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August 1997 Reevaluation of Shallow Reef Fish Populations at French Frigate Shoals and Midway Atoll

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ABSTRACT

Divers visually resurveyed reef fishes at two sites: French Frigate Shoals (FFS) and Midway Atoll (MWAY), in August 1997. Surveys were repeated at the same stations at which fishes were surveyed in July 1992 (at FFS), in August 1993 (MWAY), in September 1995 at both sites, and in August (FFS) and September (MWAY) 1996. Nine stations in two habitats (four on inner and outer barrier reefs and five on lagoonal patch reefs) were surveyed at FFS; nine stations were similarly sampled at MWAY. Three divers repeated the identical surveying protocols initiated in 1992-93: two divers simultaneously tallied all larger-than-recruit-sized ($\geq$2 cm Standard Length, SL) fish individuals, encountered within a band transect or other fixed area of reef, by species or lowest recognizable taxon. A third diver, meanwhile, estimated the body lengths of a random sample of fishes encountered within the same delimited area. As on previous surveys, divers rotated between the two (counting, size estimation) tasks.

At FFS, the estimated mean total numerical density (all fish taxa) in 1997 (14.9 ± 2.9[se] fish·10 m^{-2}) was indistinguishable from the analogous 1996 estimate (16.8 ± 4.0). Young-of-year (YOY) and other small-bodied ($\leq$7 cm SL) post-recruits represented about 48% of total fish counts in 1997 compared to 56% in 1996. Between-year differences in length distributions were the net result of disproportionately more 2-6 cm YOY-sized fishes at barrier reef stations in 1997 and relatively greater numbers of 4-7 cm YOY on patch reefs in 1996. The 23-mo (Sep 95-Aug 97) grow-out of strong 1995 year-classes, however, has not resulted in an increase in overall biomass densities. Standing biomass has been indistinguishable among recent years (1997: 0.6-1.0 kg·10 m^{-2}; 1996: 0.5-0.6 kg·10 m^{-2}; 1995: 0.6-1.9 kg·10 m^{-2}, depending on habitat).

At MWAY, the numerical densities of total fishes did not differ between 1997 (20.8 ± 8.3 fish·10 m^{-2}) and 1996 (19.2 ± 4.6). YOY and other small-bodied fishes comprised 54% and 33% of total counts in 1997 and 1996, respectively. Length-frequency distributions differed between 1997 and 1996, with relatively greater numbers of 2-5 cm YOY-sized and 11-20 cm adult-sized fishes at barrier reef stations in 1997 and disproportionately more 5-7 cm fishes (primarily recruits of aweoweo, *Priacanthus* sp.) on patch reefs in 1997. Biomass densities (kg·10 m^{-2}) have been similar among recent years (1997: 0.6-0.9; 1996: 0.8-0.9; 1995: 0.8 to <2).

Patterns of numbers and biomass at FFS and MWAY are discussed relative to the possible current and future food limitation of Hawaiian monk seals, *Monachus schauinslandi*, at FFS.

INTRODUCTION

The Hawaiian monk seal, *Monachus schauinslandi*, is endemic to the Hawaiian Archipelago where its present distribution in the Northwestern Hawaiian Islands (NWHI) is restricted to five main breeding populations, including French Frigate Shoals (FFS; 24°N, 166°W) and Midway Atoll (MWAY; 28°N, 177°W). Beginning in 1988 and continuing through 1997, the monk seal population at FFS, where about 30% of all NWHI monk seals currently reside, has declined by more than 50%. These declines at FFS, particularly of juvenile seals, are thought to be related to decreases in the forage base of monk seals whose broad diet consists primarily of benthic and other reef fishes, cephalopods, and crustacea (DeLong et al., 1984; Craig and Ragen, in review; Goodman-Lowe, 1998).

In order to evaluate whether reef fish populations had recently declined from prior levels, shallow water reef fishes were surveyed at FFS and MWAY in the early 1990s. Surveys were then repeated at stations previously surveyed by U.S. Fish and Wildlife personnel during 1980-83 (at FFS) and 1980 (MWAY). These repeated surveys were first conducted at FFS in July 1992 (DeMartini et al., 1993) and at MWAY in August 1993 (DeMartini et al., 1994). DeMartini et al. (1996) provides a comprehensive interpretation of temporal comparisons at both sites. In general, the numerical densities of post-recruit-sized ($\geq$2 cm Standard Length, SL) reef fishes declined by about one-third between the early eighties and surveys made during the first part of the following decade. At least at MWAY, these declines included both herbivorous and carnivorous fishes and occurred in both major habitat types (DeMartini et al., 1996). When resurveyed in September 1995, densities at FFS had increased by >60% compared to July 1992, and densities at MWAY had nominally increased about 30% over August 1993 (DeMartini and Parrish, 1996). Densities reestimated in August-September 1996, however, were indistinguishable from 1995 estimates at the respective site (DeMartini and Parrish, 1997). In this report, we update our shallow-water reef fish time series for surveys conducted at FFS and at MWAY during August 1997.

METHODS AND MATERIALS

Field Surveys

FFS

Surveys were conducted over a 4-day period (August 7-10, 1997). Reef fishes were surveyed at historical ("test") stations using the same recording protocols as those used in July 1992 and August 1996. (In September 1995, the data used for analysis were collected by two, rather than three, persons; three-person datasets were used in 1992, August 1996, and August 1997.) As in 1992, a total of four test stations on the barrier reef (BR: two Inner [Sta. Nos. 7, 8] and two Outer [Nos. 4, 6]), and five patch reef (PR) stations [Nos. 5c, 5d, 5e, 5f, 23] were surveyed in 1997. Each station was surveyed once; two divers tallied densities on a 500 m^2 band transect (BR stations) or within a delimited area (PR stations), while a third diver simultaneously characterized the body length distribution (by 1- to 10-cm Standard Length, SL, classes) of fishes in the same station area. Divers rotated fish counting and size estimation tasks. Fishes were tallied by species or lowest recognizable taxon; nomenclature was updated according to Randall (1996). DeMartini et al. (1993) specifies recording protocols, and DeMartini et al. (1996) describes station locations and habitats.

MWAY

Surveys were conducted over a 3-day period (August 14-16, 1997). Reef fishes were surveyed at test and other stations using recording protocols fundamentally the same as those used in August 1993 and September 1996. Four test stations on the barrier reef (BR: two Inner [Nos. 14, 21] and two Outer [Nos. 10, 19]) plus five patch reef (PR) stations were resurveyed in 1997. Outer BR station No. 10 was missed in 1996 because of unsafe diving conditions (DeMartini and Parrish, 1996); thus, 1996-97 comparisons were based on eight stations even though nine stations were surveyed in 1997. The PRs sampled included test stations Nos. 5, 11, and 17, plus 17A (a reference station used as replacement for test station No. 18; see DeMartini et al., 1994) and a patch reef first surveyed in 1996 (No. 6X; similar in area to test station No. 6 and used as its replacement). Use of the two replacement PRs was first necessitated by sand burial of PR test stations Nos. 6 and 18 in September 1996. These two test stations remained buried in sand when resurveyed in August 1997. DeMartini et al. (1994, 1996) provide additional details.

Data Analyses

Species rankings were used to evaluate assemblage structure. Some species of parrotfishes (adult *Scarus/Chlorurus* spp.) and surgeonfishes (*Acanthurus* spp.) that were at times difficult to distinguish underwater were pooled for analyses. Potential changes in numerical densities were evaluated for total fishes, herbivore and carnivore trophic levels, and each of four carnivore feeding guilds (benthic invertebrate-feeders or "benthic carnivores," corallivores, piscivores, and planktivores). Data were too few to partition analyses of size-frequency distributions and biomass densities finer than the two major trophic levels (herbivores, carnivores) within total fishes. Data were post classified into trophic levels and carnivore guilds as described by DeMartini et al. (1996). Analyses again focused on higher taxa for two principal reasons:

(1) the existing data for fish in the monk seal diet have family and grosser taxonomic resolution and (2) the statistical power to detect changes $\geq$50% in NWHI reef fish densities using diver visual surveys is generally insufficient at the species level (power = [1-ß] <0.80 at $\alpha_2 = 0.10$; DeMartini et al., 1996).

