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ABSTRACT

This document represents the sixth and last of a series of Honolulu Laboratory reports providing estimates of shallow (< 15-m-deep) reef fish population densities based on diver-surveys conducted at roughly annual intervals at two sites (French Frigate Shoals (FFS) and Midway Atoll (Midway) in the Northwestern Hawaiian Islands (NWHI)). The purpose of the time series has been to develop the capability to characterize the standing stock densities of shallow reef fishes, as one potentially important component of the monk seal (*Monachus schauinslandii*) forage base with precision sufficient to detect twofold changes over a decadal time scale when sampled at a yearly frequency. This recent series of surveys began in 1992 (at FFS) and 1993 (Midway). Updated results for 3 survey years (1998-2000, inclusive), plus a comprehensive evaluation of key variables for the entire 8/9-yr time series, are herein presented. Statistical analyses emphasize those temporal and spatial variables likely to have the greatest influence on the distribution and abundance of reef fishes as a forage base. The results of two types of special diver-survey are also provided: (1) a one-time (August 1998) survey of the fishes and macroinvertebrates (potential monk seal prey) in deep (52, 61 m) talus slope habitat at FFS; and (2) a methods-calibration survey conducted at the two sites in the year 2000. The former one-time survey provides a limited but significant complementary interpretative base for the shallow-water time series. The latter calibration study links the reported time series with analogous data on resident reef fish stocks, complemented by data on apex predator fishes (sharks and jacks), corals, macroinvertebrates, algae, and their habitat distributions, being collected at all 10 major NWHI reef and atolls (including FFS and Midway), as part of the Northwestern Hawaiian Islands–Resource Assessment and Monitoring Program (NOW-RAMP), a multiagency study newly established in September-October 2000.

INTRODUCTION

The endangered Hawaiian monk seal, *Monachus schauinslandi*, is endemic to the Hawaiian Archipelago where its present distribution in the Northwestern Hawaiian Islands (NWHI) is restricted to six main breeding subpopulations, including French Frigate Shoals (FFS; 24°N, 166°W) and Midway Atoll (Midway; 28°N, 177°W). Beginning in 1988 and continuing through 1998, the monk seal population at FFS, where about 30% of all NWHI monk seals currently reside, has declined by nearly 60% (Forney et al., 1999; Johanos and Baker, 2000). The decline at FFS, particularly of juvenile seals, is thought to be related to a decrease 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; Goodman-Lowe, 1998; Craig and Ragen, 1999). Fluctuations in this forage base are thought to be effected by natural temporal cycles (Polovina et al., 1994); recently, evidence has been presented that important, within-archipelago spatial variation in productivity exists as well (Schmelzer, 2000). Efforts to enhance the recovery of the Hawaiian monk seal require a thorough understanding of the factors that may be limiting population growth. Determining the abundance of available prey resources is a key element in evaluating the possible influence of food on monk seal population trends. Fatty acid analysis has lately been used by S. Iverson of Dalhousie University to begin building a library of signatures for possible identification of prey in the monk seal diet. However, specimen collections and analyses of monk seal fatty acid composition are incomplete (although promising), and species-level quantification of the monk seal diet is still not possible. Characterization of monk seal foraging habitat using seal-mounted (CRITTERCAM) underwater video has met with some recent success (Parrish et al., 2000), but the technique cannot provide detailed enumeration of the species and sizes of the prey present within foraging habitats or utilized by the seals. At present the assessment of monk seal prey abundance is primarily limited to conventional methods--e.g., in situ diver-surveys at shallow (< 15-m-deep) scuba depths--for estimating the more conspicuous, diurnal potential prey types occurring in one segment of the monk seals' foraging habitats.

A lengthy time series of diver surveys was conducted during 1992/93 and 1995-2000 to develop the capability to characterize the standing stock densities of shallow reef fishes as one potentially important component of the monk seal forage base, with precision sufficient to detect twofold changes over a decadal time scale when sampled at a yearly frequency. The observations reported herein contribute to this time series.

