

Abstract.—Samples of *Plectropomus leopardus* collected at two reefs (Glow and Yankee) that have been closed to fishing since 1987 were compared with samples collected at two reefs (Grub and Hopkinson) that were open to fishing to investigate the effects of a 3–4 year closure on the size, age, and sex structure of leopard coral-grouper (also known as “coral trout”) populations. There were no significant differences in mean size and age between protected reefs and unprotected reefs. However, mean size and age varied significantly between the two protected and the two unprotected reefs. In the two reefs closed to fishing, the population structure was dominated by the presence of a strong year class which settled in early 1984, indicating the occurrence of strong interannual fluctuations in recruitment. A similar pattern was not observed on the reefs open to fishing, suggesting that fishing mortality may have caused the decrease in abundance of this strong year class on the open reefs. Sex change occurred over a wide range of sizes and ages on the four reefs. A comparison of the frequency of developmental stages between reefs indicated significant variation. The two unprotected reefs had a smaller proportion of males, but that seemed to be compensated for by a larger proportion of transitional-stage fish and young males. Although the distribution of developmental stages in the populations was different, the same final female: male balance was achieved. This suggests that for the leopard coral-grouper, sex change results from a combination of developmental and behavioral processes. Differences in age structure were more obvious than differences in the size structure between closed and open reefs, suggesting that age structure may be far more useful than size structure for comparisons of fishing effects on long-lived fishes such as Epinephelinae serranids. Comparisons of open and closed reefs based solely on mean sizes may fail to detect important differences.

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Population structure of the leopard coral grouper, *Plectropomus leopardus*, on fished and unfished reefs off Townsville, Central Great Barrier Reef, Australia

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Fishing is one of the most important human exploitative activities on coral reefs (Munro, 1983; Munro and Williams, 1985; Russ, 1991). It has been suggested that fishing may have a greater impact upon fish populations and communities of coral reefs than upon those of temperate seas because of the more territorial nature of most coral reef fish (Russ, 1991). Therefore, the impact of fishing on populations and communities of coral reef fishes has been of considerable interest. Large predatory species are especially affected by overfishing owing to life history characteristics such as slow growth, high longevity, low rates of natural mortality, and limited adult mobility (Plan Development Team [PTD], 1990; Russ, 1991).

Fishing is known to cause selective removal of larger (and presumably older) individuals, thus reducing their proportion in the population (Ricker 1969; Miranda et al., 1987). Although evidence for effects of fishing on the size structure of populations of coral reef fishes is strong (Munro, 1983; PDT, 1990), there is little evidence for effects of fishing on age structure, probably

because of the perceived difficulties in age determination of tropical fishes (Manooch, 1987). On the Great Barrier Reef, for example, information on age structure from a number of reefs exists for only one species, the damselfish *Pomacentrus moluccensis* (Doherty and Fowler, 1994). In the presence of high variability in size at age, information on age structure can provide information on harvesting effects not obtainable by size-structured data alone. Different growth processes can also be associated with selective fishing mortality (Parma and Deriso, 1990), enhancing the importance of analyzing age in assessments of the effects of fishing on such populations.

Sequential hermaphroditism is common among coral reef fishes (Thresher, 1984). Bannerot et al. (1987) modelled the resilience of protogynous populations to exploitation and concluded that a definite risk existed in managing these stocks by traditional yield-per-recruit models under high fishing pressure. The effects of selective removal of larger individuals (presumably mostly males) on the sex

ratio of a population, however, will depend on the mechanisms controlling sex reversal. For example, for protogynous populations, if female to male sex change is determined by size or age, a decline in the proportion of males will be expected. Such effects have been reported by Thompson and Munro (1983) in comparing populations of serranids subjected to different levels of fishing pressure in the Caribbean. In contrast, no fishing-related effects were detected by Reeson (1983) on populations of scarids. Social induction of sex change is known or claimed for many species of fish (Shapiro, 1987). If this is the case, selective removal of larger individuals would induce female to male sex change, compensating for the effects of fishing on the sex ratio. Consequently, a reduction in the average size and age of sex change would be expected.

A widely recognized management strategy in the conservation of reefs is the implementation of marine fisheries reserves, areas designed to protect stocks of reef fish and habitats from all forms of exploitation (PDT, 1990; Williams and Russ, 1994). The first marine protected area was established in Florida in 1930. Since then, protected marine areas have been implemented all over the world (PDT, 1990). In Australia, the first protected marine areas were established in the Capricornia Section of the Great Barrier Reef Marine Park in 1981, under the first zoning plan to come into operation (Craik, 1989).

Evidence suggests that long-term spatial closure to fishing increases the density, biomass, average size, and fecundity of reef fishes (see PDT, 1990; Russ, 1991; Russ et al., in press, for reviews, but see DeMartini, 1993). Furthermore, by enabling populations of reef fishes to attain or maintain natural levels, marine reserves have been suggested as a means to help maintain or even enhance yields of fishes from areas adjacent to the reserves (Russ, 1985; Alcala and Russ, 1990).

The spatial structure of coral reefs provides an excellent opportunity to test for the effects of different management alternatives (Hilborn and Walters, 1992). The importance of experimental investigations on the effects of fishing on coral reefs that are used as replicate experimental units has been pointed out by various authors (Russ, 1991; Hilborn and Walters, 1992; Walters and Sainsbury¹). Yet, in spite of the high expectations placed on marine reserves, few direct tests exist on the effects of such protection on yields of marine resources (Alcala and Russ, 1990).

¹ Walters, C., and K. Sainsbury. 1990. Design of a large scale experiment for measuring effects of fishing on the Great Barrier Reef. Unpubl. Rep. to the Great Barrier Reef Marine Park Authority (GBRMPA), Australia, 47 p.

