs of a higher prey to predator ratio. The observation that in March 1997 feeding rates were higher on experimental reefs than on natural reefs was initially surprising, given the pattern of prey to predator ratios. The low prey to predator ratios on experimental reefs at that time were largely due to the high abundance of lutjanid recruits. Although these lutjanids may be piscivorous at settlement (Sweatman 1993), they may have been out competed for prey by *Cephalopholis boenak*. Individuals of *C. boenak* on the patch reefs were much larger than the lutjanids (10 to 20 cm compared to less than 5 cm) and were generally the largest resident piscivores. The importance of size in competitive interactions has been frequently demonstrated (Begon et al. 1986). *C. boenak* also displayed aggressive territoriality towards the lutjanids and other piscivorous species (pers. obs.) which may have inhibited their access to prey. By comparison, on the natural patch reefs there were many piscivores present which were larger than *C. boenak* (Chapter 3) and hence on these reefs *C. boenak* may have been under greater competitive pressure.

The higher prey to predator ratios on experimental reefs in August and November 1996 were probably the main reason *Cephalopholis boenak* grew much faster on experimental reefs than on natural reefs (the developmental response). Differences between the patch reefs used in the experiment and those in the natural community must be considered, however. Patch reefs in the experiment were much smaller (3 m^2) than those studied in the natural community (approximately 100 m^2). Along with differences in competitive pressure (see above), the large serranid, *Plectropomus leopardus*, a known predator of *C. boenak* (St John 1995), was not present on the experimental reefs. This predator was thought to have inhibited feeding rates of *C. boenak* on natural patch reefs (see Chapter 4).

The experimental reefs also provided an abundant supply of prey within a very small area. Fish on experimental reefs may therefore have expended less energy travelling in search of food and defending their territories, than fish on natural reefs (Krebs & Davies 1978). Interestingly, however, the mean home range size of *Cephalopholis boenak* on natural patch reefs (5.43 m^2, Chapter 3) was not much larger than the size of the experimental reefs. Hence energetic costs may have not been dramatically different on the two reef types.

Whether prey density had a direct effect on prey consumption rates, an indirect effect on energetic costs, or whether differences in competitive and predation pressure were responsible for the results, the patch reef experiment provided evidence that growth of *Cephalopholis boenak* was limited by the availability of prey on natural reefs. Food-limited growth of coral reef fish has been demonstrated previously for planktivorous (Jones 1986, Forrester 1990) and herbivorous (Clifton 1995, Hart & Russ 1996) species, but not for piscivores.

Although *Cephalopholis boenak* individuals could not have been on the experimental reefs for more than 3 years, size-at-age was also greater on experimental reefs than on natural reefs. This indicates that differences in growth rate extended beyond the course of the experiment and illustrates the influence prey abundance may have on life history characteristics of a fish species. Elevated growth rates may in turn lead to reduced mortality, earlier maturation and greater reproductive output over the life time of an individual (Jones 1991).

The findings of this study therefore reinforce the traditional view that both predator abundance and growth is likely to be food-limited (Hairston et al. 1960, Menge & Sutherland 1987), although it contrasts with other views (eg. Parrish 1987) which imply that the generalist nature of the diet of piscivores on coral reefs would make food-limitation unlikely.

This study has also paved the way for more detailed investigations into how predators respond to variation in the abundance of their prey on coral reefs. For example, a more comprehensive tagging program may reveal the distances from which predators are attracted to areas of high prey abundance. Video surveillance of small patch reefs (eg. Martin 1994), may also provide more detailed information on feeding rates of predators. Alternatively, laboratory experiments (eg. Mattila & Bonsdorff 1998) may allow the shape of functional response curves to be modelled. *Cephalopholis boenak* is already known to be well suited to laboratory experimentation (Chapter 4).

Responses of predators to variation in prey abundance may have a stabilising effect on prey populations and communities (Fretwell & Lucas 1970, Hassell & May 1974, Murdoch & Oaten 1975, Hassell 1978). Aggregation of predators in sites of high prey abundance has been implicated as a possible mechanism responsible for recent observations of density-dependent mortality of coral reef fish (Forrester 1995, Beukers & Jones 1997, Hixon & Carr 1997; Chapter 3). Despite evidence of such aggregation in this experiment, prey to predator ratios remained higher in areas of high prey density throughout the study. This pattern was also observed in natural communities (Chapter 3). This suggests that prey in living in high density populations would actually have been afforded some protection from predation (inverse density-dependence, Begon et al. 1986). However, the combined effect of both an aggregative and functional response by predators, as observed in this study, could still produce density-dependent mortality of prey (Murdoch & Oaten 1975).