The entire series of surveys can be briefly recapitulated as follows. In order to evaluate whether reef fish populations had recently declined from prior levels, shallow water reef fishes were surveyed at FFS and Midway in the early 1990s, revisiting stations previously surveyed by U.S. Fish and Wildlife Service (USFWS) personnel during 1980-83 (at FFS) and 1980 (Midway). These repeated surveys were conducted at FFS in July 1992 (DeMartini et al., 1993) and at Midway in August 1993 (DeMartini et al., 1994). DeMartini et al. (1996) provides an interpretation of temporal comparisons at both sites based on all data available through 1994. In general, the numerical densities of post-recruit-sized (≥2 cm standard length, SL) reef fishes declined by about one-third between the early eighties and early nineties. At least at Midway, these declines included both herbivorous and carnivorous fishes and occurred in both major habitat types (DeMartini et al., 1996). It was then thought that these changes might have been reflecting interdecadal-scale regime shifts in oceanic productivity (Polovina et al., 1994). Surveys were repeated annually at each site starting in 1995, but these lacked resolution necessary to detect smaller two- to threefold changes between adjacent surveys (DeMartini and Parrish, 1996, 1997, 1998).

In this report, we update our shallow-water reef fish time series for surveys conducted at FFS and Midway during 1998, 1999, and 2000 and provide a comprehensive evaluation of the combined 1992/93 and 1995 through 2000 data. Additional estimates of fish densities (numbers only) are provided for several, deep (52, 61 m) windward talus slope stations surveyed at FFS in August 1998 using technical dive gear. The results of two series of method-calibration surveys, conducted in summer 2000 at both sites, are presented as a bridge between the 8/9-yr time series and newly derived results using methods for estimating reef fish densities which were introduced in 2000 as part of the NOW-RAMP.

METHODS AND MATERIALS

Standard Field Surveys

FFS.--In 1998, surveys were conducted over a 5-day period (August 23-27); in 1999, surveys spanned 5 days from August 18 to 22. The year 2000 survey also extended 5 days from August 13-17. Reef fishes were monitored at the same series of historical station-areas ("stations") used throughout the entire time series which began in1992 (DeMartini et al., 1996). Four 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 1998, 1999, and 2000, as previously. Each station was surveyed once per survey. Recording protocols used on the 1998 and 1999 surveys were identical to those used in 1992, 1996, and 1997; i.e., 3-person data sets were obtained in each of these 5 years. On the 1995 and 2000 surveys, the data used for analysis were collected by two, rather than three, persons. Specifically, on the 1998 and 1999 surveys at FFS, three NMFS, Honolulu Laboratory divers--E. DeMartini (EED), F. Parrish (FAP), and R. Boland (RCB)--repeated the identical surveying protocols initiated in 1992: two divers tallied by 1- to 10-cm standard length, SL, classes, all larger-than-recruit-sized ($\geq$2 cm SL) fish individuals, encountered during 30 min within a band transect (at BR stations) or other fixed area of reef (PR stations). The dimensions of all band transects were 50-m long by 10-m wide (500 m^2 area). Delimited areas at patch reefs averaged 160±70(std) m^2. Fishes were recorded by species or lowest recognizable taxon, with nomenclature updated according to Randall (1996). A third diver, meanwhile, visually estimated the body lengths of a random sample of fishes encountered during 30 min within the same delimited area. As on previous surveys, divers typically rotated between the two (counting, size estimation) tasks to distribute sampling error and avoid bias. On the 1995 and 2000 surveys, two divers (FAP, RCB) performed both tasks. Whenever surveys lacked a third diver, both divers estimated fish lengths during a 15-min period immediately following each fish count. Initial (DeMartini et al., 1996) and subsequent (E. DeMartini, unpubl. data) evaluations of among-diver error have had coefficients of variation (CV, std/mean x 100%) of 15% or less for fish tallies made by these three personnel. DeMartini et al. (1993) describes habitats and provides a map of the station locations. P-coded GPS positions of the monitoring stations are listed in Appendix Table A.

At FFS only, additional stations on the talus slope of the outside (windward, exposed) barrier reef were sampled on the August 1998 survey. Fishes and conspicuous invertebrates were enumerated on timed (20-min), 2-m wide belt transects conducted at two depths (52, 61 m) at each of four stations by two divers (FAP, RCB) using open-circuit technical diving gear and mixed gases (heliox and nitrox), during August 24-27. Counts of organisms on each transect at each depth and station were tallied by five noncontiguous, 3-min segments to facilitate data recording and analysis. Organisms sheltering beneath talus were included in the counts; pieces of talus were flipped (and replaced) if moveable by a single diver (< 22 kg). Body sizes of tallied organisms were not estimated because of bottom time constraints.