Temporal changes (1997 vs. 1996) in numerical densities were evaluated using bootstrapped-paired comparisons (Manly, 1991), with data paired by station between surveys. The results of 1,000 iterations were evaluated at $\alpha_2 = 0.10$ (Manly, 1991), and Bonferroni's correction was used to control Type I error in multiple comparisons ($\alpha_{crit} = \alpha/m$, where *m* = number of comparisons; Manly, 1991, p. 52). Analogous comparisons of size-frequency distributions were made using 2-Sample Kolmogorov-Smirnov (K-S) tests (Siegel and Castellan, 1988). Among-year patterns in the densities of total, including young-of-year (YOY) and other small-bodied fishes, were analyzed by apportioning numerical counts into YOY- (1-7 cm SL) and larger-sized (>7 cm) fishes based on size-frequency distributions; the effects of survey year (1992-93, 1995, 1996, 1997) and site (FFS, MWAY) were then evaluated by 2-Way ANOVA. Biomass densities were calculated first for each taxon as the cross product of mean body weight per fish and mean numerical density ($N \cdot 10\ m^{-2}$) and then summed over taxa. Variances were estimated by the delta method excluding covariances (Seber, 1982, p. 9) because analyses indicated that covariances were trivial. Large-bodied transient predators (sharks and the two jacks *Caranx ignobilis* and *C. melampygus*) were excluded from the biomass estimates.

Bootstrap comparisons were coded in Microsoft Quick Basic 4.5. All remaining analyses used PC SAS v. 6.04 (SAS Institute, Inc., 1990).

RESULTS

Relative Densities

FFS

Count data were log normally distributed among species. The 10 most numerous species dominated total fish densities (76-81%, depending on habitat) during the August 1997 survey. The top 20 and top 30 taxa contributed 89-91% and 95-96% to total densities, depending on habitat. Within habitats, rankings among taxa were generally similar in 1996 and 1997 (Table 1).

MWAY

The 10 most numerous species dominated total densities (80-90%, depending on habitat) in August 1997. The top 20 and top 30 taxa contributed 92-96% and 97-99% to total densities. Rankings within habitat generally persisted between 1996 and 1997, with the notable exception of zooplanktivorous aweoweo (*Priacanthus* sp.), which, although absent in 1996, ranked first in 1997 (Table 2) as a result of heavy but patchy YOY recruitment in 1997 only (elaborated below).

Numerical Densities

FFS

In August 1997, total fish densities averaged 14.9 ± 2.9(se) individuals·10 m^{-2} overall, with herbivores (33% of total) and carnivores (67%) averaging 4.9 fish·10 m^{-2} and 10.0 fish·10 m^{-2}, respectively (Tables 1 and 3). Herbivores were slightly less numerous (44% of total) than carnivores on the barrier reef; conversely, carnivores were much more numerous (69%) than herbivores on patch reefs (Tables 1 and 3). The benthic carnivore guild dominated numerically in both barrier and patch reef habitats (33-35% of total fishes; Tables 1 and 3). Densities were more than threefold greater overall on patch reefs.

Bootstrapped-paired comparisons of densities for pooled (barrier and patch reef) habitats did not generally differ between 1997 and 1996 for benthic carnivores (nominally 33% lower), planktivores (12% higher), or corallivores (45% higher). An apparent 19% increase in piscivores was significant (Table 3). Other significant changes that were inconsistent between habitats occurred for total fishes on the barrier reef (23% increase) and for herbivores at barrier (29% increase) and patch reef (24% decrease) stations (Table 3). Patterns of apparent density change between August 1997 and August 1996 were qualitatively dissimilar in barrier and patch reef habitats for total fishes, herbivores and pooled carnivores, all of which trended higher at barrier reef but lower at patch reef stations in 1997 (Table 3).

The overall numerical similarities between 1996 and 1997 at FFS included most component taxa. Differences were not apparent at the species level within major functional groups (Table 4).

MWAY

Total densities averaged 20.8 ± 8.3 fish·10 m^{-2} overall in August 1997, with herbivores (16% of total) and carnivores (84%) averaging 3.4 and 17.4 fish·10 m^{-2}, respectively (Tables 2 and 5). Herbivores were slightly more abundant (55%) than carnivores on the barrier reef, whereas carnivores were much more abundant (89%) on patch reefs (Tables 2 and 5). The benthic carnivore guild dominated numerically in the two habitats (36-41% of total fishes; Tables 2 and 5). Fishes were more than fourfold denser overall on patch reefs.

Bootstrapped-paired comparisons indicated significant declines between September 1996 and August 1997 for total fishes at BR stations and for herbivores (43%) in both habitats (Table 5). Between-year comparisons, however, differed insignificantly (or inconsistently between habitats) for total fishes, pooled carnivores, benthic carnivores, planktivores, and corallivores (Table 5). The significant 53% decline in piscivores (Table 5) should be considered especially suspect because estimates for these patchily distributed and relatively uncommon fishes are extremely imprecise.

Most of the 1996-97 declines in numerical densities (Table 5) were not taxonomically general at MWAY (Table 4). Conversely, those nominal declines that were taxonomically general--for benthic carnivores and planktivores (Table 4)--were not statistically significant at the guild level (Table 5).

General

Fish densities have been indistinguishable at FFS and MWAY since the inception of the recent series of size-specific surveys in 1992/93 (Table 6A). However, at both sites the densities of total fishes and, in particular, the densities of most YOY-sized fishes have differed among recent surveys (Table 6A-C). On the 1995 survey, YOY densities increased over 1992-93 values, then returned to 1992-93 levels during 1996-97 (2-Way ANOVA on site and survey effects: survey effect $P < 0.001$, Table 6C). YOY damselfish densities, though, have not differed among recent years (Table 6D).

Length-Frequency Composition

FFS

Roughly equivalent proportions of young-of-year (YOY) and other small-bodied ($\leq$7 cm) fish contributed to length-frequency tallies in August 1997 and August 1996; overall, YOY-sized fishes comprised 48% and 56% of all fishes tallied in August 1997 and August 1996, respectively. Length-frequency distributions differed between years for fishes sampled in each major habitat and both habitats pooled (2-sample K-S tests, all $P < 0.001$; Fig. 1A,B). Relatively greater numbers of 2-6 cm YOY were observed at BR stations in 1997, whereas disproportionately more 4-7 cm fishes were observed on patch reefs in 1996.

MWAY

Length-frequency distributions differed between August 1997 and September 1996 in each and both habitats pooled (K-S tests, all $P < 0.001$; Fig. 2A,B). These 1996-97 differences reflected relatively greater numbers of 2-5 cm YOY-sized and 11-20 cm adult-sized fishes at BR stations in 1997 and disproportionately more 5-7 cm YOY aweoweo at patch reefs in 1997. The overall contributions of YOY-sized ($\leq$7 cm) fishes were 54% and 33% in August 1997 and September 1996, respectively. Excluding aweoweo, the proportion of YOY-sized fishes in 1997 was 36%.