The leopard coral grouper (also known as "coral trout"), *Plectropomus leopardus*, is a long-lived, protogynous hermaphroditic fish that represents a very important fishery resource over the Great Barrier Reef, Australia. With approximately 1,200 tonnes caught annually, the leopard coral grouper is the largest single component in the annual commercial catch of Queensland line-fishing (Trainor, 1991). Because of its importance, the leopard coral grouper has been the subject of many studies on the effects of fishing. These studies have compared the abundance and size structure of populations from open and closed reefs on the Great Barrier Reef (see Williams and Russ, 1994, for review). Most of these studies were conducted by using underwater visual census (UVC) techniques. Increased average size of the leopard coral grouper on reefs closed to fishing was detected in most cases (Craik, 1981; Ayling and Ayling^{2,3}; Ayling and Mapstone⁴). Beinssen⁵ used UVC, line fishing, and mark-release-recapture techniques to investigate the effects of a 3.5 year closure on Boulton Reef and detected a significant increase in average size of leopard coral grouper. The same reef was subsequently opened to fishing and after 18 months a significant decrease in the average size of leopard coral grouper was detected (Beinssen⁵). No study, however, has investigated the effects of fishing on the age and sex structure of leopard coral grouper populations. The age and growth of *Plectropomus leopardus* has been recently validated (Ferreira and Russ, 1994), making it possible to use age as an indicator of changes in population structure under different levels of fishing pressure and through time.

In 1987 a zoning plan was established in the central section of the Great Barrier Reef Marine Park, Australia, dividing the area into zones that allowed different activities. Under this plan, fishing was excluded from some areas. In this study, samples taken from reefs in the central section of the Great Barrier Reef located in areas closed to fishing (National Park Zones) since 1987, are compared with samples taken from reefs located in areas open to fishing (General Use Zones). The effects of this 3–4 year closure on

² Ayling, A. M., and A. L. Ayling. 1984. A biological survey of selected reefs in the Capricorn section of the Great Barrier Reef Marine Park. Unpubl. Rep. to GBRMPA, Australia, 25 p.

³ Ayling, A. M., and A. L. Ayling. 1986. A biological survey of selected reefs in the Capricorn section of the Great Barrier Reef Marine Park. Unpubl. Rep. to GBRMPA, Australia, 25 p.

⁴ Ayling, A. M., and B. P. Mapstone. 1991. Unpubl. data collected for GBRMPA from a biological survey of reefs in the Cairns section of the Great Barrier Reef Marine Park. Unpubl. Rep. to GBRMPA, Australia, 30 p.

⁵ Beinssen, K. 1989. Results of the Boulton Reef replenishment area study. Rep. to GBRMPA, Australia, 28 p.

the size, age, and sex structure of leopard coral-grouper populations are investigated.

Materials and methods

Four mid-shelf reefs off Townsville, Central Great Barrier Reef (Fig. 1), were chosen as the sample reefs for this experiment. Two reefs, Grub and Hopkinson, were located in the General Use Zones and were open to spear-fishing, whereas the other two, Glow and Yankee, were located in National Park Zones, and had been closed to line fishing since September 1987. The four reefs were sampled twice a year, during June–July and September–October, in 1990 and 1991

(Table 1). During each sampling trip, a crew of four line fishermen fished one reef per day (during the daylight hours) for a period of approximately four hours. The same vessel was used for each trip. The fishing crew was relatively consistent in composition, and overall fishing ability was presumably consistent between trips.

Laboratory analysis

All fish were measured and weighed, and their otoliths and gonads were removed. The gonads were preserved in FAAC (formaldehyde 4%, acetic acid 5%, calcium chloride 1.3%) on board, sectioned, and stained by using the standard techniques described in Ferreira (1993). Each gonad was classified into one of the following gonadal developmental stages, following Ferreira (1993, 1995):

Immature female: no evidence of prior spawning.

Mature female: evidence of prior spawning or active vitellogenesis.

Transitional-stage: gonads with proliferating testicular tissue in the presence of degenerating ovarian tissue. Dorsal sperm sinuses absent.

Young male: post-transitional, newly transformed testis. Dorsal sperm sinuses formed. Ovarian tissue dominating the lamellae.

Mature male: developed testes, presenting typical lobular form and presence of intra-lobular or "central" sperm sinuses.

To determine the age of each fish, the otoliths were read whole and sectioned by following the method described by Ferreira and Russ (1992). The number of opaque zones or rings were counted from the center to the margin of each otolith. Because leopard coral grouper recruitment occurs in the first months of the year (Doherty et al., 1994), the birth date was assigned as 1 January. Opaque zones are formed once a year, from July to November (Ferreira and Russ, 1994); therefore, they were counted only when there was further deposition of a translucent zone, i.e. from December onwards. In this way, the number of rings corresponded to the real age of the fishes.

Statistical analysis

Nested analyses of variance (reefs nested within fishing status) were used to compare mean age and size of leopard coral grouper between closed and open reefs (=fishing status). Factorial analyses of variance and Kruskal-Wallis tests

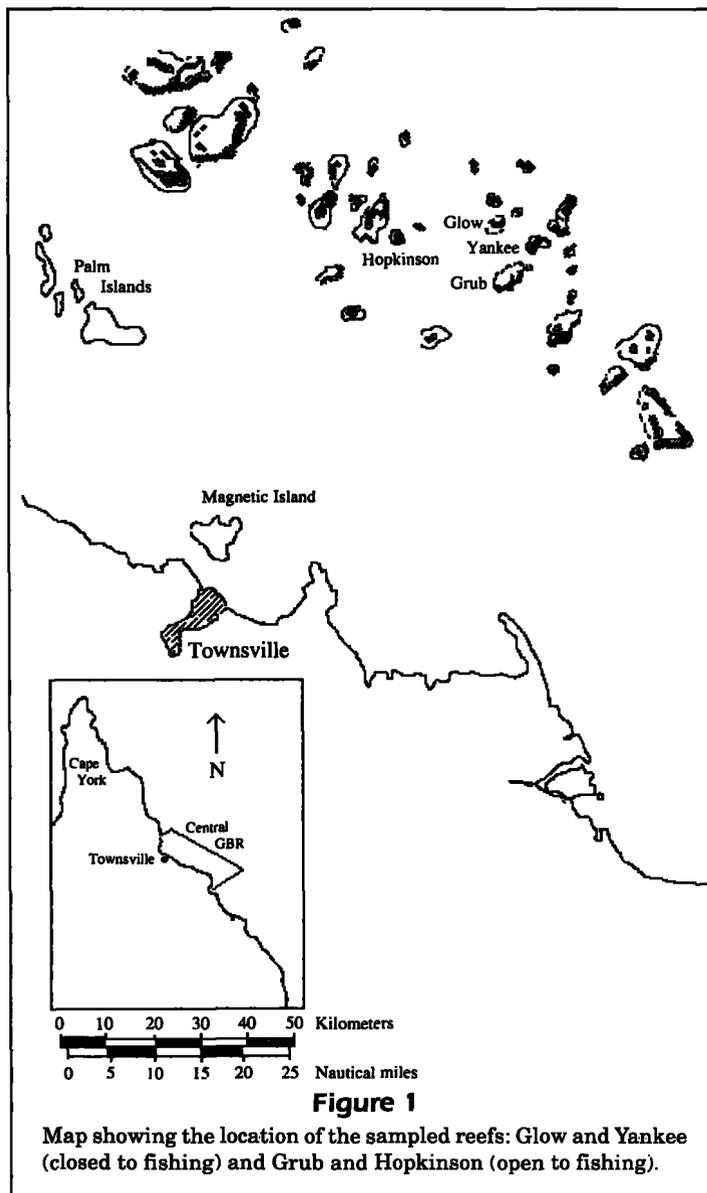


Table 1

Dates and number of leopard coralgroupers, *Plectropomus leopardus*, collected with standardized fishing effort in each one-day sampling trip.

