

Abstract—The diet of *Plectropomus leopardus* (Serranidae, Lacepede 1802) was examined on two pairs of reefs in the Cairns Section of the Great Barrier Reef Marine Park, Australia. For both pairs, one reef was open to fishing and the other had been closed to fishing for eight years; however zoning appeared to be ineffective as there was no difference in the size structure of leopard coralgrouper populations on either open or closed reefs. Two fishing methods were used to sample reefs concurrently, and the size structure and diet of *P. leopardus* that were speared randomly ($n=587$) were compared to samples caught by line ($n=85$). Adult *P. leopardus* were highly piscivorous (96% of prey was fish by number), and two families of fishes, Pomacentridae and Labridae, composed approximately half of their diet (index of relative importance=48.4%). Numerical composition of fish in the diet varied significantly among reefs, but there were no patterns related to reef closures when fish prey were classified by taxa or by their habitat. Fishes categorized as living in the demersal reef habitat were the dominant prey consumed, followed by mid-water fishes. When the data from reefs were pooled, the abundance of families in the diet differed between locations (north and south) but not between fishing zones. Dietary overlap was high between the different fishing zones and was very high in relation to naturally occurring spatial and temporal variability in the diet of *P. leopardus* found in other studies. With line fishing larger and hungry fish are caught, and the few data on natural prey suggest tentatively that line catches are biased toward *P. leopardus* feeding on pelagic fishes. The coral reefs and surrounding waters provide the major food source of *P. leopardus*, whereas sandy areas are much less important. Our data suggest that the coral trout fishery is resilient to changes in abundances of particular prey species because the diet of *P. leopardus* is broad and because the two major prey families are diverse and abundant on coral reefs.

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The diet of the large coral reef serranid *Plectropomus leopardus* in two fishing zones on the Great Barrier Reef, Australia

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Groupers (Serranidae) are an important fishery resource throughout the tropics (Ralston, 1987; Heemstra and Randall, 1993; Polunin and Roberts, 1996) and are a favored target species of fishermen (Bohnsack, 1982; Randall, 1987; Koslow et al., 1988; Russ and Alcala, 1996). Like many other large piscine predators, the life history characteristics of groupers (Bohnsack, 1982; Russ, 1991) make them vulnerable to overfishing (Sluka and Sullivan, 1998).

Unlike most other multispecies tropical habitats, the Great Barrier Reef (GBR) supports a line fishery that targets relatively few genera (Russ, 1991). The groupers of the genus *Plectropomus* support the most valuable commercial fin-fishery in Queensland (Trainor, 1991), with an annual value of \$A10 million. Groupers bring a consistently high price (about \$20/kilogram retail for fillet) on the Australian market and are highly valued in the "live export" market to Asia (Miles¹). Also, groupers are targeted by recreational line (Blamey and Hundloe²) and spear fishermen (Steven³), and recreational fishing is expanding with the rapid growth of the tourist industry on the GBR. *Plectropomus leopardus*⁴ is the domi-

nant component of the three main coral trout species caught on the GBR by all fishermen (Williams and Russ, 1994; Steven³), and by Australian standards, this species is subjected to considerable fishing pressure.

Intense fishing pressure has been implicated in the drastic declines of grouper populations off Florida and the Caribbean (Sadovy, 1994; Bohnsack et al., 1994). In Australia, fishery managers have already detected a decline in abun-

¹ Miles, A. 1997. Research, not rumors, needed for live fishing industry. Exploring Reef Science. May newsl. [Available from CRC Reef Research Centre, James Cook University, Townsville 4811, Australia.]

² Blamey, R. K., and T. J. Hundloe. 1991. Characteristics of recreational boat fishing in the Great Barrier Reef region. Unpubl. report to the Great Barrier Reef Marine Park Authority (GBRMPA) PO Box 1379, Townsville, Queensland 4810, Australia.

³ Steven, A. 1988. An analysis of fishing activities on possible predators of the crown of thorns starfish (*Acanthaster planci*) on the Great Barrier Reef. Unpubl. report to GBRMPA, PO Box 1379, Townsville, Queensland 4810, Australia. 131 p.

⁴ The official common name of *Plectropomus leopardus* is leopard coralgrouper, formerly known as bluedotted coraltrout (Heemstra and Randall, 1993).

dance of *P. leopardus* in some parts of the GBR, particularly close to centers of human population (Craik, 1981). Furthermore, fishing pressure is expected to intensify owing to increases in both commercial and recreational demand for this species. Maintaining grouper stocks on coral reefs depends on careful management of these fisheries.

Strategies of coral reef management include closing reefs to all forms of exploitation. This strategy is designed to protect reef-fish stocks and habitats (Williams and Russ, 1994), which enables populations of reef fishes to regain or maintain natural levels of abundance (see review by Roberts and Polunin, 1991). Since the establishment of the Great Barrier Reef Marine Park (GBRMP) in 1981, the major management strategy has involved partitioning of reefs into six main zones that permit different levels and types of fishing.⁵ Actual fishing pressure on reefs in these zones, however, has not been measured in many areas of the marine park (Williams and Russ, 1994).

Most concerns about the impact of fishing have focused on the reduction of stock abundance (Russ, 1991). Both direct and indirect trophic effects on the structure of coral reef-fish communities by the removal of piscivores remain poorly understood (Hixon, 1991; Russ, 1991; Steneck, 1998). Some authors have argued that the removal of large piscivorous fishes leads to compensatory increases in overall abundance or changes in relative abundance of prey often termed "prey release" (Beddington and May, 1982; Goeden, 1982; Beddington, 1984; Grigg et al., 1984; Koslow et al., 1988). Russ (1991) and Jennings and Lock (1996), however, argued that the evidence for "prey release" on coral reefs is limited and equivocal. In 1978 Goeden suggested that depleting the abundance of *P. leopardus* may irreversibly alter the structure of the community of coral-reef fishes on the GBR, and yet, 20 years later, nothing is known about the trophic impacts of this fishery.

Coral reefs with different fishing histories represent valuable large scale manipulations of predator densities (Jennings and Polunin, 1997). In contrast to results of smaller-scale predator-removal experiments on site-attached coral reef fishes (Caley, 1993; Hixon and Beets, 1993; Carr and Hixon, 1995), large-scale "experiments" of predator removal by fishing have not demonstrated that predators play an important role in structuring fish communities. Several studies have compared prey populations on fished and unfished reefs but have found no evidence for corresponding changes in diversity or biomass of potential prey species (Bohnsack, 1982; Russ, 1985; Jennings and Polunin, 1997; Russ and Alcala, 1998a, 1988b). These studies, however, were hampered by a lack of dietary information necessary to determine exactly which prey fishes are important in the diet of the fished species. For coral reef piscivores, commercially important or otherwise, quantitative studies on food consumption, feeding strategies, and comprehensive lists of prey species are rare (but see Norris, 1985; Norris and Parrish, 1988; Sweatman, 1984; St John, 1999). Studies of predator-prey relationships on coral reefs

cannot progress further without knowledge of the prey consumed (Jennings and Polunin, 1997).

Information on the trophic biology of groupers is important for protecting the stocks and ensuring a healthy fishery for the future. Knowledge of the breadth of the diet and the specific habitat of important prey will indicate the resilience of stocks to changes in prey abundance or habitat destruction. Furthermore, baseline information on the diet of unfished populations is needed as a comparison for diets of fished populations. Such information should include some measure of spatial variation in regard to the diet. Fishing activities may alter the trophic ecology of the species targeted by altering the structure or the behavior of the wild population or both. For example, removing larger individuals of *P. leopardus* may alter the diet of the population because larger predators eat larger prey. St John (1999) found that the composition of the fish diet of *P. leopardus* on the GBR varied with size until predators attained 35 cm (TL). If this result applies to other geographic areas, fishing could affect the trophic impact of *P. leopardus* populations where legal minimum size limits are less than 35 cm (TL) or do not exist (e.g. Okinawa, Japan). On the GBR, however, such effects would be minimal because the legal minimum length is 38 cm (TL).

