

# The influence of prey abundance on the feeding ecology of two piscivorous species of coral reef fish

B.D. Beukers-Stewart\*, G.P. Jones

*Department of Marine Biology, James Cook University, Townsville, Qld 4810, Australia*

Received 16 July 2002; received in revised form 8 April 2003; accepted 29 August 2003

## 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* (Valenciennes, 1828) and *Cephalopholis boenak* (Bloch, 1790) (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 2-year period. The abundance of the rock-cods and the abundance and family composition of their prey were monitored at the same time. Dietary information was largely collected from regurgitated samples, which represented approximately 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, dominated 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 mainly 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. However, there was little variation in feeding rates between habitats, despite apparent differences in prey abundance. In summary, our observations of how the feeding ecology of

\* Corresponding author. Present address: Port Erin Marine Laboratory, University of Liverpool, Port Erin, Isle of Man IM9 6JA, UK. Tel.: +44-1624-831038; fax: +44-1624-831001.

E-mail address: brycebs@liverpool.ac.uk (B.D. Beukers-Stewart).

predatory fish responded to variation in prey abundance provide potential mechanisms for how predation may affect the community structure of coral reef fishes.

© 2003 Elsevier B.V. All rights reserved.

*Keywords:* Coral reef fishes; Diet; Predation; Prey selection; Feeding rates; Predator impacts

---

## 1. Introduction

Predation may have an important influence on the dynamics of populations (Murdoch and Oaten, 1975; Taylor, 1984) and the structure of ecological communities (Paine, 1966; Connell, 1975; Menge and Sutherland, 1987). Despite a long history of research in other ecosystems, predation received relatively little attention, until recently, as a process that may be structuring coral reef fish communities (Hixon, 1991). Over the last decade, a number of researchers (Caley, 1993; Hixon and Beets, 1993; Carr and Hixon, 1995; Connell, 1996; 1997; 1998a; Beets, 1997; Beukers and Jones, 1997; Eggleston et al., 1997; Hixon and Carr, 1997; Planes and Lecaillon, 2001; Webster, 2002) 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. 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 et al., 1997), interspecific variation in mortality patterns (Carr and Hixon, 1995; Planes and Lecaillon, 2001; Webster, 2002), mediation of predation by habitat structure (Hixon and Beets, 1993; Beukers and Jones, 1997; Eggleston et al., 1997) and effects of prey density on mortality rates (Hixon and Carr, 1997; Connell, 1998a; Webster, 2002). However, in almost all of these studies, 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). However, the use of descriptive studies for studying the role of piscivorous fish on coral reefs may be problematic (Connell and Kingsford, 1997). The most common method for elucidating the identity and diet of coral reef piscivores has been the study of gut contents (e.g. Hiatt and Strasburg, 1960; Randall, 1967; Harmelin-Vivien and Bouchon, 1976; Norris and Parrish, 1988; Blaber et al., 1990; Connell, 1998b). Many of these studies examined a large number of potentially piscivorous species and so were very useful for identifying piscivores, but 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 (Connell and Kingsford, 1997; but for exceptions see Kingsford, 1992; Nakai et al., 2001; St. John, 1999, 2001; St. John et al., 2001). 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 and Miller, 1978), but has only rarely been attempted for coral reef fish (Light, 1995).

Piscivorous coral reef fish are often considered to be generalist, opportunistic predators, whose diet reflects the abundance of prey available (Harmelin-Vivien and Bouchon, 1976; Parrish, 1987). This common perception is surprising given that only one study on coral reefs (Shpigel and Fishelson, 1989) has attempted to compare 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 and Ebeling, 1983; Jones, 1984; Schmitt and Holbrook, 1984; Cowen, 1986). The predators studied by Shpigel and Fishelson (1989) did appear to concentrate on the most common prey available, but results were only reported in qualitative terms.

A more detailed study of how predatory coral reef fish respond to variation in prey availability could reveal the mechanisms for several recent observations in coral reef fish ecology. These include higher mortality of schooling/grouping prey species compared to more solitary species (Connell and Gillanders, 1997), high mortality of slow growing individuals or small species of fish (Jones and McCormick, 2002) and density dependent mortality within species (Hixon and Webster, 2002; Jones and McCormick, 2002). Indeed, Hixon and Webster (2002) state that further mechanistic studies of piscivory in reef fishes are sorely needed. For example, the high mortality of schooling species of fish could be related to patterns of prey selection by piscivorous fish. If some species suffer proportionally higher predation than others, this will have important implications for community structure (Carr and Hixon, 1995). Likewise, if predators exhibit a functional response (an increase in feeding rate with an increase in prey density) in combination with aggregation at high-density patches of prey (e.g. Hixon and Carr, 1997; Stewart and Jones, 2001), this could account for observations of density-dependent mortality (Murdoch and Oaten, 1975). In fact, a type 3 functional response alone, whereby predators feed disproportionately on certain types of prey when they are abundant but ignore them when they are scarce (Begon et al., 1986), could also induce density-dependent mortality (Hixon and Webster, 2002). Strong density-dependent mortality has the potential to regulate populations of coral reef fish (Caley et al., 1996; Hixon and Webster, 2002).

This study examined the diet and feeding rates of two piscivorous species of rock-cod, *Cephalopholis cyanostigma* and *Cephalopholis boenak* (Serranidae) at Lizard Island on the northern Great Barrier Reef, Australia. Dietary information was largely collected 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 that had been monitored at the same sites and times. It was therefore possible to measure prey selectivity and to investigate how the feeding rates of predators

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 (Stewart and Beukers, 2000) and were strongly site attached during the study (Stewart and Jones, 2001). This made monitoring of the prey available to these species relatively simple compared to more mobile piscivores. Finally, consumption rates and densities of the two rock-cod species were used to assess their impact on standing stocks of prey. This was related to known declines in prey abundance during the same period to determine the relative contribution of each piscivorous species to observed patterns of mortality.

## 2. Materials and methods

The study was conducted between February 1995 and April 1997 on the western (predominantly sheltered) side of Lizard Island (14°40'S, 145°28'E) on the northern Great Barrier Reef, Australia. Six sites were selected in 5–10 m of water depth, three on contiguous reef and three on patch reefs. Each site on contiguous reef was situated on the slope of the fringing reef and measured 30 × 30 m (area 900 m<sup>2</sup>). Each of the patch reef sites consisted of six reefs, ranging in size from 40 to 306 m<sup>2</sup> (mean = 114 m<sup>2</sup>). Total area of reef at each of the patch reef sites ranged from 506 to 960 m<sup>2</sup>. The fish studied were almost completely restricted to each site during the study (Stewart and Jones, 2001).

### 2.1. Abundance and composition of prey communities

The abundance and composition of the prey communities at the above study sites was censused once every 3 months between August 1995 and February 1997 as part of a related study (Stewart and Jones, 2001). Prey censuses included all fish less than 5 cm in standard length (SL) belonging to the families Pomacentridae, Apogonidae, Clupeidae, Caesionidae and Atherinidae. This size and type of fish was expected to be the main prey of *C. cyanostigma* and *C. boenak* at Lizard Island (Martin, 1994). Full details of the census method are described in Stewart and Jones (2001).

Throughout the study prey densities were consistently higher on patch reefs than on contiguous reef (Table 1a). Prey densities also increased dramatically in February each year after the summer recruitment season. The family composition of prey communities also varied between patch and contiguous reef habitats and throughout the year (Table 1b). On both reef types, pomacentrids, followed by apogonids, were consistently the most abundant type of prey. However, apogonids made up a much higher proportion of the prey available on patch reefs. In the summer of 1995/1996, there was a large increase in the density of clupeids on patch reefs but in the summer of 1996/1997, there was only a small increase. The other two families, Caesionidae and Atherinidae, only made up a small proportion of the remainder.

The availability of this detailed information on spatial and temporal variation in prey abundance and composition was the basis for examining the effect of fluctuations in prey abundance on the feeding ecology of the two rock-cod species.

Table 1

(a) The mean density (no./100 m<sup>2</sup> ± S.E.) of prey fish on patch and contiguous reef at Lizard Island

Date	Patch	S.E.	Contiguous	S.E.
August 1995	883.75	118.86	265.56	29.47
November 1995	863.70	119.51	280.60	46.77
February 1996	2748.83	512.79	548.07	57.59
May 1996	1697.58	233.54	328.00	42.87
August 1996	1200.61	155.57	316.76	36.60
November 1996	1143.44	152.97	319.93	34.19
February 1997	2825.61	393.68	478.40	76.83

(b) The percentage composition of different families of prey fish on patch and contiguous reef at Lizard Island

Date	Pomacentrid	Apogonids	Clupeids	Caesionids	Atherinids
<i>Patch reef</i>					
August 1995	90.49	9.51	0	0	0
November 1995	91.46	8.54	0	0	0
February 1996	42.93	38.79	16.37	1.91	0
May 1996	60.34	37.59	1.45	0.62	0
August 1996	68.94	29.57	0	0.21	1.29
November 1996	72.10	26.83	0	0.27	0.81
February 1997	55.04	37.15	1.27	5.73	0.80
<i>Contiguous reef</i>					
August 1995	100.00	0	0	0	0
November 1995	98.94	1.06	0	0	0
February 1996	91.26	8.79	0	0	0
May 1996	94.13	5.87	0	0	0
August 1996	97.66	2.34	0	0	0
November 1996	98.10	1.90	0	0	0
February 1997	86.45	8.44	0	3.56	1.55

## 2.2. Dietary composition

Over the course of a tag and release study (Stewart and Jones, 2001), a total of 548 *C. cyanostigma* and 311 *C. boenak* were captured underwater by baited hook and line at the 6 sites. Sampling dates corresponded with the above censuses of prey fish communities (generally within a few days). Fish captured ranged in total length from 12.6 to 31.4 cm for *C. cyanostigma* and from 9.8 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.