Biomass

FFS

In August 1997, the biomass density of total fishes was 0.6-1.0 kg·10 m^{-2}, depending on habitat. Herbivores comprised 78% and 44% of total fish biomass in barrier and patch reef habitats, respectively; the corresponding estimates for carnivores were 22% and 56%. The 1997 estimates are statistically equivalent to the respective August 1996 estimates for herbivores, carnivores, and total fishes (Fig. 3A). Variances were large (Fig. 3A), and statistical power was insufficient to resolve suggestions of change between years. YOY-sized fishes contributed <1% to total biomass on both the 1997 and 1996 surveys.

MWAY

Biomass densities in August 1997 averaged 0.6-0.9 kg·10 m^{-2}. About 30% comprised carnivores and 70% were herbivores at BR stations; conversely, about 70% were carnivores and 30% were herbivores on patch reefs. Biomass estimates in 1997 were similar and statistically indistinguishable from September 1996 values (Fig. 3B). YOY-sized fishes represented <1% of total biomass in 1997 as well as 1996.

DISCUSSION

Temporal Comparisons of Relative Abundance

FFS and MWAY

The distributions of counts among taxa were fundamentally similar between the August 1997 and the August (FFS)-September (MWAY) 1996 surveys. At FFS, the overall rank composition of species within the shallow reef fish assemblage has persisted despite quantitative changes in the abundance and size structure of reef fishes that occurred between July 1992 and September 1995 (DeMartini and Parrish, 1996) and more recent changes in size structure during 1995-97. At MWAY, species rankings remained concordant along with numerical densities and size distributions from August 1993 to September 1995, and despite changes in size structure between 1995-97 (the latter, in part, reflecting the exceptional recruitment of aweoweo at only two out of five patch reefs in 1997). We continue to interpret these observations as indicating general stability in fish assemblage structure at both FFS and MWAY.

Temporal Changes in Numerical Density

FFS

Between July 1992 and September 1995, the numerical densities of shallow reef fishes had generally increased >60% over 1992 levels at FFS (DeMartini and Parrish, 1996). These increases had been spatially general--an estimated 37% on the barrier reef and 63% on patch reefs (DeMartini and Parrish, 1996)--indicating that numerical increases had occurred on larger-than-physiographic spatial scales (Sale et al., 1994). Marginally lower overall densities occurred on the August 1996 survey, equivalent to those observed in August 1997 (Table 6A). These similarly low (relative to 1995) 1996-97 estimates introduce doubt as to whether the numerical increases evident in 1995 have persisted since that time (Fig. 4A).

MWAY

Total fish densities had appeared to increase by 31% overall at MWAY between August 1993 and September 1995, but the 1995 increase was then not statistically demonstrable (DeMartini and Parrish, 1996, Table 5). With the benefit of additional years' data, total fish densities at MWAY can now be recognized as higher in 1995 (vs. 1993) and have been either intermediate (between 1993 and 1995 levels) or similar to 1993 during 1996-97 (Table 6A; Fig. 4B). Numerical densities of YOY-sized fishes in particular were higher during 1995 than when first estimated on the 1993 survey, but have questionably remained at 1995 levels during 1996-97 (Table 6B,C; Fig. 4B).

Other 1996-97 comparison data reinforce the notion that fish densities have declined from 1995 levels at MWAY. The magnitude of the various 1997 estimates, relative to the respective estimates of 1996, ranged broadly around no net change (from 90% less to 183% greater) among the trophic levels and component feeding guilds examined. However, the observation that a nominal (P = 0.09) 52% decline (Table 5) in benthic carnivores included qualitative declines in 12 of 14 component species within the Top 30 suggests that lower densities in 1997, although statistically insignificant, might be real.

General

Equivalent fish densities during 1996-97 at FFS and MWAY, at levels perhaps lower than those observed in 1995, suggest that, at least for total fishes, densities generally persisted during 1996-97 at levels equivalent to those that occurred during the early nineties (DeMartini et al., 1996; Table 6A-C this study). YOY-sized fishes in particular illustrate the pattern of 1995 increases followed by lower levels in 1996-97 (Table 6C). Much of the pattern of temporal variation in YOY excludes damselfishes, a group with an atypically brief (2-3 weeks) pelagic larval stage (Wellington and Victor, 1989) that is arguably less susceptible to advection loss. This observation is consistent with recruitment variation being driven by advection losses of the majority of reef fishes having more typical, several-month-long planktonic durations.

The early 1970s through mid-1980s was an unusually turbulent and productive period in the central North Pacific; conversely, the late 1980s and early 1990s signaled a return to more "normal," lower productivity in the NWHI ecosystem (Polovina et al., 1994; 1995). Productivity during and since the mid 1990s has presumably persisted at normally lower levels, and the 1995 increases and subsequent marginal declines in fish densities at FFS and MWAY have occurred during a period of typical and unexceptional planktonic productivity. The inconstancy of reef fish recruitment during 1995-97 therefore suggests that the year-class success of most reef fishes in the NWHI is not strongly determined by water-column productivity. Rather, chance temporal and spatial vagaries of larval transport are likely important components of recruitment success.

Temporal Patterns of Size Composition and Biomass

FFS

YOY had been relatively more numerous at FFS in September 1995 compared to July 1992 due to strong year-classes of many species of shallow reef fishes in 1995 (DeMartini and Parrish, 1996; E. DeMartini, unpubl. obser.). The relative increase in YOY numbers between the 1992 and 1995 surveys (42%) was substantial. Although the 1995 increase in YOY counts was less than that necessary to explain the then observed increase of >60% in total fish density, the higher YOY counts partly contributed to the general increase in numbers. In 1995, YOY contributed only about 2% to the standing biomass of shallow reef fish at FFS (DeMartini and Parrish, 1996). Higher apparent biomass densities in 1995 reflected the greater numerical densities of larger-bodied fish that perhaps represented the grow-out of juveniles from successful year classes established between 1992 and 1995 (DeMartini and Parrish, 1996).

In 1996, YOY again contributed little to overall standing biomass. Biomass densities remained indistinguishable from 1995 despite the relative increase in 1996 of yearling-sized fish. This is not surprising because in 1996 yearling-sized (7-11 cm) fish, although larger-bodied than YOY (1-7 cm, 0.1-12 g), still averaged only about an ounce (27-32 g) per individual, depending on habitat. More than several highly successful year classes in succession would have been needed to appreciably increase standing biomass.

In 1997, YOY once more contributed little to overall standing biomass, and biomass densities remained similar to those estimated in 1996. The observed 1996-97 differences in size composition resulted from changes in relative abundance of various YOY fishes whose small body mass (<10g·individual) minimally influenced overall standing biomass.

MWAY

The equivalent proportions of YOY-sized fish in August 1993 and September 1995 (31-33% of all fishes tallied) remained unchanged in September 1996 (33%) despite the observed 1995-96 changes in length-frequency distributions. In 1997, the total YOY proportion jumped to 54%, but this primarily reflected the large but patchy recruitment of 5-7 cm aweoweo at only 40% of the patch reefs sampled. Like FFS, the changes in size composition observed at MWAY occurred in both major habitats; however, unlike FFS, the changes noted at MWAY in 1997 were qualitatively similar increases in the proportion of YOY in both habitat types. The 1996 increase in yearlings had suggested that successful 1995 year classes became established at MWAY even though our estimates in 1995 were then too imprecise to adequately describe them. The geographic scope of reef fish recruitment success in 1995 may have extended farther upchain in the NWHI than we had originally surmised (DeMartini and Parrish, 1996). Continued YOY increases in 1997 may result in the buildup of some shallow reef fish stocks at MWAY in the future, particularly if the 1997 year-class of aweoweo becomes well established.

The increase in relative numbers of small adult-sized (11-20 cm SL) fish noted in 1997 was insufficient to promote an increase in standing biomass that was detectable within the precision limits of a single survey. At present, our estimates of biomass density at MWAY (and FFS) indicate that values have ranged broadly around 1 $kg \cdot 10\ m^{-2}$ from 1992/3 through 1997 (DeMartini and Parrish, 1997; Fig. 3, this study).