	Closed		Open	
	Glow	Yankee	Grub	Hopkinson
Jun-Jul 1990	51	18	9	14
Sep-Oct 1990	49	42	11	17
Jun-Jul 1991	74	54	14	30
Sep-Oct 1991	23	11	15	15
Total	197	125	49	76

were used to compare mean size and age of leopard coralgroupers on the four reefs, independent of the reef fishing status. Multiple comparisons were performed by using post hoc tests (Tukey-Kramer, level of significance $P < 0.05$), and pair-wise comparisons by using Kolmogorov-Smirnov tests. Schnute's growth function (1981) was used to fit length-at-age data of leopard coralgroupers for each reef by using standard nonlinear optimization methods (Wilkinson, 1989). Schnute's model includes the von Bertalanffy, Richards, Gompertz, logistic, and linear growth models, which correspond simply to limiting parameter values. To test for differences in size at age between reefs, the linear regressions were compared by using analysis of covariance. Chi-square contingency tables were used to compare the frequency of sexes between reefs. The assumptions of normality and homoscedasticity were examined and data were transformed if needed (transformed data are indicated in tables). Level of significance used was $P < 0.05$.

Results

There were no significant differences in mean size and age between protected reefs and unprotected reefs (fishing status). However, the mean sizes and ages varied significantly between reefs within fishing status level (Table 2).

Post hoc tests showed that mean size and mean age were larger for Glow (closed) than for all other reefs, whereas mean ages for Grub (open) were smaller than for all other reefs. The mean sizes were not significantly different for Yankee, Hopkinson, and Grub, and the mean ages were not significantly different for Yankee and Hopkinson (Fig. 2).

Growth

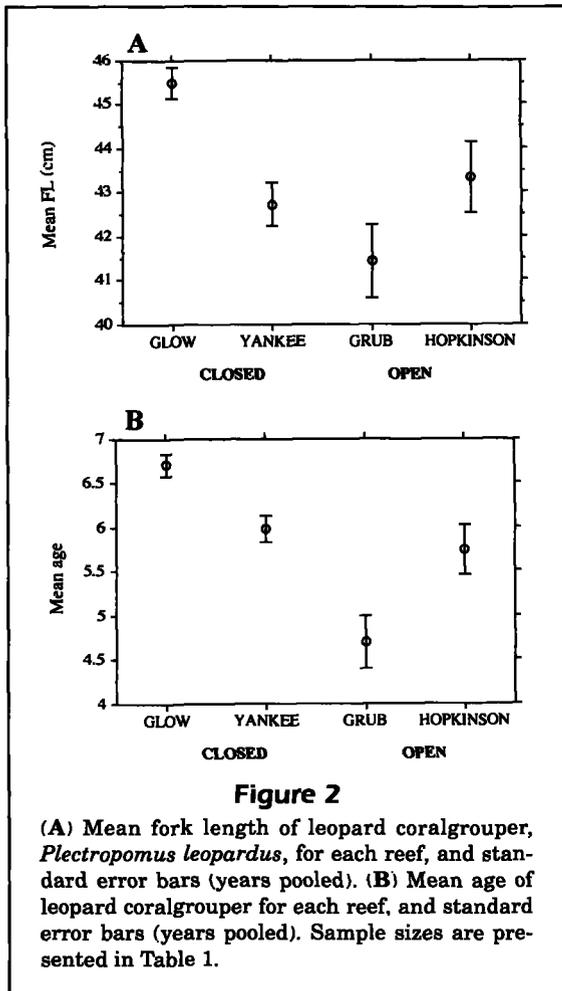
Schnute's growth function was fitted to size-at-age data for each reef. The submodel corresponding to the von Bertalanffy formula ($b=1$) provided a good fit to the data from all reefs (Fig. 3). The estimated "a" (corresponding to the von Bertalanffy K) for Grub, however, approached zero, indicating that the data could be described also by a linear regression model.

Ferreira and Russ (1994) found that for the leopard coralgroupers, estimates of growth parameters are affected greatly by different age ranges of size-at-age data. Therefore, for comparison of growth between reefs, the age range was limited to age classes occurring at all four reefs (2 to 10 years), and Schnute's growth function was fitted to these truncated data. For Hopkinson, Grub, and Glow, estimates of "a" approached zero (Table 3), indicating close to linear growth over the age range 2 to 10 years. As the estimate of "a" for Yankee was also low, simple linear models were fitted to the data from all four reefs for comparative purposes (Table 3). Analysis of the sum of squares indicated that linear models were

Table 2

Nested analysis of variance comparing mean size and age of leopard coralgroupers, *Plectropomus leopardus*, from reefs open and closed to fishing. The difference between residual degrees of freedom in the two tables is due to the fact that for some individuals age was not determined. df = degrees of freedom; SS = sum of squares; MS = mean square.

Source	df	SS	MS	F-value	P-value
Dependent variable: FL (cm)					
Fishing status	1	393.6	393.6	1.48	0.35
Reef (fishing status)	2	531.1	265.5	6.23	0.002
Residual	443	18870.6	42.6		
Dependent variable: Log age (years)					
Fishing status	1	0.931	0.931	4.41	0.17
Reef (fishing status)	2	0.422	0.211	9.07	0.0001
Residual	413	9.61	0.023		



more appropriate to describe the growth data over the age range 2 to 10 years for all reefs with the exception of Yankee, for which an asymptotic model was more appropriate. No significant differences were observed between the linear regressions obtained for each reef ($P=0.276$), indicating that the mean size at age (and therefore growth) did not vary significantly between the four reefs.