### 2.2.1. Validation of dietary analysis using regurgitated prey

To validate the accuracy of the regurgitated gut content samples we also dissected fish from which regurgitated material had already been collected. In August 1996 (winter), 26 *C. 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 2–4 h 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 two samples. This was to determine if the regurgitated samples were biased.

#### 2.2.2. Estimation of digestion rates

Information on digestion rates was already available for *C. 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 to 290 mm total length (TL), were captured in the field and then kept in 2000-l outdoor aquaria for 2 days to acclimatise. Each individual was then fed one fish (Pomacentridae—either *Pomacentrus moluccensis* or *Pomacentrus amboinensis*) and one crab (Xanthidae). Prey fish size ranged from 23 to 33 mm standard length (mean = 28.25 mm), while crab size ranged from 13 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 the Results section). At each of four different time periods after fish were fed (1, 4, 12 and 24 h), three individuals were sacrificed in an ice/seawater slurry. Fish were then gut injected with a 10% buffered formalin solution and kept on ice for 2–4 h before being dissected. Any prey remaining in the stomachs was assigned to one of five categories denoting the degree of digestion, with one representing fresh prey and five completely digested prey (see Martin, 1994). This provided a typical time scale for each digestion category and determined if fish and crustaceans were digested at different rates.

#### 2.2.3. Overall dietary composition

All regurgitated and dissected prey collected were 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 (see above). The importance of different families of prey in the diet of each species was examined in four different ways. First, by percentage frequency (i.e. the number of times that family of prey was recorded as a percentage of the total number of identifiable prey items); second, by percentage occurrence (i.e. the number of fish containing that family of prey as a percentage of the total number of fish containing identifiable prey); and third, by percentage volume (i.e. 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 (i.e. relatively intact prey). 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:

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



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.

#### 2.2.4. Ontogenetic variation in dietary composition

Using both the regurgitated and dissected samples, the effect of predator size on patterns of prey fish size-selection was examined. This was done by plotting the SL of each fish containing prey against the SL of the fish prey it had consumed.

#### 2.2.5. Seasonal and spatial variation in dietary composition

Using the regurgitated and dissected samples, temporal 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 at different times of the year, using sites as replicates, was compared by one-way ANOVA. Data were 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 were 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.

### 2.3. Prey selection

#### 2.3.1. Field observations

The above data on temporal and spatial variation in dietary composition were then compared to the abundance of prey fish available at each place and time (from Table 1). In this case, data were again pooled across sites within reef types but not between years. This enabled us 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 and Scavia, 1979) was calculated using the following formula:

$$\omega_i = \frac{\frac{r_i}{P_i}}{\sum_i \frac{r_i}{P_i}}$$

and

$$E^* = \frac{\left[ \omega_i - \left( \frac{1}{n} \right) \right]}{\left[ \omega_i + \left( \frac{1}{n} \right) \right]}$$

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.

### 2.3.2. Laboratory experiment

The prey selection of *C. boenak* was further investigated in a laboratory experiment conducted during February and March 1997. In large outdoor aquaria (2000 l), small patch reefs (approx. 0.125 m<sup>3</sup>) were built from live *Porites cylindrica*, with one *C. boenak* (approx. 150 mm TL) added to each of six treatment tanks, while six identical control tanks were left free from predators. After 2 days acclimatisation, five *Apogon fragilis*, five *Neopomacentrus azysron* and five *P. moluccensis* (all between 10 and 20 mm TL) were released into each aquaria after first being floated in plastic bags for 5 min. The number of each species surviving was then monitored after 1, 2 and then every 12 h 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).

## 2.4. Feeding rates

### 2.4.1. Temporal and spatial variation in feeding rates

Temporal and spatial variation in feeding rates was examined when at least 10 individuals of each rock-cod species were captured at each site. Initially, these feeding rates (based on both frequency and volume) were calculated for the fish prey regurgitated at each site. Using sites as replicates, the mean feeding rate on each reef type at each sampling date was determined. Differences between reef types and times were examined by two-way ANOVA. The two fixed factors were time of year and reef type. Data were square root transformed when variances were heterogeneous (Cochran's *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 these data with the single fixed factor being reef type. Data were again square root transformed when necessary. Post-hoc power analysis was used to investigate the likelihood of type II errors when comparing feeding rates on the two reef types.

## 2.5. Impact of *C. cyanostigma* and *C. boenak* on prey populations

The impact of *C. cyanostigma* and *C. boenak* on prey fish populations was calculated for the period between February and August 1996 and compared to declines in the abundance of prey over the same time (calculated from Table 1). Impact represented the number of fish consumed by the two rock-cod species per 100 m<sup>2</sup>, over the 6-month period. The following formula was used to calculate impact (*I*):

$$I = n \left\{ D \frac{(\text{FFR} + \text{AFR})}{2} \right\}$$



Table 2

Summary of the overall dietary composition of the two rock-cod species (Freq. = frequency, Vol. = volume, Occ. = occurrence, IRI = index of relative importance)

<i>C. cyanostigma</i>							
(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
Total	109		1334.45		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
Total	58		46.32		53		

*C. boenak*

(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
Total	60		33.65		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

(continued on next page)

Table 2 (continued)

<i>C. boenak</i>							
(b) Identified invertebrates							
Infraorder/family	Freq.	%F	Vol.	%V	Occ.	%O	IRI
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
Total	54		14.25		44		

where  $n$  is the number of days between the prey surveys in February and August 1996,  $D$  is the density of each rock-cod species in February 1996 (from Stewart and Jones, 2001), FFR is the feeding rate in February 1996 and AFR is the feeding rate in August 1996. Stewart and Beukers (2000) have shown that the census method used in Stewart and Jones (2001) may underestimate the densities of these rock-cod species. However, as many of the rock-cods we counted were tagged and known to inhabit distinct home ranges, we felt we were able to census them more accurately than would otherwise have been the case. We therefore decided to take a conservative approach and not adjust the density estimates of the rock-cods for these calculations. The feeding rates used in the above formula were also converted from regurgitated feeding rates (RFR) to total feeding rates (TFR) using the following formula:

$$\text{TFR} = \text{RFR}(100/\%R)$$

where  $\%R$  is the amount of prey regurgitated as a percentage of the total consumed (see the Results section). Given a digestion rate of 6–12 h and no night time feeding (see Results section and personal observations), these feeding rates were assumed to be equivalent to the number fish consumed per day. An estimate of error for these values was calculated using the upper and lower limits of the standard errors of each parameter used in the equations. Impact was calculated separately for each rock-cod species on both patch and contiguous reef.

### 3. Results

#### 3.1. Dietary composition

##### 3.1.1. Validation of dietary analysis using regurgitated prey

*C. cyanostigma* regurgitated 57.14% of prey consumed in winter 1996 compared to 60.53% in summer 1997. Similarly, *C. boenak* regurgitated 62.50% of prey in summer 1997. The relative proportions of fish and invertebrates were very similar in both the regurgitated and dissected samples. For *C. cyanostigma*, the proportion of fish in the regurgitated samples was 62.50% and 78.26% in winter and summer respectively, compared to 66.66% and 70.00% in the dissected samples. For *C. boenak*, fish comprised 60.00% of the regurgitated samples compared to 57.14% of the dissected samples.