Fishing may also affect the behavior of piscivores. Line fishermen use baited hooks and throw bait into the water (termed burleying) to attract leopard coralgroupers to their fishing sites on the GBR. The use of bait to catch these fish could affect feeding behavior or feeding-related patterns of movement of *P. leopardus* in fished reefs and may have short- or long-term effects on the feeding ecology of *P. leopardus*.

Compared with commercially important fishes in many other ecosystems, relatively little is known about the diet of adult *P. leopardus* on the GBR, despite the huge numbers of *P. leopardus* fished from the reefs on the GBR annually (but see Choat, 1968; Goeden, 1978; Kingsford, 1992; St John, 1995, 1999). In all the existing studies, most samples were collected by spear, presumably to avoid possible dietary biases caused by line fishing methods. Thus, nothing is known about the trophic impacts associated with line fishing, which uses baited hooks at local fishing sites and which is by far the most common method used to catch *P. leopardus*. A comparison of stomach contents between *P. leopardus* caught by spear and those caught by hook and line at the same reefs will provide information on the selectivity of line fishing and trophic impact of this species.

Our study is the first to examine the diet of a large commercial species of coral reef fish at reefs in open and closed fishing zones. The feeding ecology of *P. leopardus*, a major coral reef piscivore, was examined at reefs zoned open and closed to fishing for eight years in the Cairns section of the GBRMP. Although the primary aim of this study was to describe and compare the diet of *P. leopardus* on reefs in two fishing zones, we pooled reefs and compared the diet by location to assess the natural spatial variability in the diet of *P. leopardus* in this region. Also, we assessed the size structure and diet of *P. leopardus* caught by two fishing methods: nonselective spear fishing (described in the "Materials

⁵ 1987. Central Zoning Information Pamphlet. GBRMPA, PO Box 1379, Townsville, Queensland 4810, Australia. Fold-out pamphlet with no pagination.

and methods" section) and baited line fishing. Fishing pressure was assessed by comparing differences in the size structure of populations of *P. leopardus* between fished and unfished reefs using size information from the catch at each reef as well as fishery independent estimates from visual surveys done just prior to sampling (Ayling and Ayling⁶; Brown et al.⁷).

Materials and methods

Study sites and sampling design

Two pairs of mid-continental shelf reefs at the southern end of the Cairns section of the GBR Marine Park were sampled in January and February 1992 (Table 1). Each pair comprised one reef that had been closed to fishing for eight years (Marine National Park (MNP) 'B') and another open to commercial and recreational fishing activities (General Use (GU) 'B'). These reefs will subsequently be referred to as "closed" and "open" zones. The northern pair, Wardle Reef (closed) and Nathan Reef (open), and the southern pair, Noreaster Reef (closed) and Potter Reef (open), were approximately 30 km apart, and the reefs within pairs were 5 and 10 km minimum distance from each other respectively (Fig. 1).

Collection of *P. leopardus*

Each reef was fished by line and spear simultaneously. Two teams of experienced fishermen collected fish by spear and line during daylight hours (0600–1800 h). Line fishermen worked in pairs from two small boats and used single hook rigs with pilchards (*Sardinops neopilchardus*) as bait. Spear fishermen worked in two pairs and hunted each fish as soon as it was seen in an attempt to obtain a sample representative of the size distribution of the actual population of coral trout. If two or more grouper were spotted simultaneously, the choice of the target was not based on size, and spear fishermen were deliberately not size selective. Spear fishing, however, has some inherent biases. Larger fish will be sighted first by spear fisher-

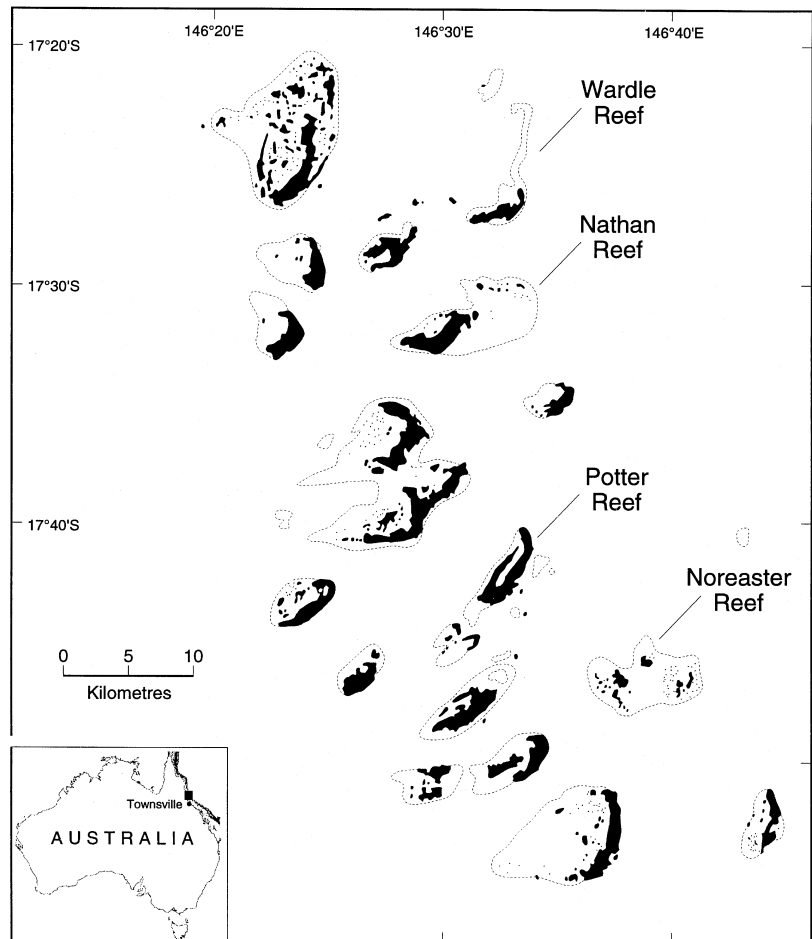


Figure 1

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

men because they will approach a diver more readily than smaller fish and are more conspicuous at distances (Kulbicki, 1998). These biases, however, should be similar at all reefs. Furthermore, the detection of camouflaged species, such as *P. leopardus*, increases with disturbance of the habitat when divers flush out these fish earlier at disturbed or fished reefs (Kulbicki, 1998), and this disturbance may increase the speared catch. Amount of catch, however, was not the focus of this study.

Samples were stored on ice in the small boats and frozen on board the mother ship (up to several hours later). Fork length (FL) of captured coral trout was measured to the nearest 0.5 cm.

Stomach contents

Only stomach contents were used in dietary analysis of *P. leopardus* (St John, 1995). The mouth and gills of each specimen were examined for regurgitated prey (Parrish, 1987). The stomach was opened and any contents were removed. Stomach contents were fixed in 10%

⁶ Ayling, A. M. and A. L. Ayling. 1992. Effects of fishing pilot study: visual surveys on Cairns section closed reefs that will be opened under the new zoning plan. Unpubl. report to GBRMPA, PO Box 1379, Townsville, Queensland 4810, Australia, 48 p.