Analysis of the age and size distributions at each reef

Glow and Yankee, the two closed reefs, had very strong modes in the year classes 6 and 7 (Fig. 4). In separating age distribution by year (Fig. 5), it is clear that these modes represented a strong year class that comprised 6-year-olds in 1990 and 7-year-olds in 1991. This result rules out the possibility of selection towards one year class by fishing gear or bias in age determination. This strong year class was not as obvious on the unprotected reefs (Fig. 5). At

Table 3

Schnute's (1981) parameter "a" and r^2 values for nonlinear and linear growth models for leopard coralgroupers, *Plectropomus leopardus*, ages 2 to 10 years.

	Closed		Open	
	Glow	Yankee	Grub	Hopkinson
a	0.080	0.102	0.004	-0.040
Nonlinear r^2	0.450	0.546	0.754	0.669
Linear r^2	0.445	0.448	0.754	0.666

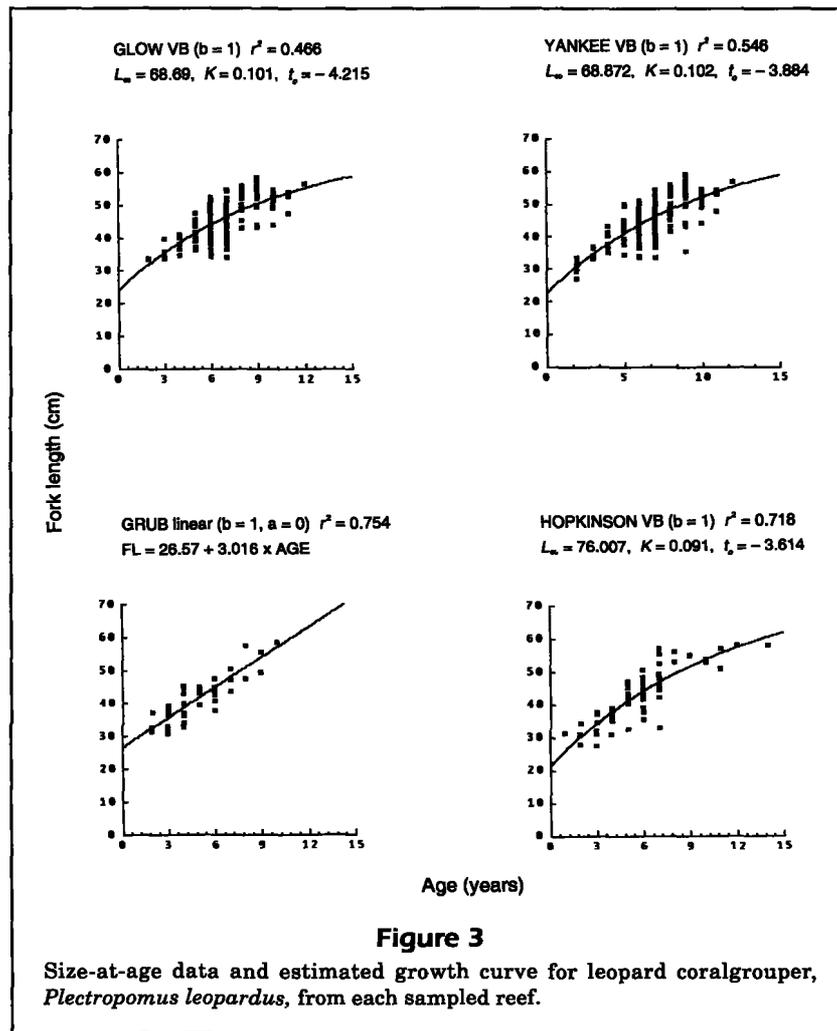
Hopkinson, year class 6 formed a small mode in 1990, but the pattern was not consistent, because year class 7 was not strong in 1991. At Grub, younger ages were proportionally more abundant; the mode was in the 3-year-old class for two consecutive years.

The 6+ year-old age class of 1990 and the 7+ year-old age class of 1991 settled onto the reefs at the beginning of 1984. Because Glow and Yankee have been closed to fishing since 1987 and age of recruitment to the fishery is approximately 3 years of age (Ferreira and Russ, 1994), the individuals settling onto Glow and Yankee in 1984 were protected from fishing for most of their lives. Modal progression was not particularly evident in the size distributions (Fig. 6).