General

Our long-term average estimates of fish biomass densities (1 $kg \cdot 10\ m^{-2}$) on relatively pristine, shallow NWHI reefs are about twice the average level of fish standing biomass on shallow, exploited reefs in the main Hawaiian Islands (MHI) (Grigg, 1994; DeMartini et al., 1996). We reemphasize the importance of these differences as evidence for the high present and continuing level of exploitation of reef fishes in the MHI.

SUMMARY AND CONCLUSIONS

At FFS, the numerical density of reef fishes (all taxa, both major habitats) in August 1997 was equivalent (mean ± se = 14.9 ± 2.9 fish$\cdot$10 m^{-2}) to the estimate made in August 1996 (16.8 ± 4.0 fish$\cdot$10 m^{-2}). At MWAY, the analogous estimate made in August 1997 (20.8 ± 8.3 fish$\cdot$10 m^{-2}) was equivalent to that made in September 1996 (19.2 ± 4.6 fish$\cdot$10 m^{-2}).

The length frequency distributions of fishes differed between 1997 and 1996 at both FFS and MWAY, but in dissimilar fashion at the two sites. At FFS, YOY and other small-bodied (1-7 cm) fishes were abundant (relative to MWAY) in 1996 (56% of total counts) as well as 1997 (48%) and 1995 (43%). At MWAY, YOY and other small fishes comprised 54% of total fishes tallied in August 1997, a value larger than analogous estimates made in September 1996 (33%), September 1995 (33%), or August 1993 (31%). The large proportion of YOY at MWAY in 1997 was dominated by the exceptionally heavy recruitment of aweoweo at a minority of patch reefs in 1997. Excluding aweoweo, YOY sizes comprised only about one-third (36%) of all fishes tallied at MWAY in 1997.

At FFS, estimates of standing biomass in 1997 (0.6-1.0 kg$\cdot$10 m^{-2}, depending on habitat) were indistinguishable from values estimated in 1996 (0.5-0.6 kg$\cdot$10 m^{-2}), in 1995 (0.7-1.9 kg$\cdot$10 m^{-2}), and in 1992 (0.4-1.1 kg$\cdot$10 m^{-2}). Biomass estimates at MWAY in 1997 (0.6-0.9 kg$\cdot$10 m^{-2}) were similar to those estimated at MWAY in 1996 (0.8-0.9 kg$\cdot$10 m^{-2}), in 1995 (0.8 to < 2 kg$\cdot$10 m^{-2}), and in 1993 (1.0-1.1 kg$\cdot$10 m^{-2}). YOY contributed little (<1%) to overall biomass densities in 1997 at FFS as well as MWAY.

The increases in recruitment detected at FFS in September 1995 likely represented the continuation of recent increases in reef fish numbers that then had not yet fully translated to increased adult standing biomass (DeMartini and Parrish, 1996). Length frequencies observed on the August 1997 surveys, and on the August 1996 (FFS) and September 1996 (MWAY) surveys, suggest that at both sites the grow-out of successful 1995 year classes has continued, but that recruitment in 1996 and in 1997 was poor to moderate relative to 1995 and that standing reef fish biomass consequently has not increased appreciably at either site. Surveys over additional years would be necessary to document the likely sporadic establishment of year classes and the accrual of biomass by successful, sequential year classes necessary for substantial increases in the reef fish forage base at FFS. Temporal changes in reef fish abundance at MWAY need further documentation because of the importance of this site for potential translocation of seals. In general, the link between reef fish recruitment and production and meaningful increases in the reef fish component of the monk seal forage base still needs to be further described.

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Table 1.--FFS. Mean numerical densities ($N \cdot 10\ m^{-2}$) of major fish taxa on the August 1996 and August 1997 surveys. The top 30 taxa are ranked in descending order of their weighted grand means within each survey for both habitat types pooled. Trophic guild acronyms are: bc = benthic carnivores; h = herbivores; co = corallivores; zp = planktivores; pi = piscivores. A dashed horizontal line separates the top 30, 1996 taxa from lower-ranked taxa that ranked within the top 30 on the 1997 survey. Density on barrier reefs and patch reefs is indicated as DBR and DPR, respectively.

	August 1996				August 1997			
Taxon	Rank96	DBR	DPR	Dboth	Rank97	DBR	DPR	Dboth
Dascyllus albisella(zp)	1	0.03	5.40	3.01	1	0.06	4.59	2.58
Mulloid. vanicolensis(bc)	2	0.20	3.09	1.81	9	abs	0.96	0.48
Stegastes fasciolatus(h)	3	0.32	2.48	1.52	3	0.29	2.14	1.32
Thalassoma duperrey(bc)	4	0.88	1.53	1.24	4	0.61	1.78	1.26
Ctenochaetus strigosus(h)	5	0.54	1.77	1.22	6	0.53	1.15	0.88
Juvenile Scaridae(h)	6	0.34	1.60	1.04	5	0.35	1.49	0.99
Mulloid. flavolineatus(bc)	7	abs	1.82	0.91	35	abs	0.10	0.05
Chaetodon miliaris(zp)	8	0.04	1.27	0.72	11	0.02	0.69	0.39
Chlorurus/Scarus spp.[b](h)	9	0.26	0.75	0.54	13	0.30	0.29	0.29
Chromis ovalis(zp)	10	0.08	0.77	0.46	2	0.56	2.44	1.60
Chromis vanderbilti(zp)	11	0.78	abs	0.39	7	1.12	abs	0.56
Acanthurus triostegus(h)	12	0.20	0.53	0.38	8	0.84	0.33	0.56
Neoniphon sammara(bc)	13	<0.01	0.56	0.31	12	abs	0.63	0.31
Lutjanus kasmira(bc)	14	0.09	0.41	0.27	16	0.04	0.36	0.22
Acanthurus spp.[a](h)	15	0.34	0.17	0.25	10	0.75	0.17	0.43
Centropyge potteri(h)	16	<0.01	0.37	0.21	20	0.04	0.21	0.13
Stethojulis balteata(bc)	17	0.10	0.28	0.20	15	0.16	0.31	0.24
Chromis hanui(zp)	18	0.02	0.31	0.18	14	0.22	0.31	0.27
Kyphosus spp.	19	0.32	abs	0.16	73	<0.01	abs	<0.01
Paru. multifasciatus(bc)	20	0.10	0.18	0.15	17	0.04	0.28	0.18
Labroides phthirophagus(bc)	21	0.01	0.25	0.14	19	<0.04	0.22	0.13
Canthigaster jactator(bc)	22	0.12	0.15	0.13	24	0.08	0.14	0.11
Thalassoma ballieui(bc)	23	0.09	0.16	0.13	22	0.15	0.09	0.12

Table 1.--FFS (continued).