⁷ Brown, I. W., L. C. Squire, C. Baltus, and M. Sellum. 1996. Effect of zoning changes on the fish populations of unexploited reefs—stage 2: post-opening assessment. Unpubl. report to GBRMPA, PO Box 1379, Townsville, Queensland 4810, Australia, 40 p.

formal calcium acetate (FCA), a buffered formalin solution (approximately 10 mL of FCA for every gram of stomach content) for a minimum of seven days and then stored in 70% ethanol.

Stomach contents were classified broadly into natural prey or bait. All bait in our study were pilchards (*Sardinops neopilchardus*), which does not occur naturally in the area. Every natural prey item was identified under low magnification to the lowest taxonomic group possible (St John, 1995). Fish were identified following Randall et al. (1990) by using several keys (Allen, 1975; Masuda et al., 1984; Smith and Heemstra, 1986; Myers, 1991).

Families of prey fishes were classified by the area where they were most commonly found (Randall et al., 1990; senior author, personal obs.). Prey fishes from the “demersal reef substrata” habitat swam around and above coral, but used it for shelter (e.g. Pomacentridae and Scaridae). Fishes categorized as using the “benthic reef substrata” habitat were benthic dwellers that remained very close to the substrata (e.g. Blenniidae). Fishes categorized as in the “adjacent sands” habitat dwelled over, on, or within the sandy areas adjacent to reefs (e.g. Mullidae). Pelagic fishes in the “midwater” habitat were found from the water surface to a depth of approximately 1 m over the reef (e.g. Clupeidae and Caesionidae).

Wet weights of the stomach contents were measured after preservation in 70% ethanol. Before weighing, the stomach contents were emptied into a sieve (St John, 1995) and shaken or sponged, or both shaken and sponged, to remove excess surface liquid (Parker, 1963). Wet weights of stomach contents were excluded from weight analyses when there was evidence of regurgitation of food from the stomach, (e.g. digested prey in the mouth or gills or an empty stomach that was stretched or everted), but this condition was rare.

Generally, weights of digested prey reflected prey size and therefore were a useful measure of the diet (St John, 1995). Less than 14% of the prey was highly digested, and such fish could not be separated for weighing. In these cases, individual prey weights were estimated from total weights of the stomach sample, taking into account the digestion stage and the size (when known) of all individuals in the sample.

The contents of the stomach were assumed to represent daily feeding in *P. leopardus* because prey items were mostly digested after 24 hours (St John, 1995).

Data analyses

Kolmogorov-Smirnov (K-S) (Sokal and Rohlf, 1981) tests were used to compare size structures of leopard coral-grouper populations on reefs on both closed and open zones to fishing.

Fisher's exact tests were used to compare the frequency of prey items in the diet because the categories (fishing zones, reefs, habitats, fishing methods and families of prey) were all nominal (Mehta and Patel, 1992). Because Fisher's exact tests do not compare nested data sets, comparisons within zones or locations used pooled data. Data from reefs were pooled when they did not differ signifi-

cantly (i.e. $P > 0.05$). Because the differences in number of prey per family in the diet was statistically marginal in reefs in the open zone ($P = 0.056$), we used the $P = 0.01$ level of significance to compare open and closed zones when reefs were pooled. Also, the $P = 0.01$ level of significance was used when sample sizes were small (e.g. in the comparison between the natural diet of line-caught and speared fish).

An independent *t*-test was used to compare the mean number of families consumed in each fishing zone. Prior to analysis, the variances were tested for homogeneity by using Cochran's test, which was not significant (Cochran's test statistic = 0.84, $P > 0.05$). Because the null hypothesis was not rejected, the power of the test to detect specified differences was calculated following Cohen (1988). In the calculations of power, the sample means were assumed to be representative of the parametric means for each treatment group. A nonsignificant result was considered to be inconclusive unless the power of the test ($1 - \beta$) was > 0.80 .

The index of relative importance (IRI) determined for the diet of *P. leopardus* was

$$IRI = 0.5 \times (\% \text{ prey number} + \% \text{ prey weight}).$$

This measure was used in Schoener's *a* index of dietary overlap (Schoener, 1970) for pair-wise comparisons of the diet of *P. leopardus* between reefs within each of the two fishing zones. Dietary overlaps were classified by using Langton's (1982) scale: low 0–0.29, medium 0.30–0.59, and high ≥ 0.60 .

Results

Size structure of *P. leopardus*

In total, 672 *P. leopardus*, ranging in size from 13 to 58.5 cm FL, were collected by line and spear from the four reefs (Fig. 2) and fewer *P. leopardus* were caught by line ($n = 85$) than by spear ($n = 587$) (Table 1).

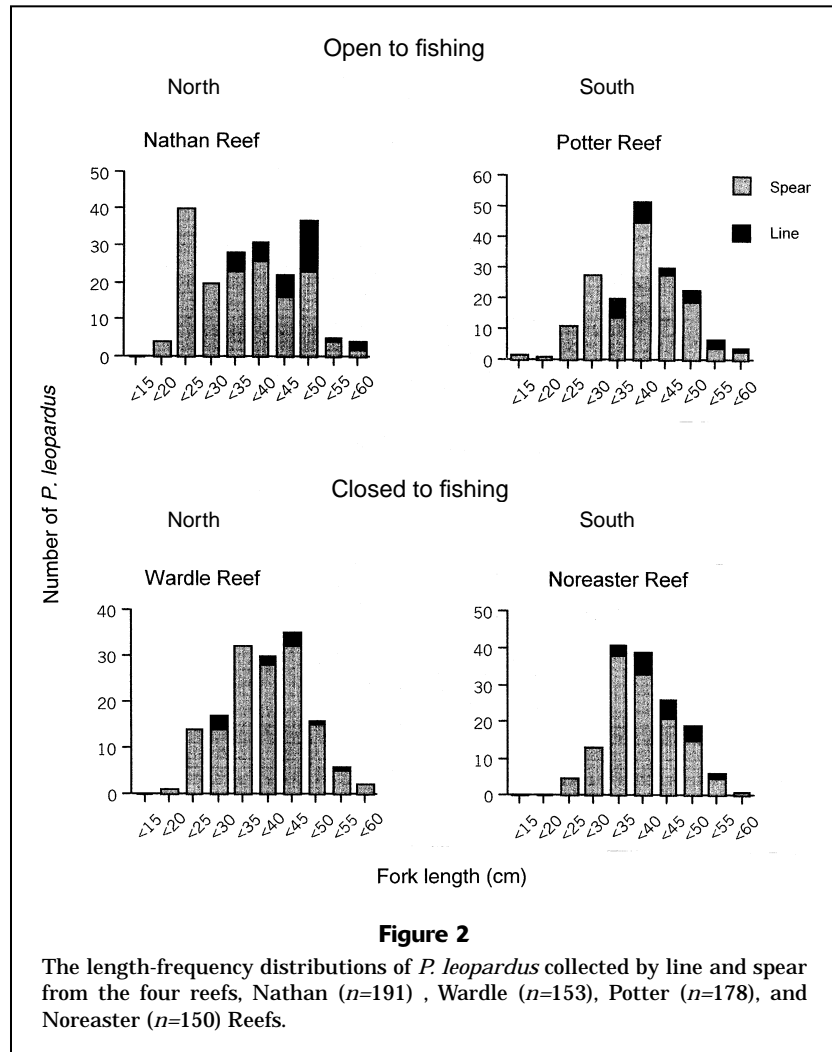
The speared catch was considered to represent populations of *P. leopardus* on reefs because spear fishermen were deliberately not size selective in this study. The size-structure of the line catch was significantly larger than that of the speared catch ($D_{\max} = 0.243$, K-S $P < 0.01$) when samples from the four reefs were pooled (Fig. 2). Thus, line caught *P. leopardus* were excluded from further analyses of population size structure.