### 3.1.2. Digestion rates

Digestion of fish prey was quite rapid in *C. cyanostigma*. After 1 h, prey were still relatively fresh (digestion stage 1), but after 4 h the superficial surfaces of prey were fully digested and the head and tail were partly digested (digestion stage 3). After 12 h, fish prey had completely disappeared. This suggests fish prey were digested in approximately 6–12 h. However, crustacean prey were much slower to digest and even after 24 h they were still

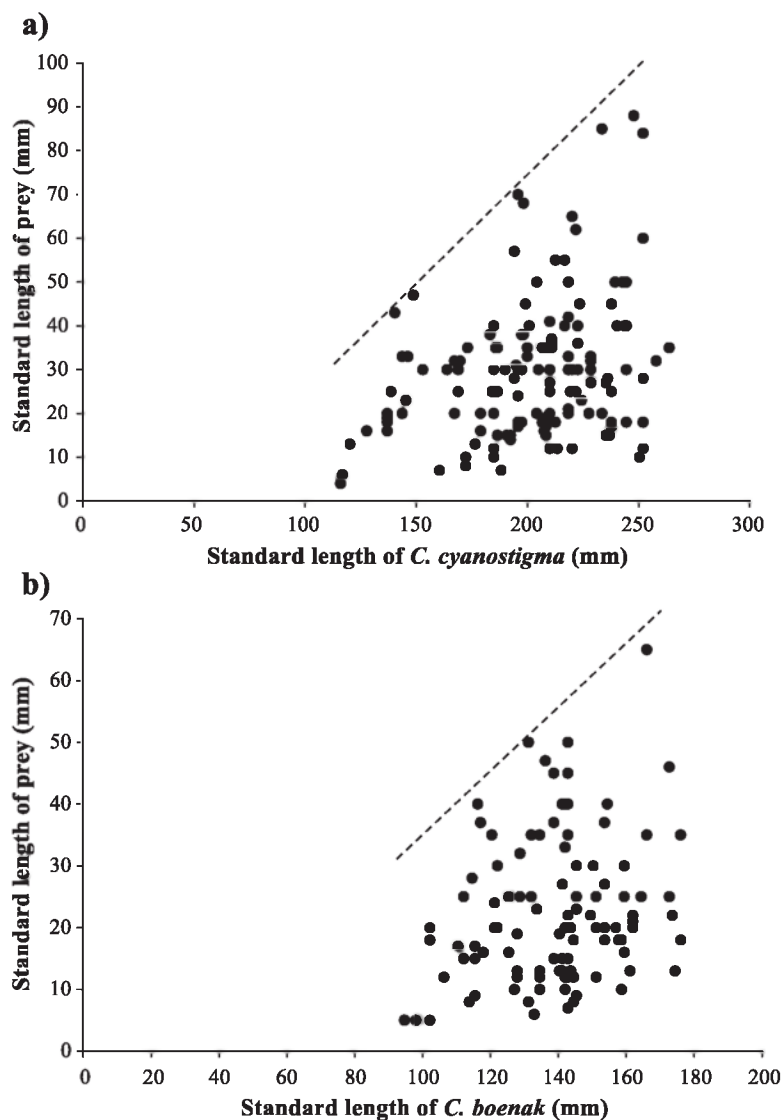


Fig. 1. The relationship between predator length and prey length for (a) *C. cyanostigma* (n = 165) and (b) *C. boenak* (n = 119). Dashed lines indicate the approximate upper limit of prey sizes that were consumed.

Table 3

Seasonal and spatial variation in the dietary composition of the two rock-cod species (Sum = summer, Win = winter, %F = percentage frequency)

*C. cyanostigma*

## (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
Galatheididae	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	

*C. boenak* (spatial variation in summer only)

## (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
Total	18		27	

Table 3 (continued)

*C. boenak* (spatial variation in summer only)

(b) Identified invertebrates

Infraorder/family	Contiguous reef		Patch reef	
	Sum	%F	Sum	%F
Caridea	4	23.53	9	50.00
Galatheididae	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	

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 by *C. boenak* was similar to that for *C. cyanostigma*, with considerable digestion after 4 h and complete digestion after 12 h (Martin, 1994).

### 3.1.3. Overall dietary composition

Overall, fish made up 74.7% by frequency of the gut contents collected from *C. 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 six families (and one separate infraorder) of invertebrates were found in the diet of *C. cyanostigma* (Table 2). Using the index of relative importance, apogonids were by far the most important fish family consumed, followed by pomacentrids, caesionids and clupeids (Table 2). 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.

The diet of *C. 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 seven families of fish were consumed and again apogonids dominated, followed by pomacentrids and clupeids (Table 2). Of the invertebrate prey, six families (and one 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).

### 3.1.4. Ontogenetic variation in dietary composition

Small prey fish (approx. 10 mm SL) were consumed by fish of all sizes belonging to both species (Fig. 1). Maximum size of prey consumed, however, appeared to be limited to approximately one third of the body length of the predator (see dashed lines, Fig. 1). The mean ratio of prey to predator length was 14.0 for *C. cyanostigma* and 15.6 for *C. boenak*.

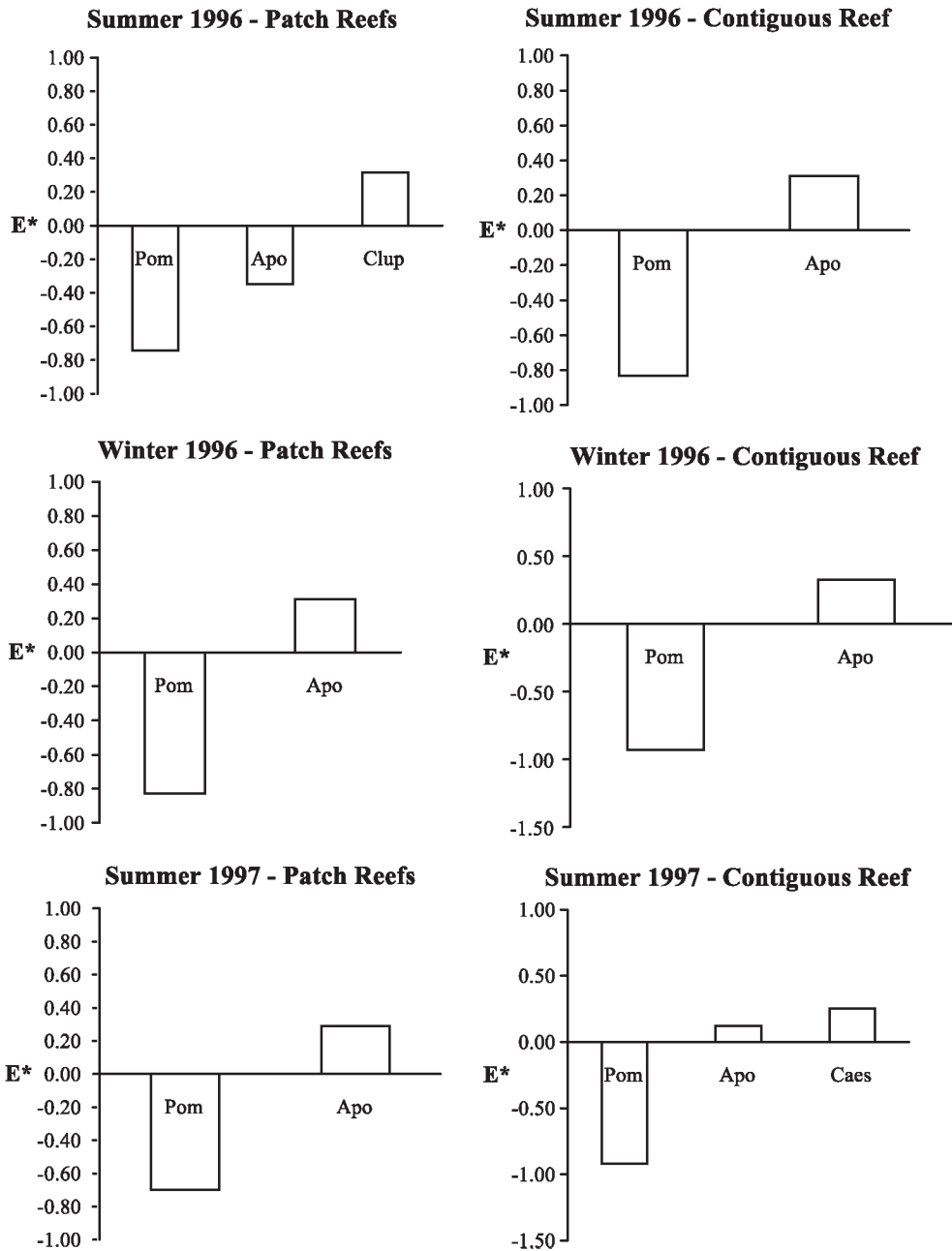


Fig. 2. Temporal and spatial variation in prey selection by *C. cyanostigma* ( $E^*$ =electivity index, Pom = Pomacentridae, Apo = Apogonidae, Clup = Clupeidae, Caes = Caesionidae).