Taxon	August 1996				August 1997			
	Rank96	DBR	DPR	Dboth	Rank97	DBR	DPR	Dboth
Macrophar. geoffroy(bc)	24	0.02	0.21	0.13	21	<0.01	0.21	0.12
Zebrasoma flavescens(h)	25	<0.01	0.21	0.12	28	0.02	0.15	<0.10
Myripristis spp.	26	0.17	0.06	0.11	36	0.03	0.06	<0.05
Plectro. johnstonianus(co)	27	0.01	0.15	0.09	18	0.03	0.27	0.16
Chaetodon fremblii(bc)	28	0.04	0.11	0.08	31	0.04	0.07	0.06
Bodianus bilunulatus(bc)	29	0.07	0.09	0.08	25	0.08	0.13	<0.11
Paru. pleurostigma(bc)	30	<0.01	0.11	0.06	26	<0.01	0.19	<0.11
Naso unicornis(h)	32	0.03	0.05	0.05	23	<0.04	0.17	0.11
Gomphosus varius(bc)	40	abs	0.06	0.03	29	0.03	0.12	0.08
Epibulus insidiator(pi)	43	0.01	0.03	0.02	30	<0.01	0.12	0.07
Top 10 taxa		4.2	20.5	12.5		5.6	16.2	10.6
Top 20 taxa		5.2	23.8	15.0		6.3	18.9	13.0
Top 30 taxa		5.5	25.0	16.1		6.6	20.2	14.0
Total fishes		5.6	25.8	16.8		6.9	21.2	14.9

[a/] *Acanthurus nigroris, A. nigrofuscus, A. blochii, A. xanthopterus, A. dussumieri, and A. olivaceus*

[b/] *Chlorurus/Scarus* spp. adults, including *S. dubius, C. perspicillatus* and *C. sordidus*

Table 2.--MWAY. Mean numerical densities (N·10 m^{-2}) of major fish taxa on the September 1996 and August 1997 surveys. The top 30 taxa are ranked in descending order of their weighted grand means within each sampling period for both habitat types pooled. For trophic guild acronyms, see Table 1 caption. A dashed horizontal line separates the top 30, 1996 taxa from lower-ranked taxa that ranked within the top 30 on the 1997 survey. August 1997 BR data include Station 10; data were not collected at Station 10 on the September 1996 survey. Density on barrier reef and patch reefs is indicated as DBR and DPR, respectively.

	September 1996				August 1997			
Taxon	Rank96	DBR	DPR	Dboth	Rank97	DBR	DPR	Dboth
Mulloid. flavolineatus(bc)	1	<0.01	5.14	3.21	59	0.01	abs	<0.01
Juvenile Scaridae(h)	2	0.45	4.08	2.72	5	0.13	1.09	0.66
Stegastes fasciolatus(h)	3	2.20	2.68	2.50	2	1.52	1.81	1.68
Dascyllus albisella(zp)	4	abs	3.22	1.61	4	abs	2.20	1.08
Thalassoma duperrey(bc)	5	1.46	1.36	1.39	3	1.40	1.66	1.55
Chaetodon miliaris(zp)	6	abs	1.99	0.99	7	<0.01	0.98	0.55
Chromis ovalis(zp)	7	0.55	0.71	0.65	6	0.82	0.44	0.61
Paru. pleurostigma(bc)	8	<0.01	1.02	0.64	10	0.01	0.51	0.29
Apogon spp.(zp)	9	abs	1.11	0.56	8	0.09	0.61	0.38
Stethojulis balteata(bc)	10	0.47	0.26	0.34	11	0.11	0.32	0.23
Thalassoma ballieui(bc)	11	0.37	0.16	0.24	9	0.38	0.21	0.29
Abudefduf abdominalis(zp)	12	0.38	<0.14	0.23	12	0.40	0.06	0.21
Neoniphon sammara(bc)	13	0.01	0.35	0.22	40	0.02	0.03	0.03
Kyphosus sp.(h)	14	0.33	0.14	0.21	13	0.30	0.13	0.21
Labroides phthirophagus(bc)	15	0.05	0.31	0.21	15	0.07	0.23	0.16
Cheilinus bimaculatus(bc)	16	abs	0.39	0.19	16	abs	0.31	0.16
Coris venusta(bc)	17	0.02	0.28	0.18	19	0.08	0.19	0.14
Chlorurus/Scarus spp.[b](h)	18	0.32	<0.05	0.15	14	0.34	0.06	0.19
Paru. multifasciatus(bc)	19	abs	0.30	0.15	35	abs	0.08	0.04
Acanthurus triostegus(h)	20	0.31	0.04	0.14	17	0.30	0.02	0.14
Mulloid. vanicolensis(bc)	21	abs	0.26	0.13	41	<0.01	0.04	0.02
Aulostomus chinensis(pisc)	22	abs	0.24	0.12	--	abs	abs	--
Chaetodon fremblii(bc)	23	<0.01	>0.16	0.10	22	0.04	0.14	0.09
Chromis hanui(zp)	24	<0.01	0.16	0.10	23	0.04	0.13	<0.09
Acanthurus leucopareius(h)	25	0.20	abs	0.10	18	0.29	abs	0.14

Table 2.--MWAY (continued).

Taxon	September 1996				August 1997			
	Rank96	DBR	DPR	Dboth	Rank97	DBR	DPR	Dboth
Synodontidae(pi)	26	abs	0.16	0.08	20	<0.01	0.23	0.13
Myripristis spp.(zp)	27	abs	>0.16	0.08	44	0.02	0.02	0.02
Ctenochaetus strigosus(h)	28	<0.02	0.11	0.07	21	0.17	0.09	0.12
Paracirrhites forsteri(bc)	29	<0.01	0.11	0.07	33	<0.01	0.08	0.04
Paru. porphyreus(bc)	30	<0.01	0.09	0.06	51	<0.01	0.02	0.01
Priacanthus sp.(zp)	abs	abs	abs	abs	1	0.02	16.82	9.36
Bodianus bilunulatus(bc)	33	0.04	0.06	0.05	24	0.05	0.07	0.06
Chaetodon auriga(bc)	45	0.03	abs	0.02	25	0.12	abs	0.06
Plectro. johnstonianus(co)	35	0.04	0.05	<0.05	26	0.02	0.09	0.06
Scorpaena ballieui[c](bc)	41	abs	.06	0.03	27	abs	0.12	0.06
Acanthurus spp.[a](h)	38	0.09	abs	0.04	28	0.12	abs	0.06
Oxycheilinus unifasciatus(bc)	62	<0.01	abs	<0.01	29	0.02	0.08	0.06
Pervagor spilosoma(co)	54	abs	0.02	<0.01	30	<0.01	0.09	0.05
Top 10 taxa		6.8	21.7	14.6		5.9	26.4	16.4
Top 20 taxa		7.5	24.2	16.6		6.8	28.2	18.1
Top 30 taxa		7.7	25.4	17.5		7.2	28.9	18.8
Total fishes		7.9	26.1	18.3		7.4	29.3	19.5

a/ *Acanthurus nigrofuscus* and/or *A. nigroris*
b/ *Chlorurus/Scarus* spp. adults, including *S. dubius, C. perspicillatus,* and *C. sordidus*
c/ *Scorpaena ballieui* coded as *Scorpaena* sp. on September 1996 survey

Table 3.--FFS. Summary comparisons between August 1996 and August 1997 densities ($N \cdot 10\ m^{-2}$), by habitat and across both major habitats, for major functional groupings of fishes. All tests were evaluated at $\alpha_{crit} < \alpha_{2,0.10/m}$ with m's as defined in the Methods section. Standard errors are listed in parentheses for the August 1996 means. Sample sizes are 4, 5, and 9 for barrier reef (BR), patch reef (PR), and both habitats, respectively. (* indicates significance at < $\alpha_{2,0.10/m}$.) Tests for stations pooled over both habitats were considered "na" if trends for BR and PR stations were opposite.