When reef pairs within locations were compared, the size structure of the speared catch on the open reefs differed significantly from the closed reefs (north: $D_{\max} = 0.20$, K-S, $n = 143$, $P < 0.01$; south: $D_{\max} = 0.13$, K-S, $n = 131$, $P < 0.05$; Fig. 2), but these zonal patterns differed between locations. The size structure of the speared catch differed significantly between the two open reefs ($D_{\max} = 0.19$, K-S, $n = 155$, $P < 0.01$, Fig. 2); the proportion of larger fish (> 35 cm FL) was 45% at Nathan Reef and 64% at Potter Reef compared with 57% at each of the closed reefs. The results of our study did not demonstrate an effect of fishing on size structure between open and closed reefs.

Stomach contents of fish caught by the two methods

Although the proportion of *P. leopardus* with empty stomachs did not differ between the line-caught and speared catch (Fisher's exact test_[1]=0.12, *P*=0.81), the proportion of

the catch with natural prey in their stomachs was significantly higher in speared fish (Fisher's exact test_[1]=7.8, *P*=0.01) (Table 2). As expected, a much higher proportion of line-caught fish had consumed the bait *S. neopilchardus* (Table 2); however, five *P. leopardus* that were speared at sites where line fishing had not occurred, also had consumed bait.



Assessment of natural diet

Type of prey *Plectropomus leopardus* on the four reefs fed mostly upon fish, some crustaceans, and a few cephalopods (Table 3). Six pieces of hard coral that were found in the stomachs of *P. leopardus* at three reefs were considered to have been ingested incidentally with prey and were excluded from the analysis. The proportions of fish, crustaceans, and cephalopods in the diet of *P. leopardus* did not vary significantly among the four reefs (Fisher's exact test_[6]=4.84, *P*=0.56, Table 3). *Plectropomus leopardus* were highly piscivorous. Fish accounted for 95.7% of their diet.

General fish diet Of the 468 prey fish in the diet of *P. leopardus*, 40% were identified to 22 families (Table 4). The abundance of fish prey in a family ranged from one (nine families, Table 4) to 47 individuals (Pomacentridae, Table 4), and total digested prey weights ranged from 0.12 g to 730 g per family (Table 5). The average weight of an individual prey item was 13.7 g.

Two families, Pomacentridae and Labridae, dominated the diet by number (Table 4) and by weight (Table 5) and were the most important prey of *P. leopardus* (*IRI*=27.8% and *IRI*=20.6% respectively, Table 6). Three families, Scaridae, Clupeidae, and Caesionidae, were the next most important prey, each representing about 10% of the diet by *IRI* and at least

Table 1

Summary of 672 *P. leopardus* collected from the Cairns section of the Great Barrier Reef Marine Park by line and spear fishing, including location of the reef pairs, names of reefs, their fishing status, and date of sampling.

Location of reef pair	Reef pair	Fishing zone	Date in 1992	Sample size (<i>n</i>)		
				Line	Spear	Total
North	Nathan	open	20–22 Jan	33	158	191
	Wardle	closed	23–25 Jan	10	143	153
South	Potter	open	24–26 Feb	23	155	178
	Noreaster	closed	27–29 Feb	19	131	150

Table 2

Stomach contents of *P. leopardus* caught by the two fishing methods. *Plectropomus leopardus* are classified into four groups by the contents of their stomachs: natural prey only, natural prey and bait, bait only, and no contents (empty). Number of *P. leopardus* and the percentage of the total catch are recorded for each group.

Stomach contents	Fishing method			
	Line		Spear	
	Number	%	Number	%
Natural prey only	36	42.4	342	58.2
Natural prey and bait	2	2.3		
Bait only	14	16.5	5	0.8
Empty	33	38.8	240	40.9
Total	85		587	

Table 3

Number of prey fish, crustaceans, and cephalopods found in *P. leopardus* collected from Nathan, Wardle, Potter, and Noreaster Reefs. Numbers of predators with natural prey in their stomachs and empty stomachs in each sample are included.

Prey groups	Reefs				Total
	Nathan	Potter	Wardle	Noreaster	
Fish	121	126	118	103	468
Crustaceans	2	2	6	3	13
Cephalopods		3	2	3	8
Unidentified	2	1	2	1	6
Total prey	125	132	128	110	495
Empty stomachs	85	76	53	59	273
<i>P. leopardus</i> with prey	92	102	100	86	380

Table 4

Number of prey per family identified in the fish diet of *P. leopardus* collected from Nathan, Wardle, Potter, and Noreaster Reefs. Total numbers of prey in families are included and expressed as percentages of the total diet. Total numbers of identified fish, unidentified fish, families of prey, and predator individuals are included. Small-size schooling fishes are underlined.

Prey families	Reefs open to fishing		Reefs closed to fishing		Total	
	North (Nathan)	South (Potter)	North (Wardle)	South (Noreaster)	Number	%
Pomacentridae	12	9	9	17	47	25.3
Labridae	9	8	9	11	37	19.9
<u>Clupeidae</u>	11	9	6	5	31	16.6
Caesionidae		9	1	2	12	6.4
Synodontidae	4	3	1	2	10	5.4
Scaridae	4	2		2	8	4.3
Blenniidae	1	1	5		7	3.8
Acanthuridae	2	3	1		6	3.2
Apogonidae	1	5			6	3.2
Serranidae	3	1		1	5	2.1
<u>Engraulidae</u>	2		1		3	1.6
Fistulariidae	1	1	1		3	1.6
Gobiidae	2				2	1.1
Balistidae			1		1	0.5
Creedidae			1		1	0.5
Lutjanidae		1			1	0.5
Monacanthidae	1				1	0.5
Nemipteridae	1				1	0.5
Platycephalidae			1		1	0.5
Plesiopidae			1		1	0.5
Scorpaenidae	1				1	0.5
Siganidae			1		1	0.5
Identified fish	55	52	39	40	186	
Unidentified fish	66	74	79	63	282	
Number of families	15	12	14	7	22	
No. of <i>P. leopardus</i> with prey	92	102	100	86	380	

Table 5

Summed digested weights (in g) of prey in each family in the diet of *P. leopardus* collected from Nathan, Wardle, Potter, and Noreaster Reefs. Total weights of prey in families are included and expressed as percentages of the total diet. Total weight of prey at each reef and number of predator individuals with prey are included. Small-size schooling fishes are underlined.