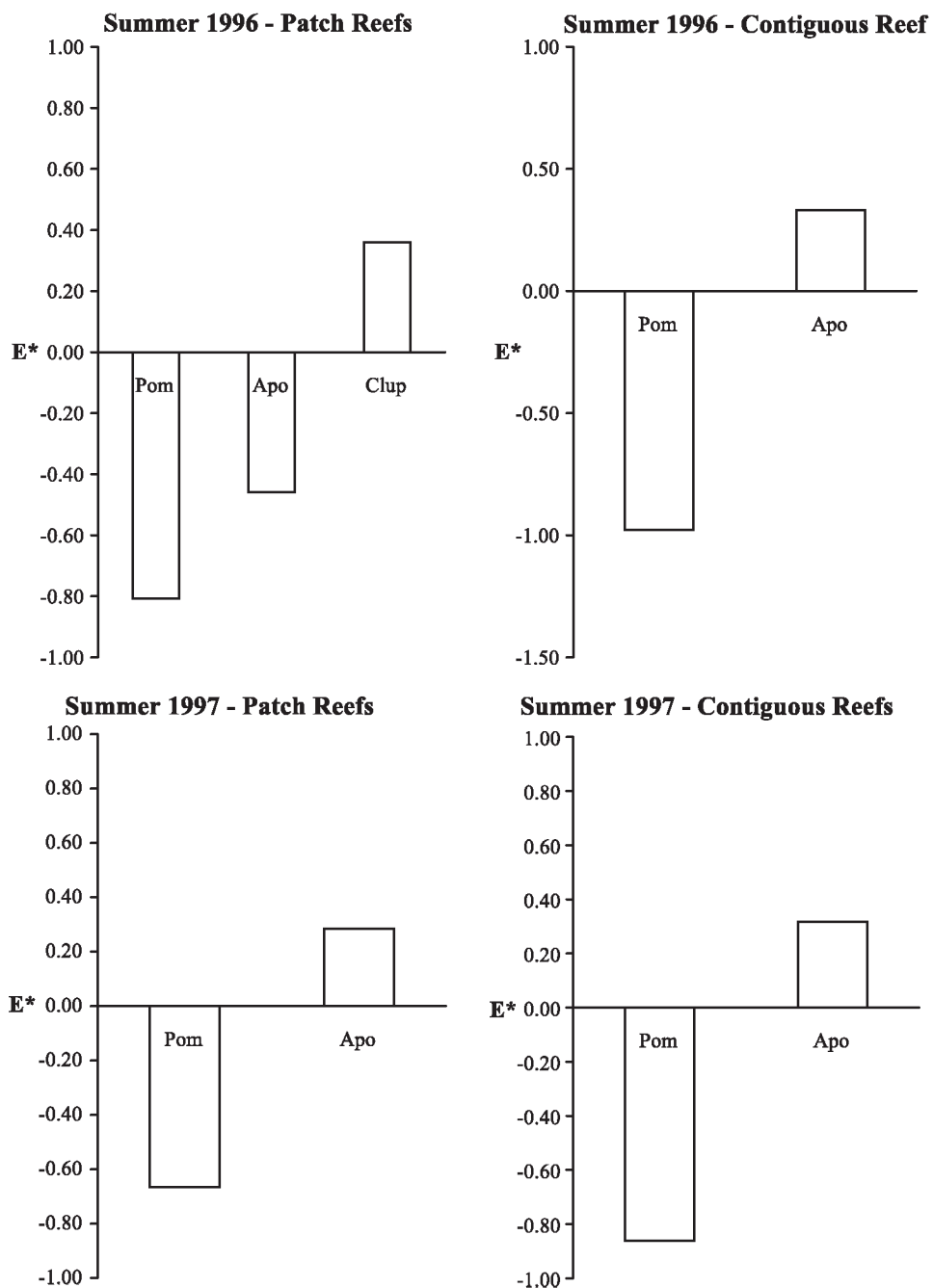


Fig. 3. Temporal and spatial variation in prey selection by *C. boenak* ( $E^*$ =electivity index, Pom = Pomacentridae, Apo = Apogonidae, Clup = Clupeidae).

### 3.1.5. Seasonal and spatial variation in dietary composition

There was no significant seasonal or temporal variation in the degree of piscivory exhibited by either species (one-way ANOVA, *C. cyanostigma*:  $F_{1,20} = 0.25$ ,  $p = 0.624$ ; *C. boenak*:  $F_{2,9} = 0.70$ ,  $p = 0.521$ ). However, at family level, there was considerable seasonal and spatial variation in dietary composition (Table 3). On contiguous reef in both summer and winter, *C. cyanostigma* fed mainly on apogonids followed by pomacentrids and caesionids. In contrast, on patch reefs in summer, *C. cyanostigma* fed equally on clupeids and apogonids, followed by pomacentrids. However, in winter, clupeids were absent from the diet on patch reefs, which was dominated by apogonids and pomacentrids. Feeding on invertebrates also varied (Table 3). 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 *C. 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 3). 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 3).

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 (*C. cyanostigma*:

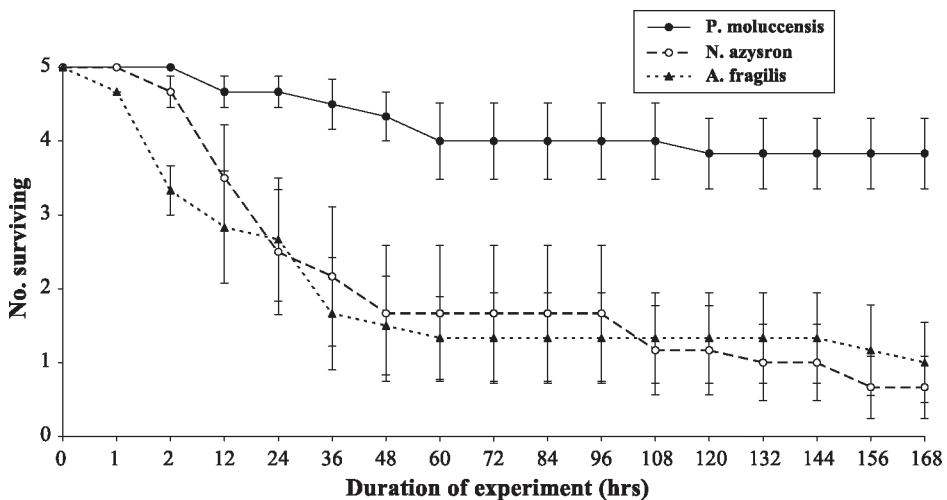


Fig. 4. Survival (mean  $\pm$  S.E.) of three different species of prey fish (*P. moluccensis*, *N. azysron* and *A. fragilis*) exposed to predation by *C. boenak* in the laboratory. Note the changing time scale.

52.78% compared to 6.45%; *C. boenak*: 66.67% compared to 35.29%). There were no real differences between the size composition of prey consumed on patch and contiguous reef, except that *C. cyanostigma* tended to take slightly more large fish (>50 mm SL) on contiguous reef (20%) compared to on patch reef (5.06%). Only 1.19% of fish prey taken by *C. boenak* were larger than 50 mm SL.

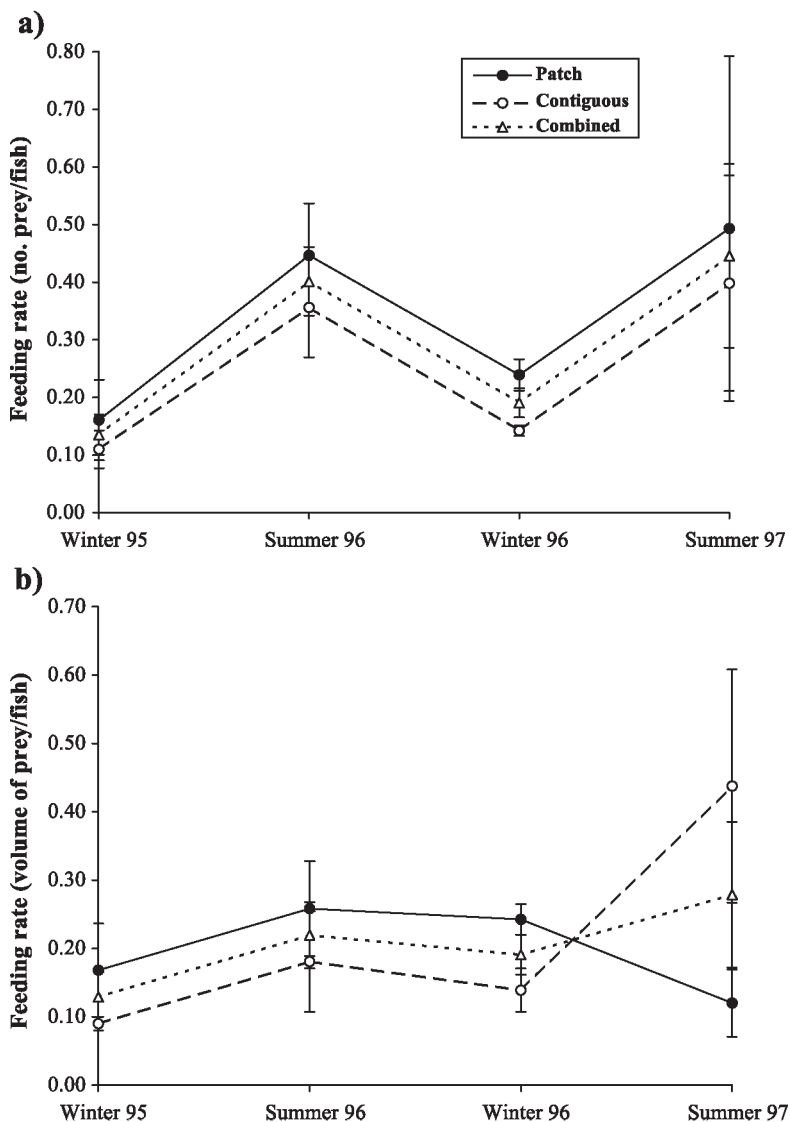


Fig. 5. Temporal variation in (a) the number of fish prey per fish (mean  $\pm$  S.E.) and (b) the volume (ml) of fish prey per fish (mean  $\pm$  S.E.), regurgitated by *C. cyanostigma* on patch reefs, contiguous reef ( $n = 3$  sites per reef type) and combined.