Trophic level/guild	Reef type	AUG 1996 mean (se)	% Total fishes	Change (%)	Prob. change = 0
Total fishes	BR	5.6 (1.5)	100	+ 23	<0.001 *
	PR	25.8 (3.3)	100	- 18	ns
	both	16.8 (4.0)	100	- 12	na
Herbivores	BR	2.5 (0.3)	44	+ 29	<0.001 *
	PR	8.0 (0.6)	31	- 24	<0.001 *
	both	5.6 (1.0)	33	- 13	na
Secondary consumers	BR	3.2 (1.4)	56	+ 18	ns
	PR	17.7 (2.8)	69	- 15	ns
	both	11.2 (3.0)	67	- 11	na
Benthic carnivores	BR	1.8 (0.3)	33	- 21	ns
	PR	9.0 (1.9)	35	- 35	ns
	both	5.8 (1.6)	35	- 33	0.07
Planktivores	BR	1.1 (1.0)	20	+ 78	ns
	PR	7.8 (1.5)	30	+ 4	ns
	both	4.8 (1.5)	29	+ 12	0.39
Corallivores	BR	0.06(.03)	<1	+ 50	<0.001 *
	PR	0.27(.04)	1	+ 44	0.15
	both	0.18(.05)	1	+ 45	0.14
Piscivores	BR	0.12(.11)	2	+ 39	ns
	PR	0.59(.40)	2	+ 16	<0.001 *
	both	0.38(.23)	2	+ 19	<0.001 *

Table 4.--FFS and MWAY. Summary of nominal (signed) changes in density within the top 30 taxa of reef fishes, grouped by major trophic level and carnivore feeding guild, between the August (FFS) or September (MWAY) 1996 and the August 1997 surveys. Noted are results for binomial tests of the relative number of nominal increases and decreases.

	French Frigate Shoals		Midway Atoll	
	Increase	Decrease	Increase	Decrease
Herbivores	2	7	3	4
Secondary consumers	10	11	3	20
Benthic carnivores	6	8	2	12
Planktivores	3	3	0	7
Corallivores	1	0	0	0
Piscivores	0	0	1	1
Total fishes	12	18	6	24

H_o : No. decreases = No. increases

H_{a2} : No. decreases $\neq$ No. increases

	French Frigate Shoals	Midway Atoll
	18/30 decreases	24/30 decreases
	P = 0.37	P = 0.002

Table 5.--MWAY. Summary comparisons between September 1996 and August 1997 densities ($N \cdot 10\ m^{-2}$), by habitat and across both major habitats, for major functional groupings of fishes. Sample sizes are 3, 5, and 8 for BR, PR, and both habitats, respectively (August 1997 data for BR Station 10 are omitted from comparisons because Station 10 was not sampled in September 1996.) Other details are noted in the Methods section and Table 3 caption.

Trophic level/guild	Reef type	SEP 1996 mean (se)	% Total fishes	Change (%)	Prob. change = 0
Total fishes	BR	7.8 (1.3)	100	- 15	<0.001 *
	PR	26.0 (5.2)	100	+ 13	ns
	both	19.2 (4.6)	100	+ 8	na
Herbivores	BR	4.0 (0.7)	51	- 8	ns
	PR	7.2 (1.7)	28	- 55	ns
	both	6.0 (1.2)	31	- 43	<0.01 *
Secondary consumers	BR	3.8 (0.7)	49	- 21	ns
	PR	18.8 (4.9)	72	+ 39	ns
	both	13.2 (4.0)	69	+ 32	na
Benthic carnivores	BR	2.8 (0.9)	36	- 11	ns
	PR	10.7 (4.6)	41	- 59	ns
	both	7.7 (3.1)	40	- 52	0.09
Planktivores	BR	0.9 (0.9)	12	- 51	ns
	PR	7.5 (2.8)	29	+183 \a	ns
	both	5.0 (2.1)	26	+167	na
Corallivores	BR	0.07 (.05)	<1	+ 20	ns
	PR	0.07 (.04)	<1	+154	ns
	both	0.07 (.03)	<1	+105	0.24
Piscivores	BR	0.07 (.03)	<1	- 90	ns
	PR	0.55 (.13)	2	- 50	ns
	both	0.37 (.12)	2	- 53	<0.001 *

Table 5.--MWAY (continued)

[a/]This huge (1997 minus 1996) difference reflects the extraordinary numbers (31-53 fish/10 m^2) of *Priacanthus* sp. young-of-year recruits observed at Patch Reef stations (Nos. 5 and 11 only) on the August 1997 survey; no YOY *Priacanthus* sp. had been observed at any station (or elsewhere) on the September 1996 survey at MWAY.

Table 6.--FFS and MWAY. Summary results of 2-Way ANOVAs testing the effects of site (FFS, MWAY) and survey (1992-93, 1995, 1996, 1997) on the numbers of (A) total fishes of all sizes, (B) YOY-sized (1-7 cm SL) fishes of all taxa, (C) YOY of all taxa excluding damselfishes, and (D) YOY-sized damselfishes only tallied on fish length surveys. Site-by-survey interaction terms were insignificant ($P > 0.5$) in all cases and are not listed. The results of Student-Newman-Keuls *a posteriori* tests are provided.

(A) Total fishes, all sizes

Source	df	SS	MS	F-ratio	Prob>F
Model	4	372,595	93,149	3.45	0.013
Site	1	53,956	53,956	2.00	0.16
Survey	3	318,639	106,213	3.94	0.012
Error	67	1,807,472	26,977		
Total	71	2,180,067			

1995 ≥ 1997 = 1996 = 1992-93

(B) YOY-sized fishes, all taxa

Source	df	SS	MS	F-ratio	Prob>F
Model	4	61,392	15,348	2.98	0.025
Site	1	2,123	2,123	0.41	0.52
Survey	3	59,268	19,756	3.83	0.014
Error	67	345,341	5,154		
Total	71	406,733			

1995 ≥ 1997 = 1996 ≥ 1992-93

(C) YOY-sized fishes, all taxa excluding damselfishes

Source	df	SS	MS	F-ratio	Prob>F
Model	4	35,881	8,970	5.98	<0.001
Site	1	5	5	0.00	0.95
Survey	3	35,876	11,959	7.97	<0.001
Error	67	100,502	1,500		
Total	71	136,383			

1995 > 1996 = 1997 = 1992-93

Table 6.--FFS and MWAY (continued).

(D) YOY-sized damselfishes only

Source	df	SS	MS	F-ratio	Prob>F
Model	4	15,243	3,811	1.17	0.33
Site	1	2,438	2,438	0.75	0.39
Survey	3	12,804	4,268	1.31	0.28
Error	67	217,482	3,246		
Total	71	232,725			