In summary, this study has supplied additional support for the view that predatory fish may be food-limited and for the regulatory role of predation on prey fish communities on coral reefs. The behavioural and developmental responses of *Cephalopholis boenak* in this study are consistent with the hypothesis that the abundance of prey controls the local abundance and or / growth of piscivores. These responses also provide potential mechanisms for recent observations of density-dependent mortality in coral reef fish populations. Before accurate models of coral reef fish communities can be generated, however, the nature of interactions between predation and other potentially important processes, such as recruitment, competition and migration, requires further investigation.

Table 1. Results of ANOVA examining spatial and temporal variation in prey and piscivore density and the ratio of prey to piscivores in the patch reef experiment. (* Indicates significant difference).

a) Prey density

SOURCE	SS	DF	MS	F	Sig of F
Date	2746366.85	2	1373183.4	6.95	0.002*
Reef Type	5915261.54	1	5915261.5	29.93	< 0.001*
Date by Reef Type	193987.62	2	96993.81	0.49	0.614
Within + Residual	14228985.85	72	197624.80		

b) Piscivore density (Data was Ln (x+1) transformed).

SOURCE	SS	DF	MS	F	Sig of F
Date	38.65	2	19.33	76.60	< 0.001*
Reef Type	1.65	1	1.65	6.53	0.013*
Date by Reef Type	0.10	2	0.05	0.19	0.827
Within + Residual	18.17	72	0.25		

c) Ratio of prey to piscivores (Data was Ln (x) transformed).

SOURCE	SS	DF	MS	F	Sig of F
Date	50.87	2	25.43	29.40	< 0.001*
Reef Type	18.13	1	18.13	20.96	< 0.001*
Date by Reef Type	3.12	2	1.56	1.80	0.172
Within + Residual	62.29	72	0.87		

Table 2. Results of ANOVA comparing piscivore and prey density and the ratio of prey to piscivores on experimental and natural patch reefs. (* Indicates significant difference).

a) Prey density (Data was Ln (x) transformed).

SOURCE	SS	DF	MS	F	Sig of F
Date	8.52	2	4.26	6.09	0.003*
Reef Type	166.9	1	166.9	238.56	< 0.001*
Date by Reef Type	7.21	2	3.60	5.15	0.007*
Within + Residual	88.16	126	0.70		

b) Piscivore density (Data was Ln (x+1) transformed).

SOURCE	SS	DF	MS	F	Sig of F
Date	16.85	2	8.43	49.12	< 0.001*
Reef Type	70.94	1	70.94	413.59	< 0.001*
Date by Reef Type	14.81	2	7.41	43.17	< 0.001*
Within + Residual	21.61	126	0.17		

c) Ratio of prey to piscivores (Data was Ln (x) transformed).

SOURCE	SS	DF	MS	F	Sig of F
Date	7.49	2	3.75	5.18	0.007*
Reef Type	1.45	1	1.45	2.01	0.159
Date by Reef Type	42.18	2	21.09	29.18	< 0.001*
Within + Residual	91.07	126	0.72		

Table 3. Results of ANOVA examining spatial and temporal variation in the density of *Cephalopholis boenak* in the patch reef experiment. Data was Ln (x+1) transformed. (* indicates significant difference).

SOURCE	SS	DF	MS	F	Sig of F
Date	1.43	3	0.48	2.87	0.040*
Reef Type	2.86	1	2.86	17.23	< 0.001*
Date by Reef Type	1.17	3	0.39	2.35	0.078
Within + Residual	15.93	96	0.17		

Table 4. Results of ANCOVA comparing growth rates of tagged *Cephalopholis boenak* on experimental and natural patch reefs. Data was Ln (x+1) transformed. (*Indicates significant difference).

SOURCE	SS	DF	MS	F	Sig of F
Reef Type	26.64	1	26.64	53.18	< 0.001*
Regression	15.31	1	15.31	30.55	< 0.000*
Within + Residual	21.04	42	0.50		