Sex structure

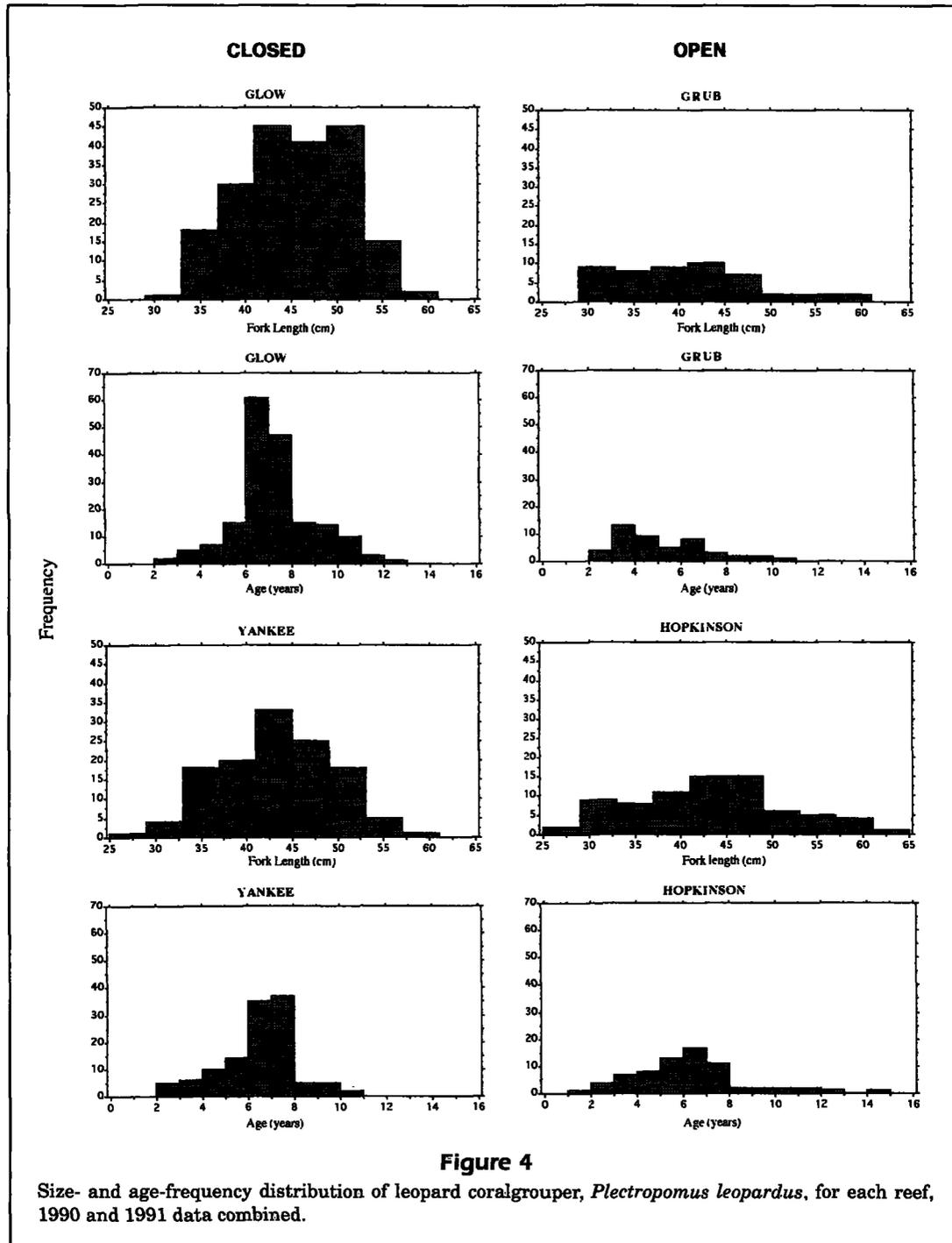
The distribution of developmental stages by size and age (Fig. 7) indicated that sex change occurs over a wide range of sizes and ages on the four reefs. The frequencies of developmental stages observed for each reef (Table 4) were compared by using chi-square analysis. The frequencies were significantly different between all reefs ($P<0.05$), with the exception of the frequencies observed for Yankee and Hopkinson ($P=0.246$). For the calculation of sex ratio, frequencies of young males were pooled with frequencies of mature males, because individuals in both categories were sexually potential males. The resulting sex ratios (Table 4) were not significantly different among reefs ($P=0.09$).

There were no significant differences between protected and unprotected reefs, but some differences between reefs were detected. The mean size of mature females was not significantly different between reefs (one-way ANOVA, $P=0.10$). The mean age of mature females, however, was significantly different between reefs (log (age), $P=0.008$); mature females from Glow were significantly older than mature females from Grub (post hoc, $P<0.05$). Age and size of

**Table 4**

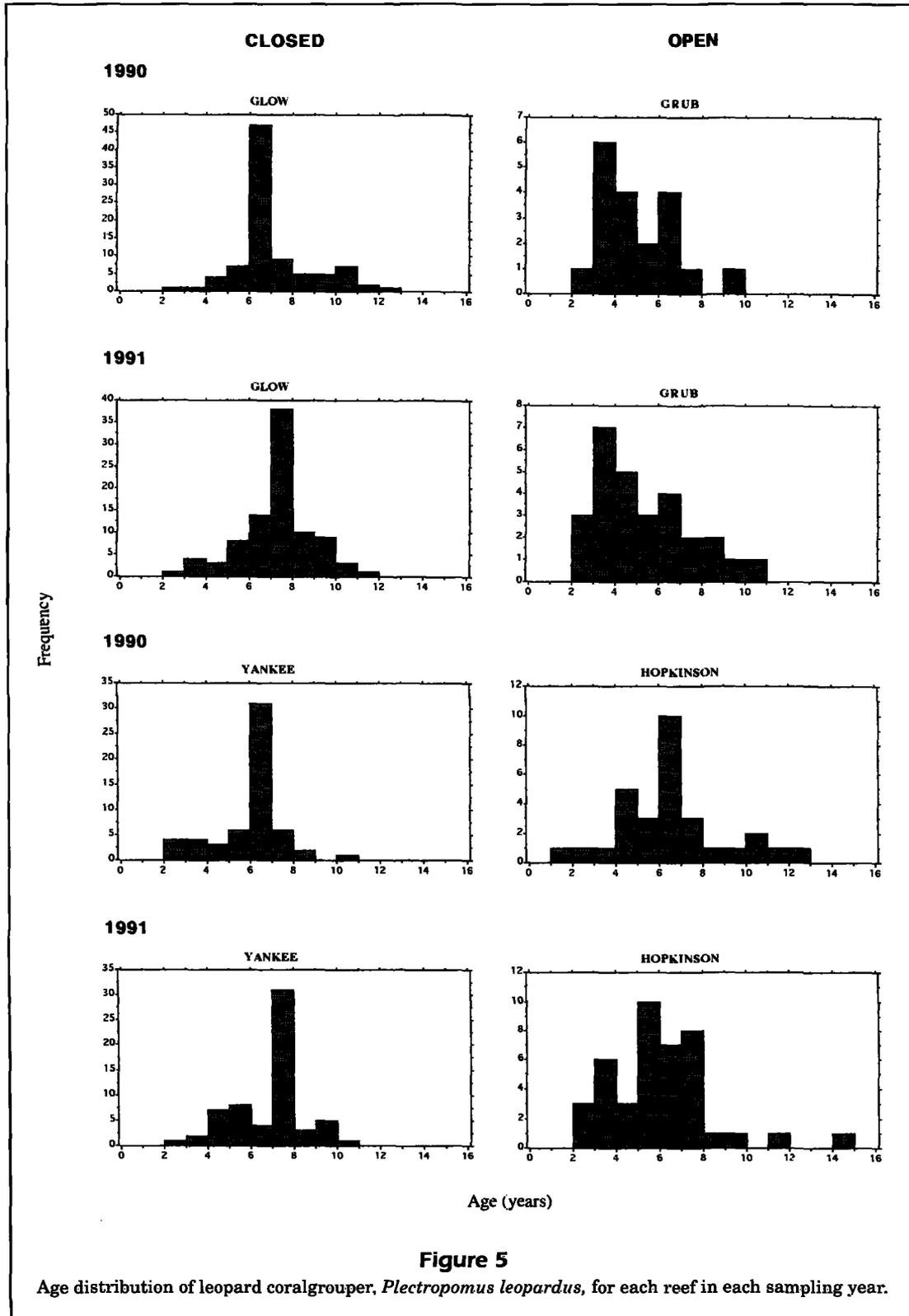
Frequency (%) of each developmental stage and sex ratio (mature females:young and mature males) of leopard coralgroupers, *Plectropomus leopardus*, at the four reefs.