Prey families	Reefs open to fishing		Reefs closed to fishing		Total	
	North (Nathan)	South (Potter)	North (Wardle)	South (Noreaster)	Number	%
Pomacentridae	235.1	85.3	195.0	215.1	730.4	28.7
Labridae	159.7	58.6	140.5	148.5	507.3	19.9
Scaridae	230.0	127.8		79.7	437.5	17.2
Caesionidae		124.6	1.0	133.3	258.9	10.2
Scorpaenidae	116.5				116.5	4.6
Synodontidae	23.4	58.3	5.6	12.0	99.4	3.9
Blenniidae	0.6	4.3	82.4		87.3	3.4
Acanthuridae	38.7	29.9	16.5		85.1	3.3
Nemipteridae	82.5				82.5	3.2
Serranidae	37.4	10.8		9.8	58.0	2.3
<u>Clupeidae</u>	12.1	10.4	5.9	10.3	38.7	1.5
Plesiopidae			13.2		13.2	.5
Fistulariidae	2.6	1.5	2.8		6.8	.3
Apogonidae	1.0	5.7			6.7	.3
<u>Engraulidae</u>	1.4		4.8		6.2	.2
Balistidae			2.3		2.3	<.1
Gobiidae	2.2				2.2	<.1
Creedidae			1.0		1.0	<.1
Platycephalidae			0.68		0.7	<.1
Siganidae			0.33		0.3	<.1
Lutjanidae		0.2			0.2	<.1
Monacanthidae	0.1				0.1	<.1
Total weight	943.5	517.4	472.0	608.8	2541.7	
No. of <i>P. leopardus</i> with prey	92	102	100	86	380	

10% by one of the other dietary measures (Tables 4–6). The body sizes of these prey families were very different, e.g. 31 Clupeidae weighed 39 g, whereas eight Scaridae weighed 438 g (Tables 4 and 5). The remaining 17 families of prey accounted for approximately one quarter of the diet (summed IRI=24.0%, Table 6). Only four families, Pomacentridae, Labridae, Clupeidae, and Synodontidae, were eaten by *P. leopardus* at every reef.

Comparisons between line-caught and speared samples In the diet of the smaller sample caught by line, 21 fish were identified into eight families that were a subset of the 22 prey families found in the speared sample (Table 7). The dietary composition of line-caught *P. leopardus* did not differ significantly from the speared catch (at $P=0.01$ level of significance, Table 8, see “Materials and methods” section for explanation). When classified by their characteristic habitat (Table 9), however, the number of prey differed significantly between fishing methods (Fisher’s exact test_[3]=18.7, $P=0.0003$). The proportion of midwater, pelagic prey in the diet was higher in the line catch (67%) than in the speared catch (21%), which was dominated by prey living in the demersal habitat (66% of the diet).

Because all prey families found in the line-caught *P. leopardus* also occurred in speared specimens, prey fishes obtained by the two types of gear identified from each reef were pooled for further analyses to increase the sample size.

Comparisons among reefs and zones The number of families in the diet of *P. leopardus* varied among reefs and ranged from seven families at Noreaster Reef to 15 at Nathan Reef (Table 4). There was no detectable difference in the number of families in the diet of *P. leopardus* between fishing zones ($t_{[2]}=1.380$, $P>0.20$, $1-\beta < 0.33$).

Dietary overlap was high between reefs within fishing zones (open reefs: Schoener $a=0.68$; closed reefs: Schoener $a=0.68$) and between fishing zones (Schoener $a=0.65$) when reefs were pooled. IRI values were higher in Pomacentridae and Labridae at the closed reefs than at the open reefs, whereas the opposite pattern occurred for Scaridae and Synodontidae (Table 6).

The number of prey per family in the diet of *P. leopardus* varied significantly among the four reefs (Table 8). This variation, however, could not be related to the zoning of reefs because the diet of *P. leopardus* did not differ

Table 6

The index of relative importance (IRI) calculated for each fish family of prey and expressed as a percentage of the total for all identified fish families in the diet of *P. leopardus*, grouped by reef, fishing zone, and total. Small-size schooling fishes are underlined.

Prey families	Reefs open to fishing			Reefs closed to fishing			Total
	North (Nathan)	South (Potter)	Both	North (Wardle)	South (Noreaster)	Both	
Pomacentridae	23.4	16.9	20.8	32.2	38.9	35.4	27.8
Labridae	16.6	13.3	15.4	26.4	25.9	26.0	20.6
Scaridae	15.8	14.3	15.0		9.0	4.9	9.8
<u>Clupeidae</u>	<u>10.6</u>	<u>9.7</u>	<u>10.1</u>	<u>8.3</u>	<u>7.1</u>	<u>7.7</u>	<u>8.9</u>
Caesionidae		20.7	8.5	1.4	13.4	8.1	8.9
Synodontidae	4.9	8.5	6.1	1.9	3.5	2.7	4.7
Blenniidae	0.9	1.4	1.1	15.1		7.0	4.4
Acanthuridae	3.9	5.8	4.7	3.0		1.4	3.2
Serranidae	4.7	2.0	3.5		2.0	1.1	2.2
Scorpaenidae	7.1		4.4				1.8
Apogonidae	1.0	5.4	3.0				1.6
Nemipteridae	5.3		3.3				1.3
Fistulariidae	1.0	1.1	1.1	1.6		0.8	0.9
<u>Engraulidae</u>	<u>1.9</u>		<u>1.0</u>	<u>1.8</u>		<u>0.8</u>	<u>0.9</u>
Plesiopidae				2.7		1.2	0.7
Gobiidae	1.9		1.0				0.5
Balistidae				1.5		0.7	0.4
Creedidae				1.4		0.7	0.3
Platycephalidae				1.3		0.7	0.3
Siganidae				1.3		0.6	0.3
Lutjanidae		1.0	0.5				0.2
Monacanthidae	0.9		0.5				0.2
No. of <i>P. leopardus</i> with prey	92	102	194	100	86	186	380

significantly between fishing zones (at $P=0.01$ level of significance, Table 8, see "Materials and methods" section for explanation). Furthermore, when pooled by location, the numerical composition of the diet of *P. leopardus* on southern and northern reefs differed significantly (Table 8).

When categorized by their characteristic habitat (Table 9), the number of prey did not differ significantly among reefs (Fisher's exact test_[9]=14.7, $P=0.10$) nor between fishing zones (Fisher's exact test_[3]=3.3, $P=0.35$, Table 10). Fishes in the majority of prey families ($n=11$) lived in the demersal reef habitat (Table 9), which was the most important source of prey for *P. leopardus* (61% by number, IRI=67%, Table 10). Prey in three or four families lived in each of the benthic reef, midwater, and adjacent sandy habitats (Table 9). The large number of midwater prey at Potter Reef (Table 10) reflected the relatively large number of Caesionidae consumed at this reef (Table 4).

Discussion

Overall, the diets of *P. leopardus* from reefs in the two fishing zones were not dissimilar. Dietary overlap was high between *P. leopardus* from the reefs with open zones and reefs with closed zones for eight years. When com-

pared to natural variation in diet among *P. leopardus* on the GBR, these values of overlap were very high because there was less similarity in the diet among regional populations of *P. leopardus* (Schoener a value of dietary overlap ranged from 0.26 to 0.42, St John, 1995) and at one reef sampled over time (Schoener a value of dietary overlap ranged from 0.44 to 0.84, St John, 1995). Generally, feeding behavior of *P. leopardus* was similar between fishing zones.

The lack of dietary differences between *P. leopardus* on open and closed reefs is consistent with the lack of meaningful trends in comparing the size and age structures of these populations. Using the catch of both fishing methods, Brown et al.⁷ found a slightly higher abundance of legal-size (>38 cm TL) leopard coral grouper on the closed reefs, as well as a greater proportion of older fish (4+ year class). But, fishing affected the size and age structure of populations on the two open reefs very differently; Nathan Reef showed a large recruitment of the one year class (Brown et al.⁷) and differed from all other reefs. In visual surveys of *P. leopardus* at the four reefs, Brown et al.⁷ detected a greater density of larger *P. leopardus* on closed reefs. In contrast, Ayling and Ayling⁶ found no differences between fishing zones in the density, average length, and recruitment of *P. leopardus* when surveying the same reefs

just prior to Brown et al.⁷ Because decreases in abundance and size of populations are widely recognized as evidence of fishing pressure (Russ, 1991; Jennings and Lock, 1996), fishing pressure between the two zones in this study did not appear to vary.