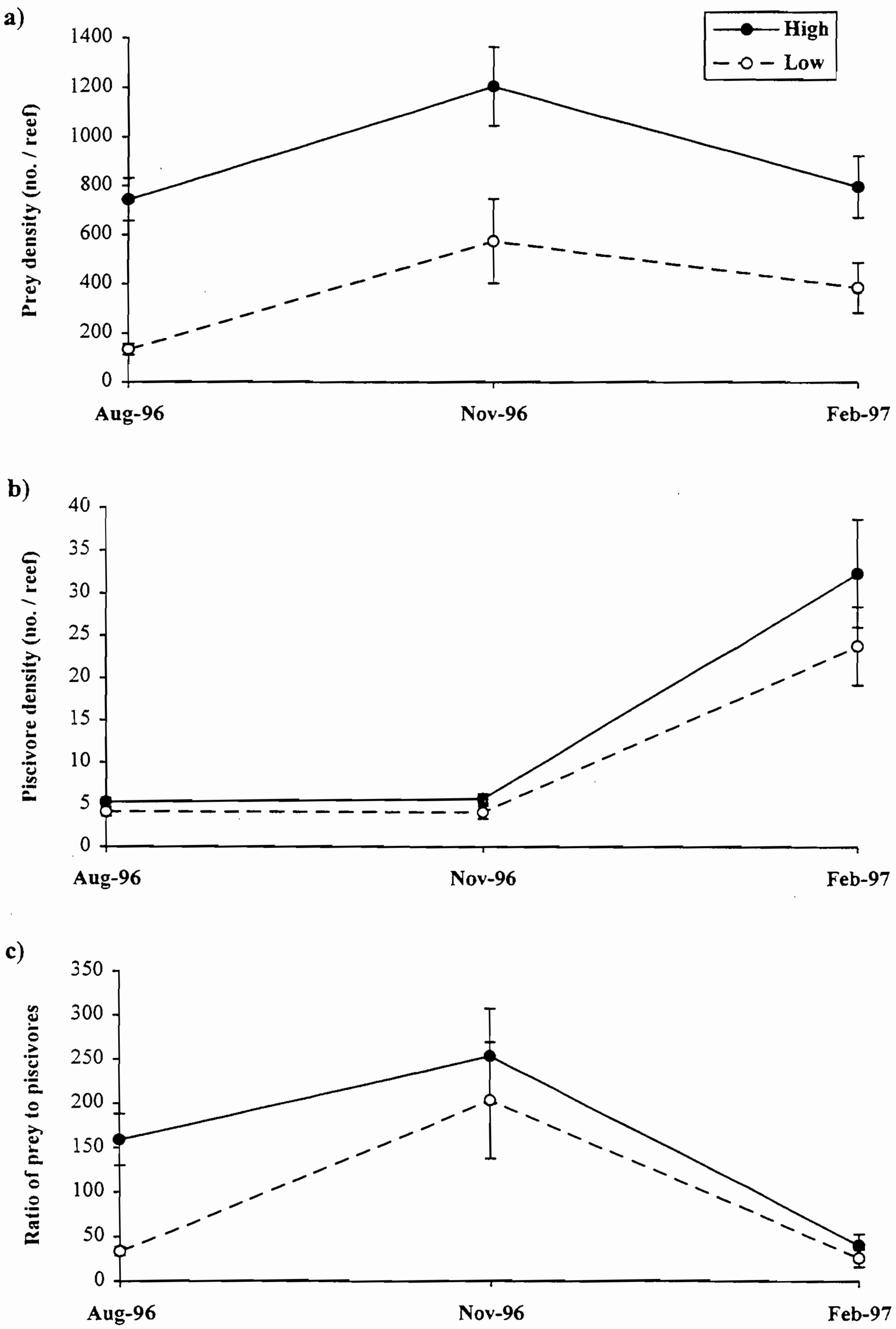


Figure 1. Spatial and temporal variation in the density (mean +/-SE) of **a)** prey, **b)** piscivores and **c)** the ratio of prey to piscivores (mean +/-SE) on experimental patch reefs (n=13 per reef type)