1997 = 1996 = 1995 = 1992-93

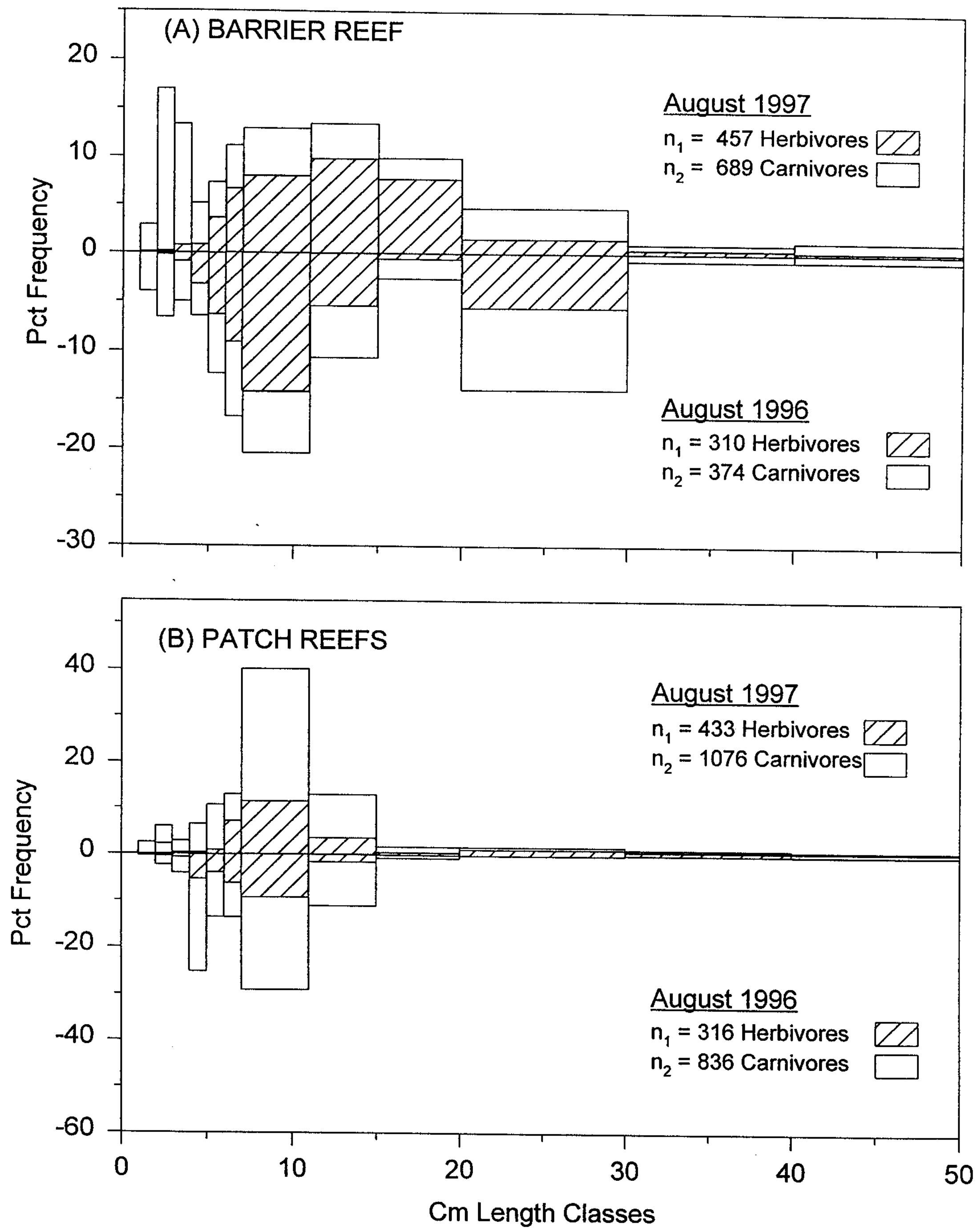

Figure 1--FFS. Percentage frequency distributions of body length classes (cm SL) for herbivores (diagonal-right histograms) and carnivores (hollow histograms). Data for the barrier reef and patch reefs are plotted in panels A and B, respectively. In each panel, data for the August 1997 and August 1996 surveys are plotted above and below the horizontal axis, respectively.

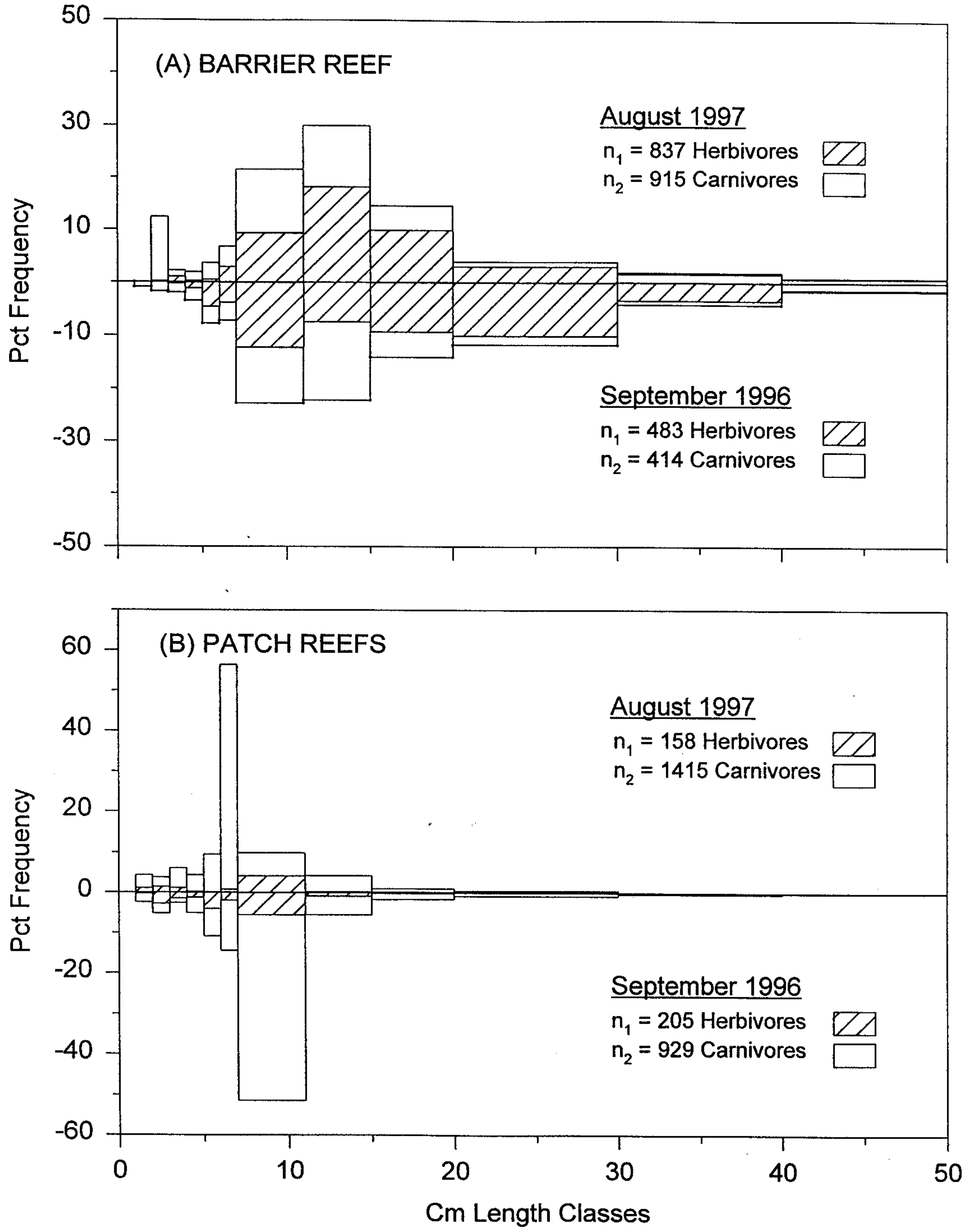

Figure 2--MWAY. Percentage frequency distributions of body length classes (cm SL) for herbivores and carnivores on the barrier reef (Panel A) and patch reefs (B), during the August 1997 (above x-axis) and September 1996 (below x-axis) surveys.