Eight years of effective protection from substantial fishing pressure should have produced detectable differences in the structure of populations of *P. leopardus* on these closed and open reefs. Generally, studies on the GBR have shown an increase in average size of *P. leopardus* popula-

Table 7

Abundance (in number and percentage) of prey belonging to families in the diet of *P. leopardus* caught by the two fishing methods. Families of fishes living in the midwaters are underlined.

Prey families	Line		Spear		Total
	Number	%	Number	%	
Pomacentridae	2	9.5	45	27.3	47
Labridae	1	4.8	36	21.8	37
<u>Clupeidae</u>	<u>11</u>	<u>52.5</u>	<u>20</u>	<u>12.1</u>	<u>31</u>
<u>Caesionidae</u>	<u>1</u>	<u>4.8</u>	<u>11</u>	<u>6.6</u>	<u>12</u>
Synodontidae	2	9.5	8	4.8	10
Scaridae			8	4.8	8
Blenniidae			7	4.2	7
Acanthuridae	1	4.8	5	3.0	6
Apogonidae			6	3.6	6
Serranidae	1	4.8	4	2.4	5
<u>Engraulidae</u>			<u>3</u>	<u>1.8</u>	<u>3</u>
<u>Fistulariidae</u>	<u>2</u>	<u>9.5</u>	<u>1</u>	<u>0.6</u>	<u>3</u>
Gobiidae			2	1.2	2
Balistidae			1	0.6	1
Creedidae			1	0.6	1
Lutjanidae			1	0.6	1
Monacanthidae			1	0.6	1
Nemipteridae			1	0.6	1
Platycephalidae			1	0.6	1
Plesiopidae			1	0.6	1
Scorpaenidae			1	0.6	1
Siganidae			1	0.6	1
Total	21		165		186
No. of <i>P. leopardus</i> with prey	38		342		380

Table 8

Results of Fisher exact tests for the number of prey per family. Information in brackets is Fisher's exact test statistic, degrees of freedom (df), and exact probability levels (*P*). Significance of tests is denoted by ** for $P < 0.01$ and * for $P < 0.05$, and ns is nonsignificant. Comparisons between fishing zones and fishing methods are tested at $P = 0.01$ level of significance (see "Materials and methods" section for explanation).

Dietary differences among <i>P. leopardus</i>				
Fishing zones		Locations		Fishing methods
Open vs. closed (reefs pooled)		North vs. south (reefs pooled)		Spearred vs. line caught (reefs pooled)
ns (28.3, df= 21, $P=0.046$)		*		ns (34.2, df=21, $P=0.034$)
(29.0, df=21, $P=0.040$)		(23.2, df=20, $P=0.135$)		(19.8, df=11, $P=0.155$)
Open reefs	Closed reefs	North reefs	South reefs	Among 4 reefs
*	ns	ns	ns	**
(22.5, df=16, $P=0.056$)	(18.5, df=15, $P=0.908$)	(23.2, df=20, $P=0.135$)	(19.8, df=11, $P=0.155$)	(75.2, df=63, $P=0.007$)

tions on reefs after closure (summarized in Williams and Russ, 1994). Also, population density of *P. leopardus* has differed in other closed-versus-open fishing zones in the Marine Park (Ayling et al., 1991). In contrast, the size structure of populations of *P. leopardus* on four reefs in the GBR showed no effect of protection from fishing after 3–4 years of reef closure (Ferreira and Russ, 1995). Possible reasons for an absence of the effects of fishing include migration by *P. leopardus* among reefs and small differences in the actual fishing pressure between open and closed zones. Other studies on movement of *P. leopardus* indicate that migration of 5–10 km between reefs would be highly unlikely (Davies, 1995; Zeller, 1997). Of a tagged population of 4627 *P. leopardus* on five reefs on the GBR, only 1% moved between reefs in a period of 22 months and only 2% travelled distances of 5–7.5 km (Davies, 1995). Fishing pressure was not measured on any of our four reefs during the eight years of protection, so it is possible that fishing pressure was low on the open reefs; however it seems more likely that the “closed” reefs were fished illegally.

Such violations are thought to be relatively common on the GBR, and illegal fishing of these prized food fishes is probably widespread throughout tropical waters. Another documented example of violations of a fishing regulation for a large grouper is found in the Florida Keys, where bans on harvesting Nassau grouper (*Epinephelus striatus*) appeared to be ineffective (Sluka and Sullivan, 1998).

The diet of *P. leopardus* in our study did not differ between fishing zones when families of prey were assessed by either their relative importance in the diet (dietary overlap) or their number of prey. Patterns between fishing zones occurred in four of the 22 families but were considered weak because they were not detected statistically. Pomacentridae and Labridae, which ranked first and second respectively at all four reefs, were more important in the diet in the closed reefs, whereas Scaridae and Synodontidae were more important in the diet on open reefs. Information on prey availability on each reef may explain these results. Lastly, proportions of prey consumed from each of the four habitats were similar among reefs, suggesting that feeding behavior of *P. leopardus* did not differ among these reefs.

Two aspects of the diet of *P. leopardus* differed between the locations of the reef pairs. Rare prey families, which occurred only once in the diet in the entire study, were more common at the two northern reefs (eight families) than at the southern pair (one family). Also, *P. leopardus* from the two southern reefs consumed more of the large schooling Caesionidae. However, location of the reefs alone may not explain these patterns because reef location is confounded with time of sampling in our study. The southern pair of reefs was sampled one month after the northern pair.

Similar to other dietary studies of adult *P. leopardus* on the GBR (Choat, 1968; Goeden, 1978; Kingsford, 1992; St John 1995, 1999), our study confirmed that leopard coralgroupers are highly

Table 9

The 22 families of prey classified into four broad habitats on the reef: demersal reef (associated with substrata), benthic reef (strongly associated with reef substrata), midwater and adjacent sands.

Demersal	Benthic	Midwater	Adjacent sands
Acanthuridae	Blenniidae	Caesionidae	Creedidae
Apogonidae	Gobiidae	Clupeidae	Nemipteridae
Balistidae	Scorpaenidae	Engraulidae	Platycephalidae
Labridae		Fistulariidae	Synodontidae
Lutjanidae			
Monacanthidae			
Pomacentridae			
Plesiopidae			
Scaridae			
Serranidae			
Siganidae			

Table 10

Number of prey in the diet of *P. leopardus* on the four reefs in each of the four habitats (demersal reef, benthic reef, midwater, and adjacent sands). Total number and percentage of prey as well as importance of prey in the diet (IRI, index of relative importance) in each habitat are included.

Habitat	Open		Closed		Total		IRI %
	North (Nathan)	South (Potter)	North (Wardle)	South (Noreaster)	Number	%	
Demersal reef	32	29	22	31	114	61.3	67.0
Benthic reef	4	1	5	0	10	5.4	6.6
Midwater	14	19	9	7	49	26.3	19.7
Adjacent sands	5	3	3	2	13	7.0	6.7
Total	55	52	39	40	186		100

piscivorous. Thus, unlike other less piscivorous coral reef serranids (Hobson, 1965; Randall, 1965; Harmelin-Vivien and Bouchon, 1976; Shpigel and Fishelson, 1989), adult *P. leopardus* rely almost entirely on one general type of food (but juveniles consume crustaceans, St John, 1999). Also, nearly half of their diet (IRI=48.4%) comprised just two families of fishes, Pomacentridae and Labridae, but this finding does not suggest that the food supply of *P. leopardus* was limited. *Plectropomus leopardus* have been reported to consume more than 20 species in each of these two families (St John, 1995), which are highly diverse and abundant on coral reefs. On the GBR, Pomacentridae, with some 120 species, is the most numerically abundant family, and Labridae represents the second most speciose family (Randall et al., 1990). Therefore, the diet of *P. leopardus* was not dependent on a few species.