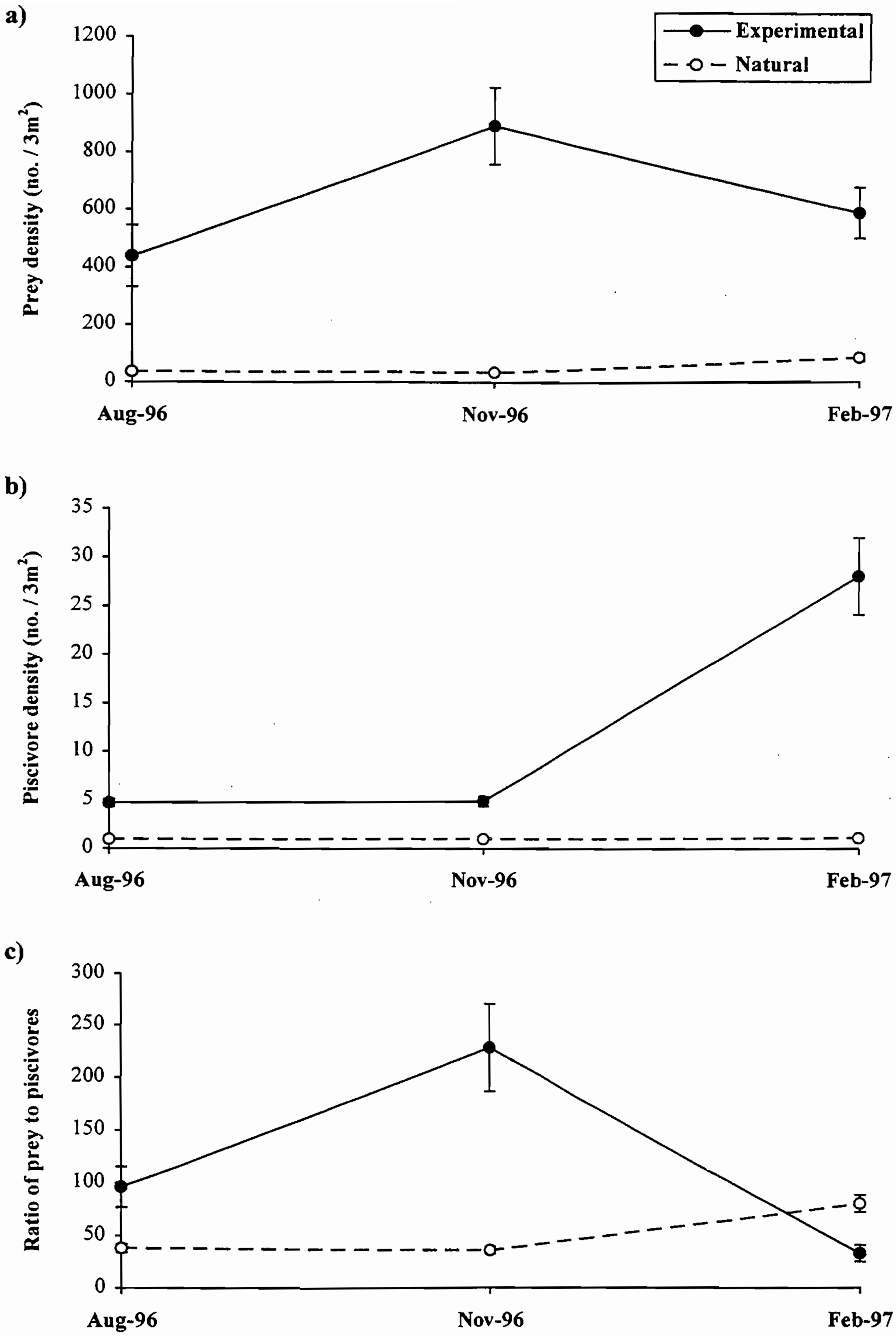


Figure 2. Comparison of the density (mean +/-SE) of **a)** prey, **b)** piscivores and **c)** the ratio of prey to piscivores (mean +/-SE) on experimental (n=26) and natural (n=18) patch reefs