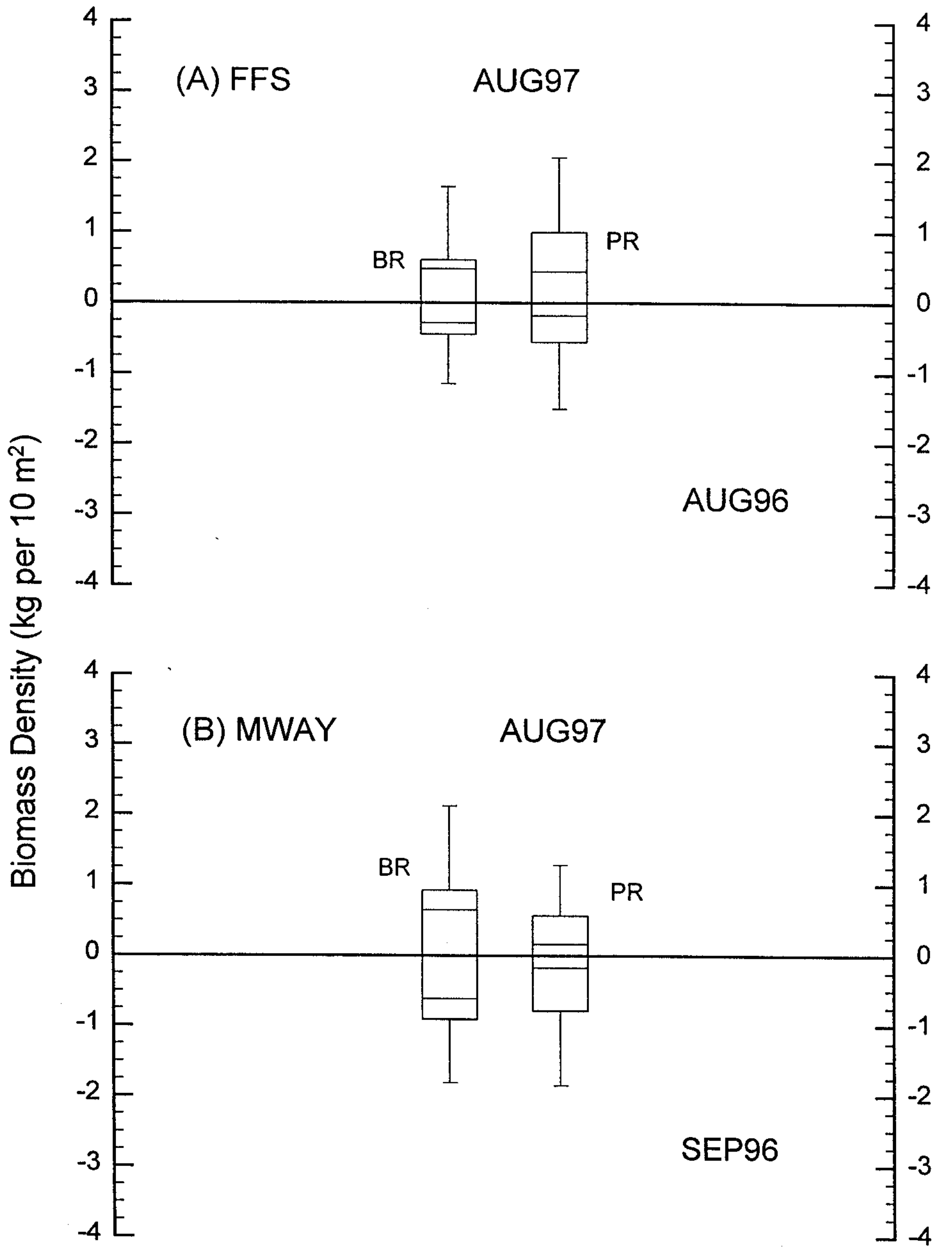

Figure 3--(A) FFS and (B) MWAY. Estimated biomass densities ($kg \cdot 10\ m^{-2}$) of herbivores (diagonal-right histograms) and carnivores (hollow histograms), during August 1997 surveys at FFS and MWAY (above x-axis) and in August (FFS) and September (MWAY) 1996 (below x-axis). Also indicated is one approximate standard error of the biomass density of total (herbivore plus carnivore) fishes in each (barrier reef, BR; patch reef, PR) habitat during each survey.

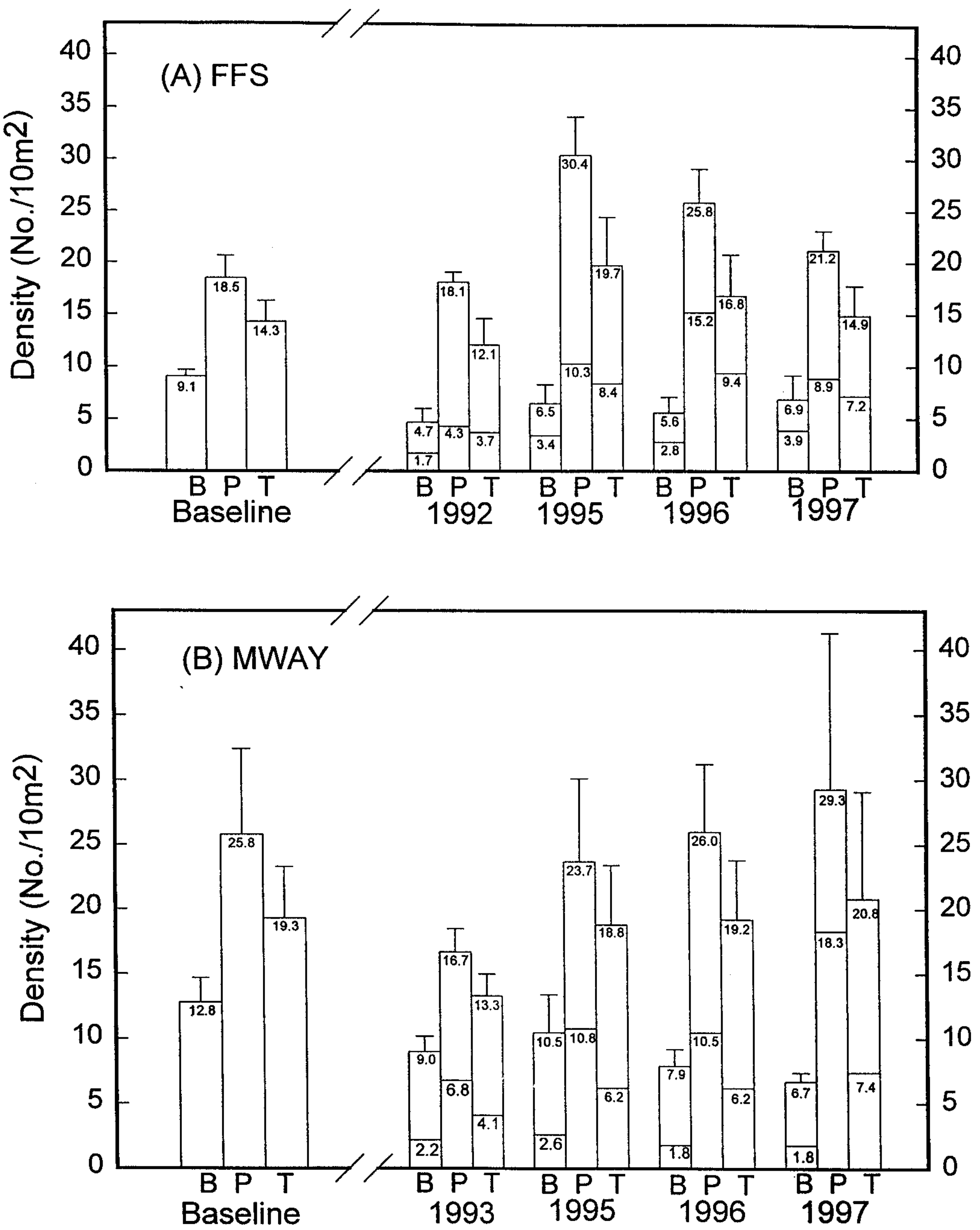

Figure 4--(A) FFS and (B) MWAY. Time series of the estimated numerical densities (N·10 m^{-2}) of total and YOY-sized (1-7 cm SL) fishes, at barrier reef (B), patch reef (P) and both habitats (T), during baseline surveys, and in 1992 (FFS), 1993 (MWAY), and 1995, 1996, and 1997 (both sites) surveys. The 1997 estimates for P and T habitats include aweoweo. Baseline survey data were collected during 1980 and 1983 at FFS and during 1980 at MWAY (DeMartini et al., 1996). Vertical bar indicates 1 se of total fish density.