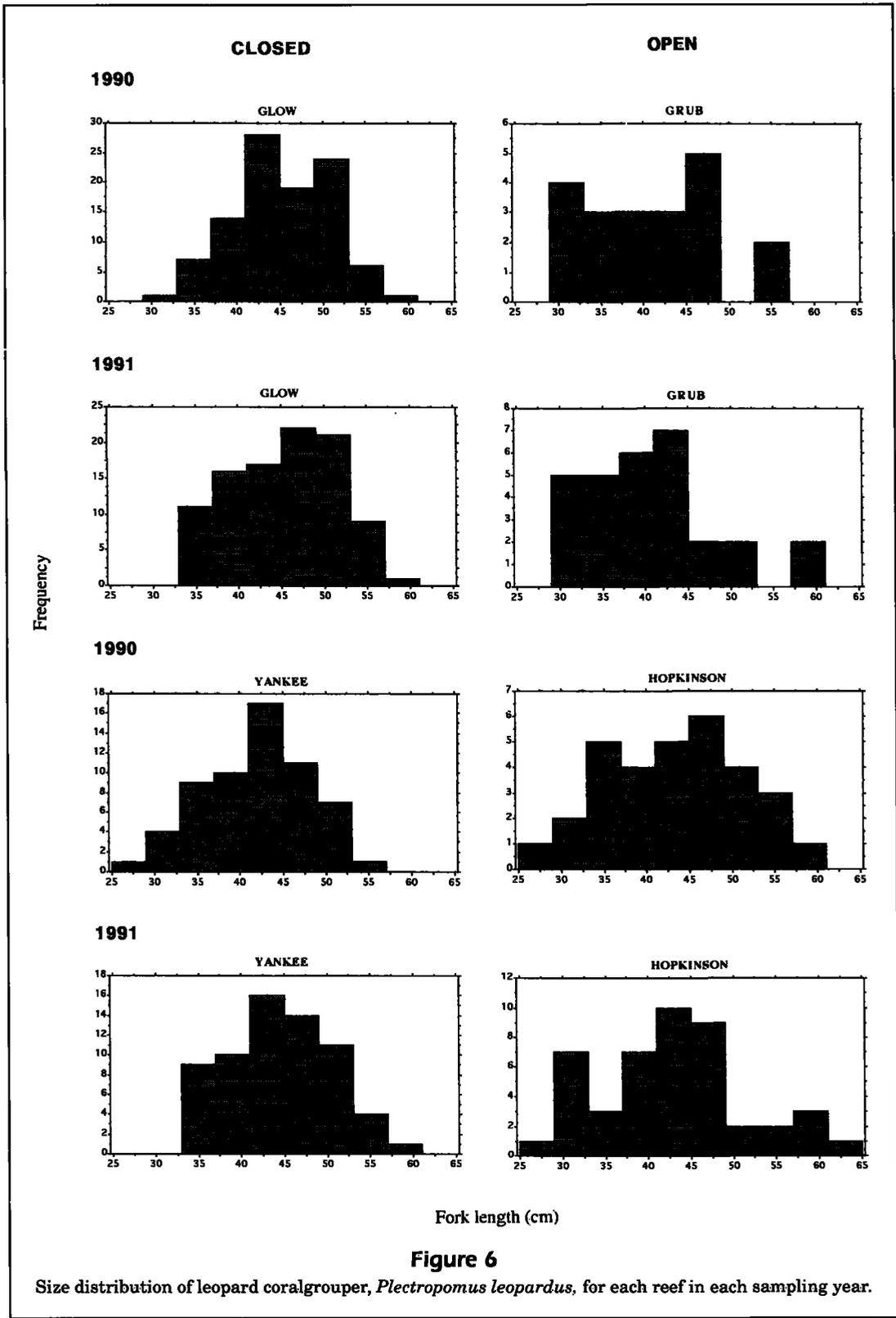
	Immature female	Mature female	Transitional	Young male	Mature male	Sex ratio
Closed						
Glow	1 (1%)	0 (59%)	8 (6%)	8 (6%)	38 (28%)	1.7:1
Yankee	4 (4%)	40 (38%)	16 (15%)	11 (11%)	3 (32%)	0.91:1
Open						
Grub	7 (16%)	15 (34%)	10 (23%)	7 (16%)	5 (11%)	1.25:1
Hopkinson	5 (7%)	36 (52%)	9 (13%)	4 (6%)	15 (22%)	1.9:1



transitional-stage fish were not significantly different between reefs (FL: $P=0.24$, log (age), $P=0.11$). Size of young males was not significantly different between reefs ($P=0.2$) but ages of young males were significantly different ($P=0.03$); young males from Glow were significantly older than young males from

Grub (post hoc, $P<0.05$). Age of mature males was not significantly different between reefs ($P=0.22$). However size of mature males varied significantly between reefs ($P=0.001$); mature males at Yankee were significantly smaller than mature males at Hopkinson (post hoc $P<0.05$).