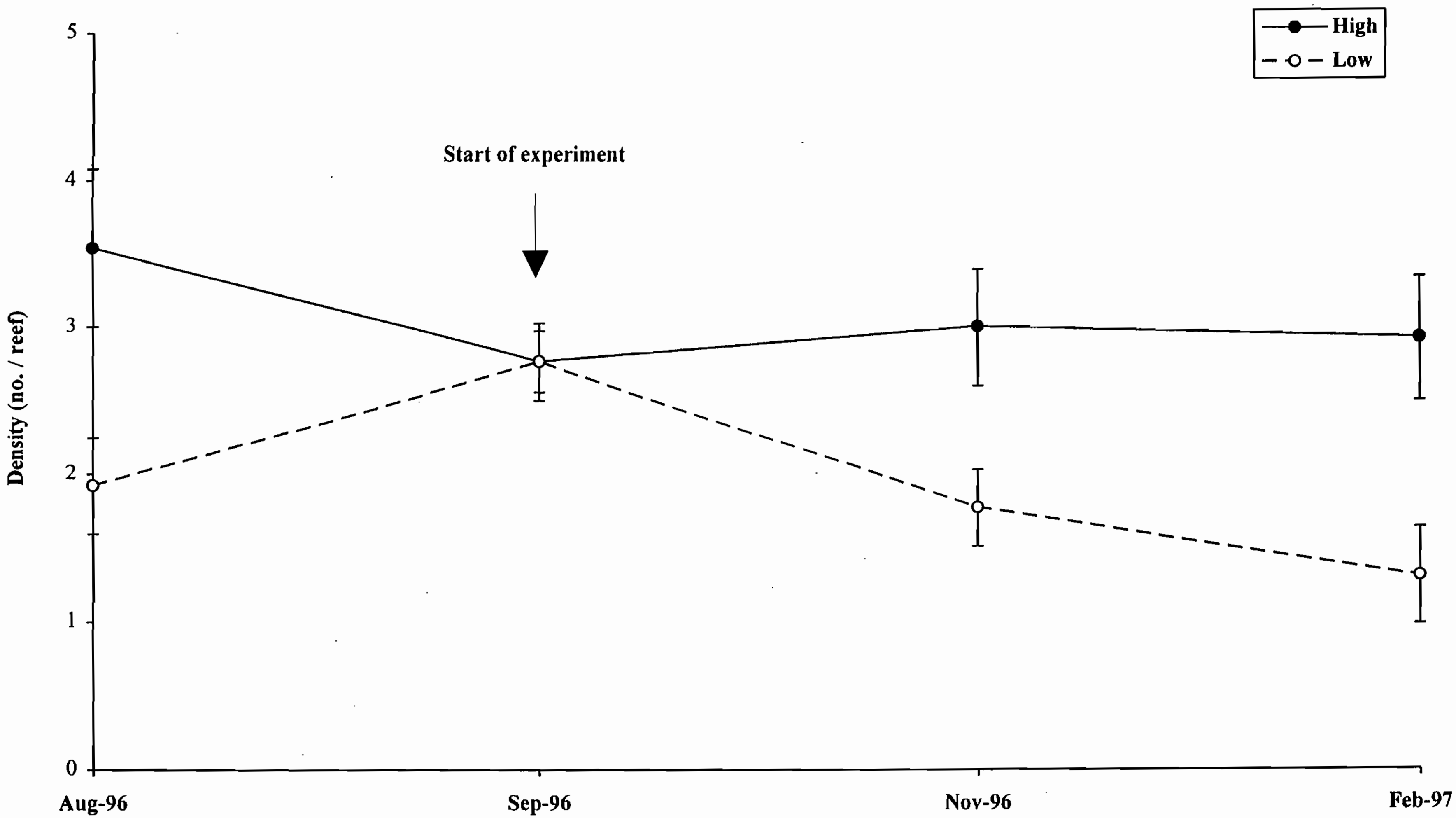


Figure 3. Spatial and temporal variation in the density of *Cephalopholis boenak* on experimental patch reefs (n=13 per reef type). Note the changing time scale of censuses.