### 3.2. Prey selection

#### 3.2.1. Field observations

Relating the above information on temporal and spatial variation in dietary composition to patterns of prey abundance (Table 1) revealed that prey selection also varied temporally and spatially (Figs. 2 and 3). In summer 1996, both *C. 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 fed selectively 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.

#### 3.2.2. Laboratory experiment

The laboratory experiment examining the feeding behaviour of *C. boenak* also showed selection of some prey species over others (Fig. 4; one-way ANOVA,  $F_{2,15} = 15.00$ ,  $p < 0.001$ ). Initial mortality of *A. fragilis* was very high, closely followed by *N. azysron*, while only a few *P. moluccensis* were eaten 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. 4, Tukey's HSD method). Only one *A. fragilis* died in the control aquaria.

### 3.3. Feeding rates

#### 3.3.1. Seasonal and spatial variation in feeding rates

Feeding rates of *C. cyanostigma* could be calculated at all 6 sites in both summer and winter over the 2 years. Feeding rates of *C. boenak*, however, could only be calculated

Table 4

The influence of reef type and time of year on the feeding rate of *C. cyanostigma*

Source	SS	DF	MS	F	p-value
<i>(a) Results of ANOVA examining the influence of reef type and time of year on the number of prey fish per predator. Data were square root transformed</i>					
Reef	0.02	1	0.02	1.32	0.265
Time	0.17	1	0.17	10.47	0.005*
Reef × time	0.00	1	0.00	0.12	0.735
Residual	0.29	18	0.02		
<i>(b) Results of ANOVA examining the influence of reef type and time of year on the volume of prey fish per predator. Data were square root transformed</i>					
Reef	0.00	1	0.00	0.00	0.952
Time	0.02	1	0.02	1.06	0.317
Reef × time	0.07	1	0.07	2.93	0.104
Residual	0.41	18	0.02		

\* Indicates significant result.

at four sites and not in winter 1995. Feeding rates of both species were often highly variable at site level but some general patterns did emerge. First, the number of fish prey per predator was much higher in summer than winter for *C. cyanostigma* (Fig. 5a, Table

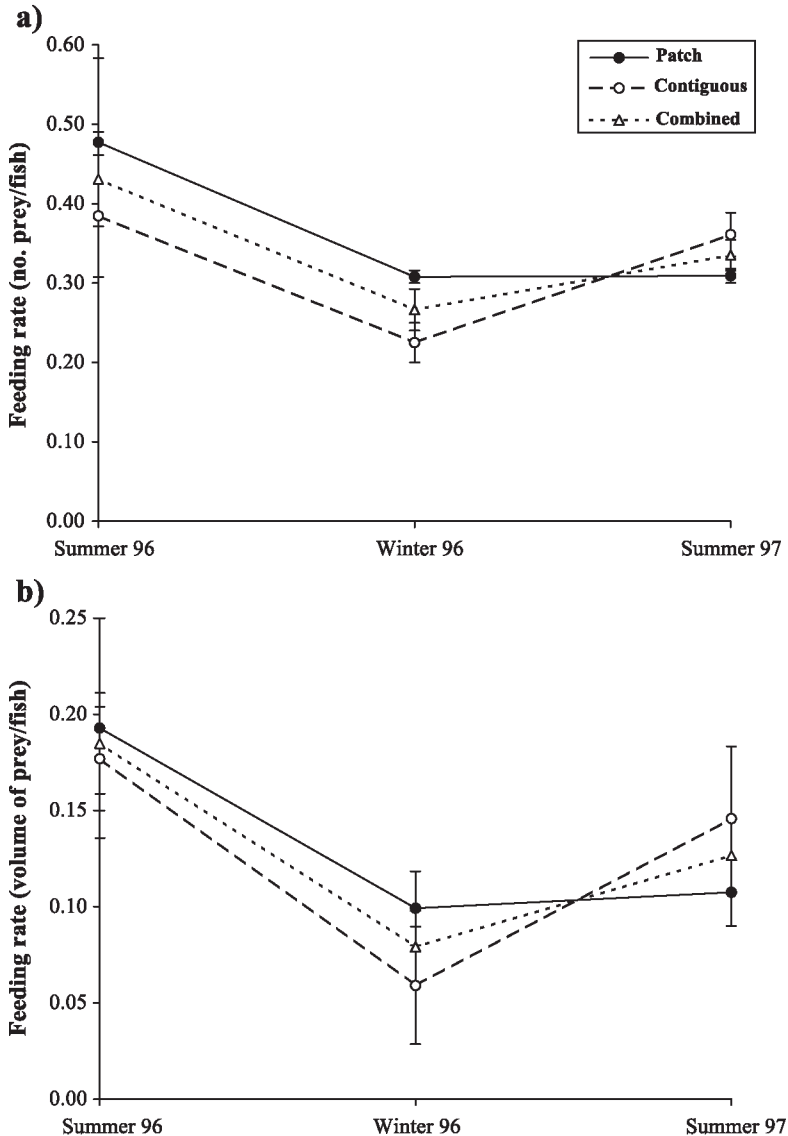


Fig. 6. Temporal variation in (a) the number of fish prey per fish (mean  $\pm$  S.E.) and (b) the volume (ml) of fish prey per fish (mean  $\pm$  S.E.), regurgitated by *C. boenak* on patch reefs, contiguous reef ( $n=2$  sites per reef type) and combined.

4a) and higher in one of the two summers for *C. boenak* (Fig. 6a, Table 5a). The volume of fish prey per predator was higher in one summer for *C. boenak* (Fig. 6b, Table 5b) but there were no differences for *C. cyanostigma* (Fig. 5b, Table 4b). 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 (Figs. 5 and 6, Tables 4 and 5), despite a general trend for feeding rates to be higher on patch reefs. The only exception to this was in February 1997 when feeding rates of both *C. cyanostigma* (volume only) and *C. boenak* (number and volume) were higher on contiguous reef than on patch reefs. Likewise, the combined regurgitated and dissected samples taken in February 1997 revealed only one significant difference, a greater volume of fish consumed by *C. cyanostigma* on contiguous reef (one-way ANOVA,  $F_{1,4}=0.212$ ,  $p=0.047$ ). Otherwise, there was no effect of reef type on the number of prey consumed by *C. cyanostigma* (one-way ANOVA,  $F_{1,4}=0.297$ ,  $p=0.615$ ) or the number (one-way ANOVA,  $F_{1,2}=0.070$ ,  $p=0.820$ ) or volume (one-way ANOVA,  $F_{1,2}=0.945$ ,  $p=0.434$ ) of prey consumed by *C. boenak*. Post-hoc power analysis revealed that the scarcity of significant differences between the two reef types was largely due to variability in the datasets. As a result, estimates of power for detecting the observed differences in feeding rate on the two reef types statistically were less than 0.2 in all cases.

Table 5

The influence of reef type and time of year on the feeding rate of *C. boenak*

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

Source	SS	DF	MS	<i>F</i>	<i>p</i> -value
Reef	0.003	1	0.003	0.963	0.364
Time	0.039	2	0.020	5.624	0.042*
Reef × time	0.009	2	0.005	1.326	0.333
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 were square root transformed

Source	SS	DF	MS	<i>F</i>	<i>p</i> -value
Reef	0.001	1	0.001	0.212	0.661
Time	0.050	2	0.025	5.942	0.038*
Reef × time	0.008	2	0.004	1.037	0.410
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

\* Indicates significant result.