The variety of prey fishes in the diet of *P. leopardus* reflects the groupers large home range (Samoilys, 1997; Zeller, 1997) that includes several habitats (Goeden, 1978; Kingsford, 1992; Samoilys, 1997). *Plectropomus leopardus* consumed fishes in families that lived in all four broad habitats on coral reefs: adjacent sands, midwater, benthic reef substrata, and demersal reef substrata. Yet, prey from the demersal reef environment and the midwaters were six times more important than prey in the other two habitats. The diverse and abundant families of fishes that live on or over adjacent sands, or dwell among the benthic reef substrata (e.g. Gobiidae and Blenniidae) were not important food for adult *P. leopardus*. Similarly, piscivores reported from coral reefs elsewhere have usually focused on prey in reef habitats. In the Caribbean, tethered prey consistently disappeared from sites close to areas of natural reef rather than from areas of adjacent sediment (Shulman, 1985), and rates of encounter with predators for surgeonfishes in bottles were highest at reef edges compared with other sediment habitats (Sweatman and Robertson, 1994).

Lastly, the results of our study suggest several differences in the catch and diet of *P. leopardus* caught by the two fishing methods. Such information is useful for managers when considering the impacts of different types of fishing methods on the fish population. Line fishing catches larger fish than nonselective spear fishing; however nonselective spear fishing probably never occurs in the real fishery. Based on the comparison of line catch and spear catch, baited lines appear to attract a higher proportion of hungry *P. leopardus* to common fishing sites, but predators may leave the site after they have eaten bait. Therefore, line fishing can affect the trophic ecology of *P. leopardus* reef-wide, even when it is concentrated at just a few sites on reefs. Also, line fishing may alter patterns of movement of *P. leopardus* temporarily, and such opportunistic behavior will be difficult to detect in movement studies on this species (e.g. Samoilys, 1997; Zeller, 1997). Thus, when reefs are partitioned into different fishing zones, line fishing could facilitate the movement of *P. leopardus* across reserve boundaries from protected areas. In one study on the GBR, *P. leopardus* had low flux rates across reserve boundaries (Zeller and Russ, 1998). Another, more tentative, result of our study is that line-

caught fish appear to eat more midwater pelagic fishes, which suggests that line fishermen or the methods used in line fishing target *P. leopardus* hunting this prey. Whether line fishermen chose sites where pelagic schooling fishes congregate (e.g. near the reef edge) or whether pelagic prey are attracted to a fishing site after fishermen burley the waters, is uncertain.

In conclusion, eight years after reefs have been closed to fishing, no differences that could be linked to zoning were detected in size structure of populations and diets of *P. leopardus*. Results of this dietary study, however, can offer some insights for the management of the *P. leopardus* fishery. Even though fish are the dominant food of this predator, and the main fish prey are associated with the coral reef substrata, *P. leopardus* are not dependent on a narrow range of species for food. A diverse mixture of Pomacentridae and Labridae species represents nearly half of their diet, and overall, the diet of *P. leopardus* is sufficiently broad to be resilient to the depletion of several species of prey.

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Literature cited

- Allen, G. R.
1975. Damselfishes of the South Seas. TFH Publications, Neptune City, NJ, 271 p.
- Ayling, A. M., A. L. Ayling, and B. D. Mapstone.
1991. Possible effects from protection by fishing pressure on recruitment rates of the coral trout (*Plectropomus leopardus*: Serranidae). In Recruitment processes (D. A. Hancock, ed.), p. 210–215. Australian Society for Fish Biology Workshop, Hobart, August 1991.
- Beddington, J. R.
1984. The responses of multispecies systems to perturbations. In Exploitation of marine communities (R. M. May, ed.), p. 209–225. Springer-Verlag, Berlin.
- Beddington, J. R., and R. M. May.
1982. The harvesting of interacting species in a natural ecosystem. *Sci. Am.* 247:42–49.
- Bohnsack, J. A.
1982. Effects of piscivorous predator removal on coral reef fish community structure. In Gutshop '81: fish food habit studies (G. M. Caillet and C. A. Simenstad, eds.), p. 258–267. Wash. Sea Grant Publ., Seattle, WA.
- Bohnsack, J. A., D. E. Harper and D. B. McClellan.
1994. Fisheries trends from Monroe County, Florida. *Bull. Mar. Sci.* 54:982–1018.
- Caley, M. J.
1993. Predation, recruitment and the dynamics of communities of coral-reef fishes. *Mar. Biol.* 117:33–43.