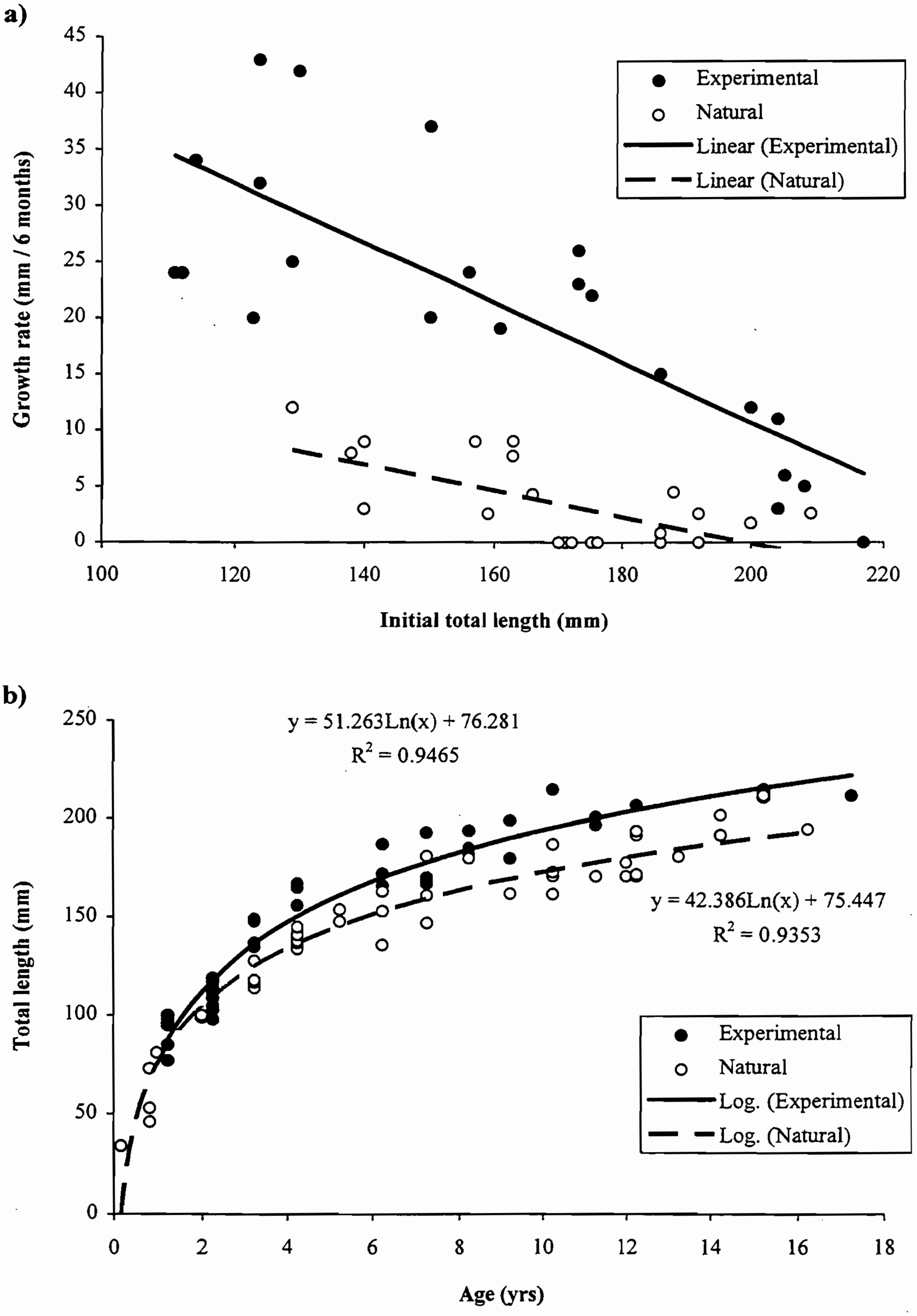


Figure 4. Comparison between **a)** the growth of tagged *Cephalopholis boenak* on experimental (n=22) and natural (n=23) patch reefs and **b)** the size-at-age curves of *C. boenak* on experimental (n=45) and natural (n=44) patch reefs.

Chapter 7

General Discussion

Interactions between Predators and Prey

Few studies have investigated interactions between predators and prey on coral reefs. In fact, only one study has monitored the diet of piscivorous coral reef fish and the abundance of their prey at the same time (Shpigel and Fishelson 1989). General ecological theory suggests that predators are limited by the availability of prey (Hairston et al. 1960; Menge & Sutherland 1976), and therefore should respond in predictable ways to fluctuations in prey abundance. Likewise, predators are known to effect the abundance of prey and the composition of ecological communities (Sih et al. 1985). Most studies examining predator / prey interactions have concentrated on freshwater lakes and streams (Zaret 1980; Kerfoot & Sih 1987; Forrester 1994) and marine intertidal areas (Paine 1966; Connell 1975; Menge 1992), where food webs are often relatively simple, consisting of only a few predator and prey species. Whether general ecological principles hold in diverse coral reef fish communities, where there may be hundreds of species of both predators and prey, and consequently complex food webs, is unknown.

The main aim of this thesis was examine how piscivorous fish respond to fluctuations in the abundance of their prey. With this information I then aimed to predict their impact on prey populations and communities. I initially concentrated on community level interactions between predators and prey. Predator abundance was consistently correlated with prey abundance and the mortality of prey at least partially explained by predator abundance. Detailed investigation of the ecology of two species of rock-cod, *Cephalopholis cyanostigma* and *C. boenak* showed that movement, feeding ecology and growth was all effected by prey abundance. The high abundance of these rock-cods and their behavioural responses to fluctuations in prey abundance suggested they were having a considerable impact on their prey populations. Hence, this study revealed that populations of predators and prey were inextricably linked at Lizard Island, and represents a significant contribution to our understanding of predator / prey relationships on coral reefs.

Effects of Prey on Predators

This study provided several lines of evidence that piscivorous fish at Lizard Island were limited by the abundance of prey. Firstly, there were strong positive relationships between the abundance of prey and predators throughout the study, despite sometimes dramatic fluctuations in prey abundance. Recruitment of prey fish to Lizard Island is known to be particularly high, up to an order of magnitude higher than other areas such as One Tree Island on the southern Great Barrier Reef (Sweatman 1985). It may therefore seem surprising that predators would be limited by the abundance of prey in such an environment. Studying experimental reefs, however, Caley (1995) found that the recruitment and abundance of piscivores was also much higher at Lizard Island than One Tree Island. It is not known if this pattern is also present in natural communities, but it would appear likely.

The mechanisms responsible for the observed correlations between predator and prey abundance could not be fully determined. Previous studies have shown that recruitment may explain patterns of adult abundance for some planktivorous species of coral reef fish (Doherty 1981; Victor 1983, 1986; Doherty & Fowler 1994). In this study, however, patterns of recruitment explained little of the variation in the abundance and distribution of piscivorous fish. In freshwater (Eklov 1997) and intertidal (Boulding & Hay 1984; Robles et al. 1995) ecosystems predators have also been shown to move into areas receiving high amounts of prey recruitment. *Cephalopholis boenak* in the lagoon experiment also moved from areas of low to high prey abundance. In contrast, movement of rock-cods between patch reefs and between patch and contiguous reef was rare in the natural communities, suggesting it had little effect on large scale patterns of abundance and distribution.