Table 6

The impact of *C. cyanostigma* and *C. boenak* on populations of prey fish on patch and contiguous reefs at Lizard Island between February and August 1996

(a) *C. cyanostigma*

Reef type	Density (no./100 m <sup>2</sup> )	S.E.	No. prey eaten (100 m <sup>2</sup> )	Error (100 m <sup>2</sup> ) (upper/lower)
Patch	5.65	0.83	586.07	789.06/413.02
Contiguous	2.00	0.44	150.33	220.09/93.81

(b) *C. boenak*

Reef type	Density (no./100 m <sup>2</sup> )	S.E.	No. prey eaten (100 m <sup>2</sup> )	Error (100 m <sup>2</sup> ) (upper/lower)
Patch	4.01	0.89	476.24	670.33/314.25
Contiguous	0.59	0.24	54.10	89.84/26.31

## (c) Combined impact

Reef type	Decline in prey density (100 m <sup>2</sup> )	No. prey eaten (100 m <sup>2</sup> )	Error (100 m <sup>2</sup> ) (upper/lower)	Impact (%)	Error (%) (upper/lower)
Patch	1548.22	1062.31	1459.39/727.27	68.61	94.26/46.97
Contiguous	231.31	204.44	309.30/120.12	88.38	133.72/51.9

Estimates of error were calculated using the upper (mean + S.E.) and lower (mean – S.E.) limits of each parameter used in the equations.

### 3.4. Impact of *C. cyanostigma* and *C. boenak* on prey populations

Based on our estimates of density and feeding rates, the two rock-cod species were calculated to have had a large impact on populations of their prey (Table 6). Over the 6 months between February and August 1996, the two rock-cod species combined were estimated to have consumed approximately 1062 prey fish per 100 m<sup>2</sup> on patch reefs and 204 prey fish per 100 m<sup>2</sup> on contiguous reef. The observed decline in mean prey fish density over the same time period was 1548 per 100 m<sup>2</sup> on patch reefs and 231 per 100 m<sup>2</sup> on contiguous reef (Table 1). The two rock-cod species were therefore estimated to have accounted for approximately 68.60% of the observed decline in prey density on patch reefs and 88.50% of the observed decline on contiguous reef.

## 4. Discussion

Few workers have investigated interactions between predators and prey on coral reefs. This study has shown that combining dietary analysis of piscivorous fish with information on the abundance and composition of their prey enables an in depth examination of predator–prey relationships. Most importantly, this approach allowed us to examine the nature of prey selection and the influence of prey abundance on the feeding rates of piscivorous fish. This in turn allowed for the impact of piscivorous fish on the abundance and composition of prey communities to be examined. Further studies of this type will

provide a much greater understanding of the role of predation in the regulation of coral reef fish communities.

The use of regurgitated gut contents in this study was a highly successful way of obtaining samples from the same populations 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. However, the application of this method may be limited to fish caught underwater as regurgitation often occurred soon after capture. Other studies (Randall and 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. We 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. However, given the generally high feeding rates we observed in this study, this did not seem to be the case. Indeed some individual fish caught with bait regurgitated as many as seven 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. Even if line fishing was biased towards hungry fish, this only makes the feeding estimates from this study even more conservative.

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). However, determination of digestion rates revealed that simply examining the frequency of crustaceans in the stomachs grossly overestimated their importance. This study showed that crustaceans probably take about 4 times longer than fish to be digested. Fish would therefore 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 that may affect digestion rate is water temperature (Reshetnikov et al., 1972; Hyslop, 1980; Elliot, 1991). However, a similar study to this one (St. John, 1995) found that 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 that 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). We aimed 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. Nevertheless, digestion in the two rock-cod species appears much more rapid than that observed for other tropical piscivores such as coral trout, (24 h; St. John, 1995) and several lutjanid species (24–33 h; Reshetnikov et al., 1972).

Like many other serranids, the two rock-cod species fed on a wide variety of prey families (Parrish, 1987; Nakai et al., 2001; St. John, 1999, 2001; St. John et al., 2001). 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 other detailed studies of the diet of coral reef piscivores (Kingsford, 1992, St. John, 1999, 2001; St. John et al., 2001) several families of prey fish dominated the gut contents of both rock-cod species. These other studies (all 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, differences between the species in terms of feeding behaviour (Kingsford, 1992) or the large size of *P. leopardus* relative to the rock-cods (Randall et al., 1990).

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; Connell, 1998b; St. John, 1999). 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. Rock-cods of the full size range we examined may therefore be contributing to the high mortality rates often observed for newly recruited fish (Doherty and Sale, 1985; Eckert, 1987; Meekan, 1988; Webster, 2002). These patterns of prey size selection may also help explain observations of high mortality in slow growing individuals or small species of fish (Jones and McCormick, 2002). Further support for these ideas is that the consistent inclusion of small prey in the diet of piscivorous fish, regardless of predator size, has been found to be almost universal in other ecosystems (Juanes, 1994).

The maximum size of prey consumed was probably limited by the depth of the prey and the gape size of the predators (Werner, 1974; Schmitt and Holbrook, 1984; St. John, 1999). In this study, prey as large as 40% of the length of the predators were taken, but the mean ratio was 14–15%. This is somewhat smaller than ratios of 20–30% that 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. However, patterns of seasonal variation in the abundance of crustacean prey were not known. Other research has shown that species such as *Epinephelus merra* (Randall and Brock, 1960) and *Lutjanus kasmira* (Oda and Parrish, 1981), which normally eat crustaceans, switch to a much more piscivorous diet during the summer months. In contrast, *P. leopardus* remains almost entirely piscivorous throughout the year (Kingsford, 1992; St. John, 2001).

Seasonal and spatial variation in dietary composition at family level, however, 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. *P. leopardus* is also known to focus on pelagic schooling fish (such as clupeids and caesionids) when they are available

(Kingsford, 1992; St. John, 2001). At One Tree Island on the southern Great Barrier Reef, this caused pelagic prey to dominate the diet during summer months (Kingsford, 1992), while on the central Great Barrier Reef clupeids appeared in the diet of *P. leopardus* sporadically throughout the year (St. John, 2001). In contrast to this study on rock-cods and Kingsford (1992), St. John (2001) 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 we also observed variation in feeding on invertebrates. We 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). The two rock-cod species therefore appear to have shown 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 (e.g. Harmelin-Vivien and Bouchon, 1976; Parrish, 1987).

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 that 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 that 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 and Beets, 1989, 1993; Caley and St. John, 1996; Beukers and Jones, 1997). The patterns of prey selection observed in this study also matched patterns of decline in prey abundance at the study sites (Stewart and Jones, 2001). 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 the most important factor influencing the risk of predation. *N. azysron*, which is unusual as a mid-water, schooling pomacentrid, suffered similar mortality to the apogonid, *A. fragilis*. Several other studies (Eckert, 1987; Connell and Gillanders, 1997) have found higher mortality among schooling prey species than among solitary prey species of the same family. In addition to their loose association with the substrate, the tendency for many clupeid and apogonid species to form into large and dense aggregations or schools may lead to higher predation rates. Predatory fish may focus on these aggregations and pay less attention to more solitary species such as many of the pomacentrids (Kingsford, 1992; Connell, 1998a, 2000). This type of predatory behaviour would also make density-dependent declines in prey abundance more likely, both between and within different species. Species level variation in mortality rates has been described for a range of species from different families (Sale and 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 and Hixon, 1995).

Prey selection by piscivorous fish may also result in interactions between community structure and the mortality suffered by different fish species. For example, the presence of schooling clupeids or apogonids may provide a type of refuge for reef-associated pomacentrids. A recent study at Lizard Island (Webster and Almany, 2002) found that a high abundance of apogonids on experimental patch reefs resulted in higher recruitment, abundance and species richness of other prey species. They hypothesized that this was due to the predators present (predominately *C. boenak*) concentrating on the highly abundant apogonids and leaving the other species relatively unmolested. The patterns of prey selection found by our study support this hypothesis. Consequently, in the absence of clupeids or apogonids, pomacentrids may be subject to unusually high predation pressure. A better understanding of this interaction could be gained by studying switching behaviour and the shape of functional response curves in predatory coral reef fish, as has been done for predator–prey relationships in other ecosystems (Begon et al., 1986). Unfortunately, during analysis of our prey selection data, it was necessary to pool the results from the study sites within each reef type. This lowered our level of replication and negated the possibility of examining functional responses in our study. Well replicated laboratory experiments, possibly conducted in large outdoor aquaria, could be used to further investigate this aspect of predatory feeding ecology.

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 appeared to feed at a constant rate throughout the year (St. John, 2001). 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 (Stewart and Jones, 2001). The dominance of small prey fish in the diet of both species in summer further reflects this pattern. However, 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, cannot 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 (Stewart, 1998; Stewart and Jones, 2001) 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 (Stewart, 1998) the rock-cods would have to travel less distance in search of prey. One possible explanation for the observed pattern of feeding is that there was 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. However, this observation is confounded by the effect of variation in temperature on metabolic rate.

Comparison between the two reef types is also confounded by several other factors that may have influenced feeding rates such as habitat type and the density of competitors and predators (Werner et al., 1983a,b; Holbrook and Schmitt, 1988). For example, densities of both competitors and predators of the rock-cods themselves (e.g. *P. leopardus*—St. John, 1995) were considerably higher on patch reefs than on contiguous reef (Stewart and Jones, 2001). Finally, due to the high variability of the observed feeding rates, power analysis revealed that the statistical tests used were only sensitive to larger differences than were actually observed. The question of whether or not the feeding rate of the rock-cods responds to the abundance of prey therefore remains unresolved.