- Carr, M. H. and M. A. Hixon.
1995. Predation effects on early post-settlement survivorship of coral reef fishes. *Mar. Ecol. Prog. Ser.* 124:31–42.
- Choat, J. H.
1968. Feeding habits of and distribution of *Plectropomus maculatus* Serranidae at Heron Island. *Proc. R. Soc. Qd.* 80(2):13–18.
- Cohen, J.
1988. Statistical power analysis for the behavioral sciences (2nd ed.). Lawrence Erlbaum Associates, Hillsdale, NJ, 567 p.
- Craik, G. J. S.
1981. Underwater survey of coral trout *Plectropomus leopardus* Serranidae populations in the Capricornia Section of the Great Barrier Reef Marine Park. *Proc. 2nd Int. Cor. Reef Symp.* 1:54–58.
- Davies, C.
1995. Patterns of movement of three species of coral reef fish on the Great Barrier Reef. Unpubl. Ph. D. diss., Dept. of Marine Biology, James Cook University of North Queensland, Australia, 170 p.
- Ferreira, B. P., and G. R. Russ.
1995. Population structure of the leopard coral grouper, *Plectropomus leopardus*, on fished and unfished reefs off Townsville, Central Great Barrier Reef, Australia. *Fish. Bull.* 93:629–642.
- Goeden, G. B.
1978. A monograph of the coral trout *Plectropomus leopardus*. *Res. Bull. Qld. Fish. Ser.* 1:1–42.
1982. Intensive fishing and a 'keystone' predator species: ingredients for community instability. *Biol. Conserv.* 22:273–281.
- Grigg, R. W., J. J. Polovina, and M. J. Atkinson.
1984. Model of a coral reef ecosystem. III: Resource limitation, community regulation, fisheries yield and resource management. *Coral Reefs* 3:23–27.
- Harmelin-Vivien, M. L., and C. Bouchon.
1976. Feeding behavior of some carnivorous fishes (Serranidae and Scorpaenidae) from Tulear (Madagascar). *Mar Biol* 37:329–340.
- Heemstra, P., and J. Randall.
1993. FAO species catalogue. Vol 16: Groupers of the world family Serranidae, subfamily Epinephelinae: an annotated and illustrated catalogue of grouper, rockcod, hind, coral grouper and lyretail species known to date. FAO Fisheries Synopsis, FAO, Rome, 383 p.
- Hixon, M. A.
1991. Predation as a process structuring coral-reef fish communities. *In* The ecology of fishes on coral reefs (P. F. Sale, ed.), p. 475–508. Academic Press, San Diego, CA.
- Hixon, M. A. and J. P. Beets.
1993. Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecol. Monogr.* 63(1):77–101.
- Hobson, E. S.
1965. Diurnal-nocturnal activity of some inshore fishes in the Gulf of California. *Copeia* 1965:291–302.
- Jennings, S., and J. M. Lock.
1996. Population and ecosystem effects of reef fishing. *In* Reef fisheries (N. V. C. Polunin and C. M. Roberts, eds.), p. 193–218. Fish and fisheries series. Chapman and Hall, London.
- Jennings, S., and N. V. C. Polunin.
1997. Impacts of predator depletion by fishing on the biomass and diversity of non-target reef fish communities. *Coral Reefs* 16:71–82.
- Kingsford, M. J.
1992. Spatial and temporal variation in predation on reef fishes by coral trout (*Plectropomus leopardus*, Serranidae). *Coral Reefs* 11:193–198.
- Koslow, J. A., F. Hanley, and R. Wicklund.
1988. Effects of fishing on reef fish communities at Pedro Bank and Port Royal Cays, Jamaica. *Mar. Ecol. Progr. Ser.* 43:210–212.
- Kulbicki, M.
1998. How the acquired behaviour of commercial reef fishes may influence the results obtained from visual censuses. *J. Exp. Mar. Biol. Ecol.* 222:11–30.
- Langton, R. W.
1982. Diet overlap between Atlantic Cod, *Gadus morhua*, silver hake, *Merluccius bilinearis*, and fifteen other north-west Atlantic finfish. *Fish. Bull.* 804:745–759.
- Masuda, H., K. Amaoka, C. Araga, T. Uyeno, and T. Yoshino.
1984. The fishes of the Japanese archipelago. Tokai Univ. Press, Tokyo, 374 p.
- Mehta, C., and N. Patel.
1992. StatXact. CYTEL Software Corporation, Cambridge, 442 p.
- Myers, R. F.
1991. Micronesian reef fishes: a practical guide to the identification of the inshore marine fishes of the tropical and central Pacific, 2nd ed. Coral Graphics, Barrigada, Guam.
- Norris, J. E.
1985. Trophic relationships of piscivorous coral reef fishes from the Northwestern Hawaiian Islands. M.S. thesis, Univ. Hawaii, Honolulu, HI, 71 p.
- Norris, J. E. and J. D. Parrish
1988. Predator-prey relationships among fishes in pristine coral reef communities. *Proc. 6th Intl. Coral Reef Symp.* 2:107–113.
- Parker, R. R.
1963. Effects of formalin on length and weight of fishes. *J. Fish. Res. Board Canada* 20(6):1441–1455.
- Parrish, J. D.
1987. The trophic biology of snappers and groupers. *In* Tropical snappers and groupers: biology and fisheries management (J. J. Polovina and S. Ralston, eds.), p. 405–463. Westview Press Inc., Boulder, CO.
- Polunin, N. V. C. and C. M. Roberts.
1996. Reef fisheries. *In* Fish and fisheries series, p. 193–218. Chapman and Hall, London.
- Ralston, S.
1987. Mortality rates of snappers and groupers. *In* Tropical snappers and groupers: biology and fisheries management (J. J. Polovina and S. Ralston, eds.), p. 375–404. Westview Press Inc., Boulder, CO.
- Randall, J. E.
1965. Food habits of the Nassau grouper (*Epinephelus striatus*) 6th meeting. *Assoc Island Mar Labs Caribb.* 6:13–16.
1987. A preliminary synopsis of the groupers (Perciformes: Serranidae: Epinephelinae) of the Indo-Pacific region. *In* Tropical snappers and groupers: biology and fisheries management (J. J. Polovina and S. Ralston, eds.), p. 89–187. Westview Press Inc., Boulder, CO.
- Randall, J. E., G. R. Allen, and R. C. Steene.
1990. Complete diver's and fisherman's guide to fishes of the Great Barrier Reef and Coral Sea. Crawford House Press, Bathurst, 507 p.
- Roberts, C. M., and N. V. C. Polunin.
1991. Are marine reserves effective in management of reef fisheries? *Rev. Fish Biol. Fisheries* 1:65–91.
- Russ, G. R.
1985. Effects of protective management on coral reef fishes

- in the central Philippines. Proc. 5th Int. Coral Reef Congr. 4:219–224.
1991. Coral reef fisheries: effects and yield. In *The ecology of fishes on coral reefs* (P. F. Sale, ed.), p. 601–636. Academic Press, San Diego, CA.
- Russ, G. R. and A. C. Alcala.
1996. Marine reserves: rates and patterns of recovery and decline of large predatory fish. *Ecol. Applic.* 6:947–961.
- 1998a. Natural fishing experiments in marine reserves 1983–1993: community and trophic responses. *Coral Reefs* 17:383–397.
- 1988b. Natural fishing experiments in marine reserves 1983–1993: roles of life history and fishing intensity in family responses. *Coral Reefs* 17:399–416.
- Sadovy, Y.
1994. Grouper stocks of the Western Central Atlantic: the need for management and management needs. *Proc. Gulf Caribb. Fish. Inst.* 43:43–64.
- Samoilys, M. A.
1997. Movement in a large predatory fish: coral trout, *Plectropomus leopardus* (Pisces: Serranidae) on Heron Reef, Australia. *Coral Reefs* 16:151–158.
- Schoener, T. W.
1970. Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology* 51:408–418.
- Shpigel, M., and L. Fishelson.
1989. Habitat partitioning between species of the genus *Cephalopholis* (Pisces Serranidae) across the fringing reef of the Gulf of Aqaba (Red Sea). *Mar. Ecol. Prog. Ser.* 58:17–22.
- Shulman, M. J.
1985. Recruitment of coral reef fishes: effects of distribution of predators and shelter. *Ecology* 66(3):1056–1066.
- Sluka, R., and K. Sullivan.
1998. The influence of spear fishing on species composition and size of groupers on patch reefs in the upper Florida Keys. *Fish. Bull.* 96:388–392.
- Smith, M. M., and P. C. Heemstra.
1986. *Smith's sea fishes*. Springer-Verlag, Berlin, 1047 p.
- Sokal, R. R., and F. J. Rohlf.
1981. *Biometry*, 2nd ed. W.H. Freeman, San Francisco, CA, 859 p.
- Steneck, R. S.
1998. Human influences on coastal ecosystems: Does over-fishing create trophic cascades? *Tree* 13(11):429–430.
- St John, J.
1995. Feeding ecology of the coral trout, *Plectropomus leopardus* Serranidae on the Great Barrier Reef, Australia. Ph.D. diss., James Cook University of North Queensland, Townsville, Australia, 277 p.
1999. Ontogenetic changes in the diet of a large coral reef grouper *Plectropomus leopardus* (Serranidae): patterns in taxa, size and habitat of prey. *Mar. Ecol. Prog. Ser.* 233–246.
- Sweatman, H. P. A.
1984. A field study of the predatory behaviour and feeding rate of a piscivorous coral reef fish, the lizardfish *Synodus englemani*. *Copeia* 84:187–193.
- Sweatman, H. P. A., and D. R. Robertson.
1994. Grazing halos and predation on juvenile Caribbean surgeonfishes. *Mar. Ecol. Prog. Ser.* 111:1–6.
- Trainor, N.
1991. Commercial line fishing. *The Queensland Fisherman*, March 9(3):17–24.
- Williams, D. M., and G. R. Russ.
1994. Review of data on fishes of commercial and recreational fishing interest on the Great Barrier Reef. Vol. I: Research publication 33. Great Barrier Reef Marine Park Authority, Townsville, Australia, 103 p.
- Zeller, D. C.
1997. Home range and activity patterns of the coral trout *Plectropomus leopardus* (Serranidae). *Mar. Ecol. Prog. Ser.* 154:65–77.
- Zeller, D. C., and G. R. Russ.
1998. Marine reserves: patterns of adult movement of the coral trout (*Plectropomus leopardus* (Serranidae)). *Can. J. Fish Aquat. Sci.* 55:917–924.