Recruitment patterns and early life histories of piscivorous fish require further investigation, however. The use of baited censuses (Chapter 2) and suction pumps (Eggleston 1995) may provide much more accurate censuses of predator recruitment. Recruitment surveys also need to be conducted over long time periods to account for potential variation in this process (Doherty & Williams 1988). The paucity of information on mortality patterns of juvenile piscivorous fish also needs to be redressed. Several recent studies have shown that post-settlement mortality of reef fish may disrupt patterns of recruitment (Forrester 1995; Beukers 1996; Steele 1997). This study did not examine movement of juvenile piscivorous fish, but ontogenetic shifts in habitat use have been described for other piscivorous species (Eggleston 1995; Light & Jones 1997). These movements may well be in response to feeding requirements as predators become more piscivorous with increases in size and age (Harmelin-Vivien & Bouchon 1976; Parrish 1987) and may be crucial in determining patterns of adult abundance. The recent development of techniques for tagging small reef fish (Beukers et al. 1995), provides a method for examining both the mortality and movement of juvenile piscivorous fish.

The movement of large piscivorous species known to be mobile (eg. *Plectropomus leopardus*, Zeller 1997a,b, 1998) also needs to be examined further. Ultrasonic telemetry has been shown to be ideal for obtaining detailed information on movements of these fish (Zeller 1997a,b, 1998). If telemetry could be combined with diver surveys of prey abundance in areas frequented by these fish, a better understanding of how these predators respond to fluctuations in prey abundance could be obtained. It is quite likely that recruitment, mortality and movement all interact to produce patterns of adult abundance of piscivorous fish, with the importance of each process varying between species (Caley et al. 1996; Steele 1997).

The interacting effect of fluctuations in prey abundance and patterns of prey selection appeared to effect the dietary composition of *Cephalopholis cyanostigma* and *C. boenak*. This caused diet to vary both spatially and temporally. Patterns of prey selection appeared to reflect the vulnerability of different types of prey to capture, with mid-water schooling prey such as clupeids selected for over other families of fish. In the absence of these types of prey, apogonids, which hover above the reef, were selected for over more reef-associated pomacentrids. Similar types of prey selection have been reported for another piscivorous coral reef fish, *Plectropomus leopardus*, at One Tree Island (Kingsford 1992). Use of habitat as a refuge from predation is emerging as common practice among various species of coral reef fish (Hixon & Beets 1989, 1993; Caley & St John 1996; Beukers & Jones 1997). The availability of prey to predators may therefore depend not only on prey abundance, but also on the type of prey present and the quality and quantity of refuges from predation.

Despite significant spatial variation in the abundance of prey at Lizard Island, there was little evidence of spatial variation in the feeding and growth rates of the rock-cods. The lagoon experiment demonstrated, however, that at least for *Cephalopholis boenak*, there was potential for higher feeding and growth rates under enhanced conditions of prey abundance. The lack of variation in natural communities was probably the result of a number of factors which cancelled out the effects of one another. For example, although prey abundance was much higher on the patch reefs in this study, so to was the abundance of competitors and predators of the rock-cods themselves. In addition, habitat complexity may also have differed between the two reef types. All of these factors may inhibit feeding and consequently growth rates (Werner et al. 1983a,b; Milinski 1986; Schmitt & Holbrook 1988). Home ranges of the rock-cods were also significantly smaller on patch reefs, although whether this was due to prey abundance or the density of conspecifics is difficult to determine. Hence it would appear that piscivorous fish at Lizard Island live in a relatively balanced community in which the profitability of living in different habitats or patches is evened out.

Effects of Predators on Prey

This thesis also provided considerable evidence that piscivorous fish at Lizard Island were having a significant impact on populations and communities of their prey. Firstly, the two rock-cod species studied were very abundant, consumed prey at high rates and selected certain sizes and types of prey. Secondly, along with several other recent studies on coral reefs (Forrester 1995; Beukers & Jones 1997; Hixon & Carr 1997) mortality of prey fish was found to be density-dependent. Mortality was correlated with predator abundance, suggesting that aggregation of predators in areas of high prey abundance was at least partially responsible for the observed patterns. Interestingly, however, mortality was also highest where the ratio of prey to predators was highest. This suggests that several other factors contributed to the observed patterns of mortality.

The role of transient predatory fish (eg. Carangidae) in predator / prey interactions requires further investigation. Personal observations suggested that these fish were responsible for a considerable amount of prey fish mortality at Lizard Island. Transient predators are difficult to census (Thresher & Gunn 1986), however, the recent use of remote video surveillance (Martin 1994; Hixon & Carr 1997) may provide a solution. Based on video recordings, Hixon & Carr (1997) found that transient predators visited reefs with high densities of prey much more often than reefs with low densities of prey. Video surveillance may also provide information on predator strike and capture rates (Martin 1994).