Taken together, all of the previous results indicated that the two rock-cod species were having a considerable impact on populations of their prey. Indeed, our calculations suggested that between February and August 1996 the rock-cods accounted for between 69% and 88% of the observed declines in prey density. These results must be viewed somewhat cautiously as the calculations involved multiplying together several estimates with associated errors, and relatively few temporal samples, but the rock-cods undoubtedly consumed a large number of prey fish. The feeding rates estimated in this study (0.41–0.63 prey fish/day) are actually considerably less than those gained from direct observation of another piscivore at Lizard Island (*Synodus variegatus*, 1.8 prey fish/day—Sweatman, 1984). We also took a conservative approach to estimating both the density of the rock-cods and rates of digestion.

Although *C. cyanostigma* and *C. boenak* were among the most common piscivores at the study sites (Stewart and Jones, 2001), 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 additional prey moved into the study sites during the year. Under this scenario, there could have been turnover of prey populations by predators, with relatively small changes in overall prey density. Little recruitment of fish is thought to occur between February and August on the Great Barrier Reef (Russell et al., 1977; Doherty, 1991), so any input of fish would have to have mainly been in the form of immigrants. Several families of prey fish (e.g. 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. Unfortunately, determining the extent of any immigration and subsequent turnover of fish populations generally requires tracking the fate of individual fish. 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 and Jones, 1997). Such patterns of mortality may largely be due to the influence of predation.

In summary, this study has demonstrated that the two rock-cod species *C. cyanostigma* and *C. boenak* have high feeding rates and show selection for certain sizes and types of prey fish. This is the first time prey-selection has been conclusively demonstrated for piscivorous coral reef fish. These results provide potential mechanisms for observations of high mortality in small or slow growing fish and in schooling prey species relative to solitary species. Our work also supports recent hypotheses that suggest the presence of



abundant, schooling prey species may lower the predation pressure on other species in the community. Further mechanistic studies of piscivory will advance our understanding of the role of predation in coral reef fish communities.

## Acknowledgements

While conducting this work, Bryce Beukers-Stewart was supported by an Australian Postgraduate Research Award. Fieldwork was funded by two Merit Research Grants and a Lizard Island Doctoral Fellowship to Bryce Beukers-Stewart and an Australian Research Council Grant to Geoff Jones. Many thanks to Ruth Adams, Matteo Barchiesi, Jo Beukers-Stewart, Justin Chidlow, Nick Gust, Morgan Pratchett, Tobin Turner and Stuart Watson who all provided spirited assistance in the field, and to Julian Caley and two anonymous reviewers who commented on the manuscript. Thanks also to Chris Alexander for assistance in identifying some of the crustaceans. This is a contribution from the Lizard Island Research Station, a facility of the Australian Museum. [AU]

## References

- Andreasson, S., 1971. Feeding habits of a sculpin (*Cottus gobio* L. Pisces) population. Rep.-Inst. Freshw. Res., Drottningholm 51, 5–30.
- Beets, J., 1997. Effects of a predatory fish on the recruitment and abundance of Caribbean coral reef fishes. Mar. Ecol. Prog. Ser. 148, 11–21.
- Begon, M., Harper, J.L., Townsend, C.R., 1986. Ecology: Individuals, Populations and Communities. Blackwell Scientific Publications, Oxford.
- Beukers, J.S., Jones, G.P., 1997. Habitat complexity modifies the impact of piscivores on a coral reef fish population. Oecology 114, 50–59.
- Blaber, S.J.M., Milton, D.A., Rawlinson, N.F.J., Tiroba, G., Nichols, P.V., 1990. Diets of lagoon fishes of the Solomon Islands: predators of tuna baitfish and trophic effects of baitfishing on the subsistence fishery. Fish. Res. 8, 263–286.
- Caley, M.J., 1993. Predation, recruitment and the dynamics of communities of coral reef fish. Mar. Biol. 117, 33–43.
- Caley, M.J., St. John, J., 1996. Refuge availability structures assemblages of tropical reef fishes. J. Anim. Ecol. 65, 414–428.
- Caley, M.J., Carr, M.H., Hixon, M.A., Hughes, T.P., Jones, G.P., Menge, B.A., 1996. Recruitment and the local dynamics of open marine populations. Ann. Rev. Ecol. Syst. 27, 477–500.
- Carr, M.H., Hixon, M.A., 1995. Predation effects on early post-settlement survivorship of coral reef fishes. Mar. Ecol. Prog. Ser. 124, 31–42.
- Connell, J.H., 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In: Cody, M.L., Diamond, J.M. (Eds.), Ecology and Evolution of Communities. Belknap-Harvard Univ. Press, Cambridge, MA, pp. 460–490.
- Connell, S.D., 1996. Variations in mortality of a coral reef fish: links with predator abundance. Mar. Biol. 126, 347–352.
- Connell, S.D., 1997. The relationship between large predatory fish and recruitment and mortality of juvenile coral reef-fish on artificial reefs. J. Exp. Mar. Biol. Ecol. 209, 261–278.
- Connell, S.D., 1998a. Effects of predators on growth, mortality and abundance of a juvenile reef fish: evidence from manipulations of predator and prey abundance. Mar. Ecol. Prog. Ser. 169, 251–261.
- Connell, S.D., 1998b. Patterns of piscivory by resident predatory reef fish at one tree reef, Great Barrier Reef. Mar. Freshw. Res. 49, 25–30.
- Connell, S.D., 2000. Is there safety-in-numbers for prey? Oikos 88, 527–532.

- Connell, S.D., Gillanders, B.M., 1997. Mortality and abundance of a schooling reef fish. Proc. 8th Int. Coral Reef Symp. 1, 1035–1038.
- Connell, S.D., Kingsford, M.J., 1997. The utility of descriptive information for assessing the impact of coral reef piscivores on their prey. Proc. 8th Int. Coral Reef Symp. 1, 999–1004.
- Cowen, R.K., 1986. Site-specific differences in the feeding ecology of the California sheephead, *Semicossyphus pulcher* (Labridae). Environ. Biol. Fish. 16, 193–203.
- Day, R.W., Quinn, G.P., 1989. Comparison of treatments after analysis of variance in ecology. Ecol. Monogr. 59, 433–463.
- Doherty, P.J., 1991. Spatial and temporal patterns in recruitment. In: Sale, P.F. (Ed.), The Ecology of Fishes on Coral Reefs. Academic Press, London, pp. 261–293.
- Doherty, P.J., Sale, P.F., 1985. Predation on juvenile coral reef fishes: an exclusion experiment. Coral Reefs 4, 225–234.
- Doherty, P.J., Williams, D.Mc.B., 1988. The replenishment of coral reef fish populations. Oceanogr. Mar. Biol., Ann. Rev. 26, 487–551.
- Eckert, G.J., 1987. Estimates of adult and juvenile mortality for labrid fishes at one tree reef, Great Barrier Reef. Mar. Biol. 95, 167–171.
- Eggleston, D.B., Lipcius, R.N., Grover, J.J., 1997. Predator and shelter-size effects on coral reef fish and spiny lobster prey. Mar. Ecol. Prog. Ser. 149, 43–59.
- Elliot, J.M., 1991. Rates of gastric evacuation in piscivorous brown trout *Salmo trutta*. Freshw. Biol. 25, 297–305.
- Harmelin-Vivien, M.L., Bouchon, C., 1976. Feeding behaviour of some carnivorous fishes (Serranidae and Scorpaenidae) from Tulear (Madagascar). Mar. Biol. 37, 329–340.
- Hiatt, R.W., Strasburg, D.W., 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecol. Monogr. 30, 65–127.
- Hixon, M.A., 1991. Predation as a process structuring coral reef fish communities. In: Sale, P.F. (Ed.), The Ecology of Fishes on Coral Reefs. Academic Press, New York, pp. 475–507.
- Hixon, M.A., Beets, J.P., 1989. Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs. Bull. Mar. Sci. 44, 666–680.
- Hixon, M.A., Beets, J.P., 1993. Predation, prey refuges and the structure of coral reef fish assemblages. Ecol. Monogr. 63, 77–101.
- Hixon, M.A., Carr, M.H., 1997. Synergistic predation, density dependence, and population regulation in marine fish. Science 277, 946–949.
- Hixon, M.A., Webster, M.S., 2002. Density dependence in reef fish populations. In: Sale, P.F. (Ed.), Coral Reef Fishes: Diversity and Dynamics in a Complex Ecosystem. Academic Press, San Diego, pp. 303–325.
- Holbrook, S.J., Schmitt, R.J., 1988. The combined effects of predation risk and food reward on patch selection. Ecology 69, 125–134.
- Hyslop, E.J., 1980. Stomach content analysis—a review of methods and their application. J. Fish Biol. 17, 411–429.
- Jones, G.P., 1984. The influence of habitat and behavioural interactions on the local distribution of the wrasse, *Pseudolabrus celidotus*. Environ. Biol. Fish. 10, 43–58.
- Jones, G.P., 1991. Postrecruitment processes in the ecology of coral reef fish populations: a multifactorial perspective. In: Sale, P.F. (Ed.), The Ecology of Fishes on Coral Reefs. Academic Press, London, pp. 294–328.
- Jones, G.P., McCormick, M.I., 2002. Interaction between energetic and numerical processes in the ecology of coral reef fish populations. Coral Reef Fishes: Diversity and Dynamics in a Complex Ecosystem. Academic Press, San Diego, pp. 221–238.
- Juanes, F., 1994. What determines prey size selectivity in piscivorous fishes? In: Stouder, D.J., Fresh, K.L., Feller, R.J. (Eds.), Theory and Application in Fish Feeding Ecology. University of South Carolina Press, Columbia, pp. 79–100.
- Keable, S.J., 1995. Structure of the marine invertebrate scavenging guild of a tropical reef ecosystem: field studies at Lizard Island, Queensland, Australia. J. Nat. Hist. 29, 27–45.
- Kingsford, M.J., 1992. Spatial and temporal variation in predation on reef fishes by coral trout (*Plectropomus leopardus*, Serranidae). Coral Reefs 11, 193–198.