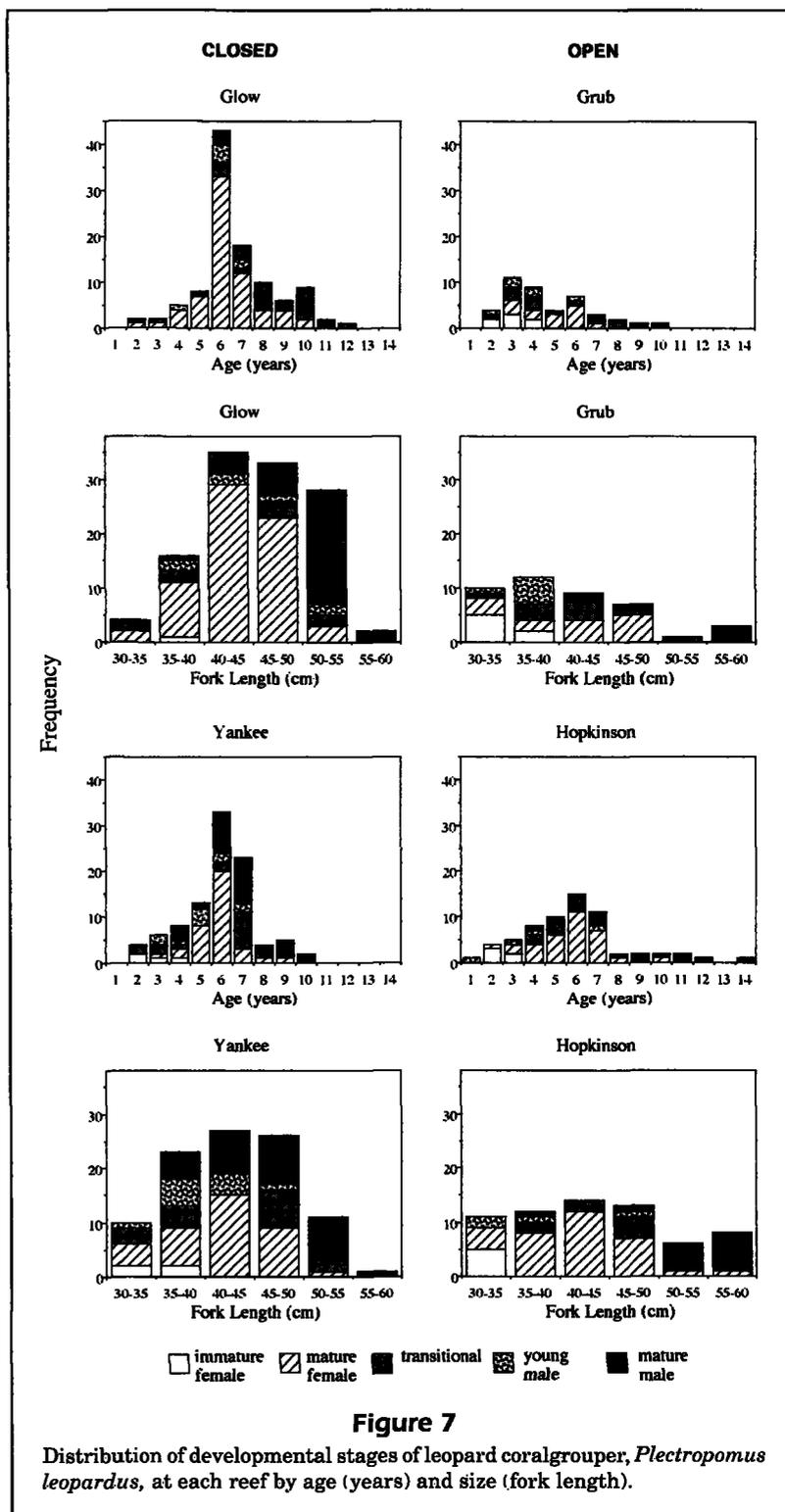




Discussion

There are several important assumptions in a comparison of the effects of fishing on populations from areas that are open with those that are closed to fishing. The first assumption is that protection is enforced so as to guarantee effective fishing closure. In the Great Barrier Reef Marine Park, aerial surveillance is conducted on a regular basis and fines are levied on those who fish illegally. Although violations still occur, the fishing pressure is likely to be considerably lower on the closed reefs. The second assumption is that the effects of fish movements across closed and open boundaries do not mask the effects of protection from fishing on the population structure. The minimum distance between two study reefs was of 1.6 km, and depth between reefs of the order of 40–60 m. Tagging studies have shown that reef fishes are highly site-attached, and most studies on movements of serranids have not shown significant movements across distances and depths such as those existing on the present study (PDT, 1990). Davies⁶ conducted extensive tagging studies on leopard coral grouper and showed that fish exhibited extremely limited inter-reef movement in a study of six reefs in the Central Great Barrier Reef.

Expected effects of fishing are a reduction in the size and age range and average size and age of the population (Russ, 1991). In addition, line fishing might select for the larger and older individuals in a population (Ricker, 1969; Miranda et al., 1987), which would exacerbate this effect. Significant differences between size and age structures on closed and open reefs, however, will depend largely on the duration of closure in relation to species longevity and fishing mortality. Therefore, a third assumption is that the duration of effective closure is great enough (in relation to the longevity of the target species



⁶ Davies, C. R. 1995. Patterns of movement of three species of coral reef fish on the Great Barrier Reef. Ph.D. diss., Department of Marine Biology, James Cook University of North Queensland, Australia, 170 p. Unpubl. data.

concerned) for an effect of closure to be detected. In this study, given the short period of time for which the reefs had been closed (3–4 years) in relation to the longevity of the leopard coral grouper (14+ years),

great differences in the size and age structure were not likely to be detected. A fourth assumption is that effects are attributable to fishing and not some other factor. The failure to detect a significant difference between either mean size or age of leopard coral-grouper on open and closed reefs, however, was due largely to variability between replicate reefs. If, in the present study, only Glow (closed) and Grub (open) had been compared, the result would reveal a classic effect-of-fishing scenario, with a larger range of sizes and ages and significantly larger mean sizes and ages observed on the reef closed to fishing. In contrast, if only Yankee (closed) and Hopkinson (open) had been compared, no effect of fishing would have been detected on the population structure. These results emphasize the importance of replicate reefs in analyses of the effects of fishing on coral reef fish populations. More replicates (i.e. more reefs per treatment group) would increase the degrees of freedom and thus the power (i.e. likelihood of detecting a given effect size) of the nested ANOVA.

One possible reason for the differences between the two open reefs is the fact that they are apparently not subject to the same fishing pressure. Grub is renowned for its excellent anchorage, and therefore is a preferred site for recreational and commercial fishing vessels. Aerial surveys conducted by the Great Barrier Reef Marine Park Authority between 1989 and 1992 (GBRMPA⁷), indicated that Grub is frequented by boats 2.2 times more frequently than Hopkinson and that fishing vessels are sighted 3 times more often at Grub than at Hopkinson. Such factors should be taken into account in designing future sampling and experimental programs on the effects of fishing on the Great Barrier Reef.