The functional response of piscivorous reef fish to increases in prey density also needs to be examined. In the lagoon experiment *Cephalopholis boenak* fed at a higher rate on reefs where the prey density was higher, however, the shape of the functional response curve could not be determined. This study has shown *C. boenak* to be ideally suitable for laboratory experimentation, and this may be the best way to further investigate functional responses. Treatments could be set up offering individual predators a range of prey densities and the resultant mortality of prey could then be monitored (eg. Mattila & Bonsdorff 1998). The presence of a type 3 functional response (ie disproportionate increases in consumption rates with increasing prey density, Holling 1959) would have strong implications for the regulatory effect of predation on prey populations (Murdoch & Oaten 1975).

Another mechanism which may be contributing to mortality of prey fish is increased piscivory during recruitment periods, by species which do not normally consume fish. At Lizard Island, the labrid *Thalassoma lunare*, which is occasionally piscivorous (Martin 1994; Connell 1998a), was extremely abundant. Hence, although each individual may not consume many prey fish, the total impact of this species may be considerable. *T. lunare* may also become more piscivorous during pulses of recruitment. For example, on one occasion I observed group of *T. lunare* (3 or 4 fish) consume an entire brood (20 to 30 individuals) of juvenile *Acanthochromis polyacanthus*. Clearly, detailed dietary studies, on a wide range of coral reef fish, must continue if trophic interactions are to be further unravelled.

This study also provided evidence of differential mortality between families of prey fish. These patterns corresponded with patterns of prey selection by the two species of rock-cod. Similar prey selection may therefore be common among other species of piscivorous fish. Indeed, several other studies have recorded variation in the mortality rates of different species of prey fish (Doherty & Sale 1985; Eckert 1987; Sale & Ferrell 1988; Connell & Gillanders 1997). The factors causing this differential mortality are not fully known, but probably relate to vulnerability of prey to capture. A greater understanding of this process could also be gained from laboratory experimentation. For example, a predator such as *Cephalopholis boenak* could be offered choices between different types of prey, with the proportion of each type being varied between treatments. This would provide information on when predators switch from one type to another (Murdoch et al. 1975), and would be useful for predicting mortality patterns of prey.

Overall, this study provided evidence that predation by piscivorous fish may cause both density-dependent mortality of prey and variation in mortality rates between families and species. Hence post-settlement predation on coral reef fish has the potential to disrupt patterns of prey fish abundance established at settlement (Jones 1991; Hixon 1991; Carr & Hixon 1995; Forrester 1995; Caley et al. 1996; Hixon & Carr 1997).

The Role of Predation in Coral Reef Fish Communities

Little is known of whether top-down (ie predation pressure) or bottom-up forces (ie the productivity of the surrounding waters) predominantly structure coral reef fish communities, or whether these forces interact with one another. Although this study joins an increasing number which show predation may influence the dynamics of prey populations and the structure of communities (eg. Doherty & Sale 1985; Caley 1993; Hixon & Beets 1993; Carr & Hixon 1995; Connell 1996, 1997, 1998b; Beukers & Jones 1997; Hixon & Carr 1997), the generality of these findings is unknown. Due to practical constraints, many of these studies (including this one) were limited to small scales, few species or artificial reefs. Extrapolation of these results to large scales or entire communities must therefore be done with caution.

Piscivorous reef fish are disproportionately targeted by commercial and recreational fishers (Russ 1991) which may cause dramatic reduction of their stocks (Russ & Alcala 1989, 1996; Jennings et al. 1995; Jennings & Polunin 1997). This fishing effort is often spread out over large areas, enabling the effects of large-scale piscivore removal to be examined (Jennings & Polunin 1997). It has been predicted that removal of piscivores by fishing should cause proliferation of prey populations and changes in community structure (Beddington & May 1982; Beddington 1984). Of the few studies which have effectively examined the effects of fishing, however, several (eg. Jennings et al. 1995; Jennings & Polunin 1997) found no effect on populations and communities of prey. These authors have consequently suggested that predation may not be an important structuring force at large scales.

I would suggest that failure to detect effects of fishing on prey species is due to the complexity of food webs on coral reefs. This study provides considerable evidence that coral reef piscivores are limited by prey abundance and are therefore likely to competing for this limited resource. Removal of top predators by fishing may provide advantages for other smaller piscivores or species which occasionally consume fish. For example, overfishing of *Plectropomus leopardus* (a large, commercially targeted predator) at Lizard Island, could result increased prey availability for the smaller rock-cod species (which are not commercially targeted) leading them to feed at higher rates. There may also be increased survivorship of the rock-cods as *P. leopardus* is probably their main predator (St John 1995). In this way the rock-cods could fill the role of *P. leopardus*, resulting in little overall change in predation pressure at Lizard Island.

If our understanding of the role predation on coral reefs is to progress, the nature of trophic interactions, including interactions between different piscivorous species, must be further studied. Only then will we be able generate accurate models able to predict how different processes such as recruitment, competition and predation interact with one another to structure coral reef fish communities.

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