- Laur, D.R., Ebeling, W., 1983. Predator–prey relationships in surfperches. *Environ. Biol. Fish.* 8, 217–229.
- Lechowicz, M.J., 1982. The sampling characteristics of electivity indices. *Oecology* 52, 22–30.
- Light, P.L., 1995. The early life history of coral trout *Plectropomus leopardus* at Green and Arlington Reefs. PhD Thesis. James Cook University, Townsville.
- Martin, J., 1994. Predation on juvenile coral-reef fish at Lizard Island, northern Great Barrier Reef: an ecological and behavioural study. BSc (Hons.) Thesis. James Cook University, Townsville.
- Meehan, W.R., Miller, R.A., 1978. Stomach flushing: effectiveness and influence on survival and condition of juvenile salmonids. *J. Fish. Res. Board Can.* 35, 1359–1363.
- Meekan, M.G., 1988. Settlement and mortality patterns of juvenile reef fishes at Lizard Island, northern Great Barrier Reef. *Proc. 6th Int. Coral Reef Symp.* 2, 779–784.
- Menge, B.A., Sutherland, J.P., 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *Am. Nat.* 130, 730–757.
- Murdoch, W.W., Oaten, A., 1975. Predation and population stability. *Adv. Ecol. Res.* 9, 1–131.
- Nakai, T., Sano, M., Kurokura, H., 2001. Feeding habits of the darkfin hind *Cephalopholis urodeta* (Serranidae) at Iriomote Island, southern Japan. *Fish. Sci.* 67, 640–643.
- Norris, J.E., Parrish, J.D., 1988. Predator–prey relationships among fishes in pristine coral reef communities. *Proc. 6th Int. Coral Reef Symp.* 2, 107–113.
- Oda, D.K., Parrish, J.D., 1981. Ecology of commercial snappers and groupers introduced to Hawaiian reefs. *Proc. 4th Int. Coral Reef Symp.* 1, 59–67.
- Paine, R.T., 1966. Food web complexity and species diversity. *Am. Nat.* 100, 65–75.
- Parrish, J.D., 1987. The trophic biology of snappers and groupers. In: Polovina, J.J., Ralston, S. (Eds.), *Tropical Snappers and Groupers: Biology and Fisheries Management*. Westview Press, Boulder, CO, pp. 405–439.
- Pinkas, L., Oliphant, M.S., Iverson, I.L.K., 1971. Food habits of albacore, bluefin tuna and bonito in Californian waters. *Calif. Fish Game* 152, 1–105.
- Planes, S., Lecaillon, G., 2001. Caging experiment to examine mortality, during metamorphosis of coral reef fish larvae. *Coral Reefs* 20, 211–218.
- Randall, J.E., 1967. Food habits of reef fishes of the West Indies. *Stud. Trop. Oceanogr.* 5, 665–847.
- Randall, J.E., Brock, V.E., 1960. Observations on the biology of epinepheline and lutjanid fishes of the Society Islands, with emphasis on food habits. *Trans. Am. Fish. Soc.* 89, 9–16.
- Randall, J.E., Allen, G.R., Steene, R.C., 1990. *Fishes of the Great Barrier Reef and Coral Sea*. Crawford House Press, Bathurst, Australia.
- Reshetnikov, Y.S., Claro, R., Silva, A., 1972. The pattern of feeding and the rate of digestion in some predatory fish. *J. Ichthyol.* 12, 818–824.
- Russell, B.C., Anderson, G.R.V., Talbot, F.H., 1977. Seasonality and recruitment of coral reef fishes. *Aust. J. Mar. Freshw. Res.* 28, 521–528.
- St. John, J., 1995. Feeding ecology of the coral trout *Plectropomus leopardus* (Serranidae) on the Great Barrier Reef, Australia. PhD Thesis. James Cook University, Townsville.
- St. John, J., 1999. Ontogenetic changes in the diet of the coral reef grouper *Plectropomus leopardus* (Serranidae): patterns in taxa, size and habitat of prey. *Mar. Ecol. Prog. Ser.* 180, 233–246.
- St. John, J., 2001. Temporal variation in the diet of a coral reef piscivore (Pisces: Serranidae) was not seasonal. *Coral Reefs* 20, 163–170.
- St. John, J., Russ, G.R., Brown, I.W., Squire, L.C., 2001. The diet of the large coral reef serranid *Plectropomus leopardus* in two fishing zones on the Great Barrier Reef, Australia. *Fish. Bull.* 99, 180–192.
- Sale, P.F., 1977. Maintenance of high diversity in coral reef fish communities. *Am. Nat.* 111, 337–359.
- Sale, P.F., Ferrell, D.J., 1988. Early survivorship of juvenile coral reef fishes. *Coral Reefs* 7, 117–124.
- Scharf, F.S., Buckel, J.A., Juanes, F., Conover, D.O., 1998. Predation by juvenile piscivorous bluefish (*Pomatomus saltatrix*): the influence of prey to predator ratio and prey type on predator capture success and prey profitability. *Can. J. Fish. Aquat. Sci.* 55, 1695–1703.
- Schmitt, R.J., Holbrook, S.J., 1984. Ontogeny of prey selection by black surfperch *Embiotoca jacksoni* (Pisces: Embiotocidae): the roles of fish morphology, foraging behaviour, and patch selection. *Mar. Ecol. Prog. Ser.* 18, 225–239.
- Shpigel, M., Fishelson, L., 1989. Food habits and prey selection of three species of groupers from the genus *Cephalopholis*. *Environ. Biol. Fish.* 24, 67–73.

- Stewart, B.D., 1998. Interactions between piscivorous coral reef fishes and their prey. PhD Thesis. James Cook University, Townsville.
- Stewart, B.D., Beukers, J.S., 2000. Baited technique improves censuses of cryptic fish in complex habitats. *Mar. Ecol. Prog. Ser.* 197, 259–272.
- Stewart, B.D., Jones, G.P., 2001. Associations between the abundance of piscivorous fishes and their prey on coral reefs: implications for prey fish mortality. *Mar. Biol.* 138, 383–397.
- Sweatman, H.P.A., 1984. A field study of the predatory behaviour and feeding rate of a piscivorous coral reef fish, the Lizardfish, *Synodus englemani*. *Copeia* 1984 (1), 187–194.
- Taylor, R.J., 1984. Predation. Chapman & Hall, London.
- Vanderploeg, H.A., Scavia, D., 1979. Calculation and use of selectivity coefficients of feeding: zooplankton grazing. *Ecol. Model.* 7, 135–149.
- Weatherley, A.H., Gill, H.S., 1987. The Biology of Fish Growth. Academic Press, San Diego, CA.
- Wellington, G.M., Victor, B.C., 1989. Planktonic larval duration of one hundred species of Pacific and Atlantic damselfishes (Pomacentridae). *Mar. Biol.* 101, 557–567.
- Webster, M.S., 2002. Role of predators in the early post-settlement demography of coral reef fishes. *Oecologia* 131, 52–60.
- Webster, M.S., Almany, G.R., 2002. Positive indirect effects in a coral reef fish community. *Ecol. Lett.* 5, 549–557.
- Werner, E.E., 1974. The fish size, prey size, handling time relation in several sunfishes and some implications. *J. Fish. Res. Board Can.* 31, 1531–1536.
- Werner, E.E., Gilliam, J.F., Hall, D.J., Mittelbach, G.G., 1983a. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64, 1540–1548.
- Werner, E.E., Mittelbach, G.G., Hall, D.J., Gilliam, J.F., 1983b. Experimental test of optimal habitat use in fish: the role of relative habitat profitability. *Ecology* 64, 1525–1539.