Nevertheless, there was a major and consistent difference between the open and closed reefs that were analyzed. For the two closed reefs, the population structure was dominated by the presence of a strong year class which settled in early 1984. A similar pattern was not obvious on the open reefs, and a corresponding strong mode was not evident at Grub or at Hopkinson. Occurrence of strong year classes is a well-documented phenomenon in commercial catches of temperate species (Hjort, 1914; Sissenwine, 1984; Rothschild, 1986). For temperate species, year-class strength has been linked to early life history processes since the beginning of this century (Hjort, 1914). However, for populations of coral reef fish, the importance of recruitment as a major driving force in the temporal variability of abundance has been recognized only recently (Williams, 1980;

Doherty and Williams, 1988, a and b; Doherty, 1991; Doherty and Fowler, 1994).

There is evidence for the possibility of strong recruitment pulses of reef fishes occurring concurrently on midshelf reefs off Townsville which are separated by distances of up to 10–30 km (Doherty and Williams, 1988, a and b; Williams, 1991). The age-structure data for the two closed reefs provides circumstantial evidence in support of pulses of recruitment being synchronous on reefs at least 10 km apart (Fig. 1). With the assumption that the four reefs received a similar pulse of recruitment in 1984, it is apparent that fishing mortality has operated to largely decrease the abundance of this year class. On the closed reefs, this strong year class was protected from fishing for almost its entire life and as a result its dominance was maintained. In contrast, on the open reefs, the same year class probably supported the fisheries disproportionately in relation to the other age classes, and consequently abundance was reduced. An alternative hypothesis is that the settlement pulse occurred only on the two closed reefs owing to some process independent of fishing.

A common question regarding the effects of fishing on protogynous hermaphroditic fishes is how the sex structure of the population would respond to fishing mortality. If sex change is determined by age and size and selective removal of larger and older individuals occurs, the result would be a decrease in the proportion of males in the population. However, if sex change is behaviorally induced, the population would be expected to compensate to some extent for the selective removal of males by female-to-male sex change, i.e. by changing sex at smaller ages and sizes.

The mean size and age observed for each stage seemed to follow the size and age structure of each population. Mature females and young males were larger and older at Glow than those at Grub. Age and size of transitional-stage fish did not differ significantly between reefs, but this is not surprising given the high variability in the age and size of sex transition characteristic of leopard coral-grouper and the small numbers of transitional individuals. Mature males from Yankee were smaller than those at Hopkinson. This is possibly a consequence of the age distribution and consequent size distribution. Yankee had proportionally more 6- and 7-year-old fish and not many in the older age classes; therefore most males would be 6- or 7-year-olds, resulting in a small overall mean size. At Hopkinson, the age frequency was more evenly distributed, without strong modal classes for years 6 and 7 and having a wider range of age classes.

The comparison of frequency of developmental stages between reefs showed significant variation.

⁷ GBRMPA data base. 1992. Great Barrier Reef Marine Park Authority. P.O. Box 1379, Townsville, Q4810, Australia.

When immature males were pooled with mature males for sex ratio calculations, the resulting sex ratio was not significantly different among reefs. Therefore, it appears that despite the differential distribution of developmental stages in the populations, the same final female:male balance was achieved. This result suggests that behavioral mechanisms are probably contributing to the determination of the distribution of sexes in the populations of leopard coralgroupers. It is possible that for the leopard coralgroupers, sex change results from a combination of a developmental process, in which individuals are more susceptible to sex change as they grow larger and older, and from a social process through behaviorally induced stimuli. Genetic variability would widen the range over which sex change can occur and phenotypic plasticity would allow individuals to respond to different social structures. Manipulative experiments are probably necessary to detect the exact mechanisms determining the distribution of sexes in leopard coralgroupers populations.

Estimations of mortality rates are essential to fishery management, and yet few studies have made estimates of the rate of total mortality of coral reef fishes (Russ, 1991). However, an important assumption of catch curve analysis, one of the most commonly employed methods to estimate mortality (Beverton and Holt, 1957), is that all age groups have been recruited with the same abundance (Pauly, 1984). The present data represent a clear example of the problems that can result from the presence of strong recruitment pulses in calculating the total mortality rate Z from age- or length-structured catch curves. Because of a strong year class, estimates of Z calculated from the right-hand slopes of the catch curves would suggest very high mortality rates for the two closed reefs, in contrast with much lower mortality rates on the open reefs. Mortality estimates drawn from the present data or from similar cases where significant recruitment fluctuation is retained in the age structure would be very imprecise.

For the leopard coralgroupers, our results suggest that the occurrence of strong interannual fluctuations in recruitment were retained in the age structure. With recruitment as a major factor driving the patterns of abundance, recovery of leopard coralgroupers populations after closure to fishing may be largely dependent on a good pulse of recruitment. Thus recoveries of populations after closure to fishing are likely to be "events" rather than gradual "processes," and recovery may be rapid or slow, depending on the timing of closure with respect to the occurrence of a very large year class.

Differences in the age structure were more obvious than differences in the size structure between

open and closed reefs. As the leopard coralgroupers is a relatively slow-growing fish, differences in the size structure of a population will take longer to become evident than will differences in the age structure. Additionally, owing to considerable variability in size at age (Ferreira and Russ, 1994), recruitment fluctuations may also pass unnoticed if size-structure data alone are examined. The results presented here indicate that age structure may be far more useful than size structure for comparisons of fishing effects on long-lived fishes such as *Epinephelinae* serranids. Comparisons based solely on mean sizes of reefs open to fishing with those closed to fishing may fail to detect important differences.

Marine fishery reserves are a management strategy with excellent potential for maintaining high abundances of reef fishes (Alcala and Russ, 1990). However, to understand better the processes determining differences in abundance, it is important that studies on the effects of closures to fishing on long-lived species include examination of age structure. Furthermore, such studies must replicate reefs, take into account strong recruitment pulses that may mask fishing effects, and consider the effects of strong recruitment pulses when estimating mortality from catch curves.

Conclusion

In this study we found 1) no significant differences between the mean size and age of leopard coralgroupers on open and closed reefs were detected (such a result could have been a consequence of the design constraints of this study, such as not accounting for variability among replicate reefs, or the duration of closure (3–4 years); 2) that there were no differences in the overall sex ratio, despite observed differences in the sex structure, suggesting social induction of sex change; 3) that a strong recruitment pulse occurred, an event that may be extremely important in determining variation in abundance of leopard coralgroupers, and therefore very relevant to the fisheries; and 4) that age structure is more useful than size structure in detecting effects of fishing on leopard coralgroupers, and, therefore, age determination should be a routine component in the management of leopard coralgroupers populations.

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