Midway.--Surveys in 1998 were conducted over a 4-day period (August 6-9); the 1999 survey also spanned 4 days, from July 25-28. Six days (July 16-21) were required for the year 2000 survey. Reef fishes were surveyed at the same monitoring stations used in previous survey-years, beginning with the first survey in 1993. Initial comparisons of monitoring with other reference stations in 1993 indicated that they were representative of their habitat type at Midway (DeMartini et al., 1996). Recording protocols were approximately the same as those used on the 1993, 1995, 1996, and 1997 surveys. As at FFS, surveys were conducted by the same personnel (EED, FAP, RCB) in all years except 1995 and 1998, when a 2-person team (1995: EED, FAP; 1998: EED, RCB) conducted all counting and sizing tasks as described for FFS in 1995 and 2000. Four 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 1998 and again in 1999. Outer BR station No. 10 was missed in 1996 because of unsafe diving conditions (DeMartini and Parrish, 1997). The PRs sampled included stations Nos. 5, 11, and 17, plus 17A (a reference station used as replacement for station No. 18; see DeMartini et al., 1994) and a patch reef first surveyed in 1996 (No. 6X; similar in area to station No. 6 and used as its replacement). Use of these two replacement PRs was first necessitated by sand burial of PR stations Nos. 6 and 18 in September 1996. These two stations remained buried in sand when resurveyed in 1998 and 1999. On the 1999 survey, continuing sand movements within Welles Harbor further necessitated replacing PR station No. 17 (then half buried) with a new patch reef, PR No. 17X. Shifting sand had uncovered an unusually large (nearly 500 m^2) expanse of reef habitat at PR station 5 on the 2000 survey. Midway patch reefs averaged 126 ± 87(std) m^2 in area (range 11-484 m^2). DeMartini et al. (1994) provides complementary details including a map of the station locations. In Appendix Table A P-coded GPS coordinates of historical monitoring stations are presented.

Methods-Calibration Study

In 2000 a special study was conducted to quantify the relationships between density and biomass estimates obtained using the historical methods of 1992/3, 1995-2000 and to obtain analogous estimates using transect protocols newly established in 2000 for baseline assessment and monitoring to be conducted by the NOW-RAMP. Two series of matched (same-dive) fish assessment exercises were conducted in addition to the usual surveys of stations at Midway in July and on *Townsend Cromwell* cruises TC00-10 and TC00-11 in August (at FFS) and October (Midway). The two types of calibration studies were the following: (1) Standard fish counts conducted using historical protocols ("Old Method": 50-m long by 5-m wide; 250-m^2 area, 15-min duration) were matched with same-diver counts in a 2-m-wide by 50-m-long (100 m^2, 10-min duration) strip centered on the wider lane but lagged by 30 minutes ("New Method"). The same diver (RCB) was used in all matched-pair surveys to remove additional variance attributable to diver differences. (2) The latter New Method diver-counts, developed for the NOW-RAMP, were matched with video records for a 2-m-wide by 50-m-long strip, surveyed concurrently by a second diver, offset about 5-m to one side of the strip in which fishes were being directly counted. The two types of calibration thus included the effects of a brief (0.5-hr) time lag and short (5-m) spatial separation, respectively, when comparing the two types of direct counts and comparing the newly developed, direct counting method with the video record. A single observer (EED) later viewed and scored all video records for the number of individual fish, by species or lowest recognizable taxon, present on the video record.

Data Analyses

Potential changes in numerical densities were evaluated for higher taxonomic and functional categories; namely, total fishes; herbivore and carnivore trophic levels; and each of four carnivore feeding guilds (benthic invertebrate-feeders or "benthic carnivores," corallivores, piscivores, and planktivores). Transient apex predators (sharks and carangid jacks) were excluded from our primary density estimates of piscivores because the densities of such large rare organisms were poorly quantified by tallies limited within small areas at few stations. The relative frequency occurrence at stations of two principal species of jacks was evaluated by factorial G-test (Zar, 1984). Analyses also included those fish families identified as among the top 3 ranked diurnal and nocturnal prey of monk seals based on examination of the hardparts present in all scat and spew samples examined by Goodman-Lowe (1998). Key life-stages (young-of-year "yoy", older) of total fishes and other selected groupings (i.e., total yoy densities adjusted for particularly variable taxa such as recruit aweoweo–see Results) were also evaluated. 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. Post-classification into trophic levels and carnivore guilds followed DeMartini et al. (1996). Trophic level and carnivore guild assignments are listed in Appendix Table B for all species encountered at quantitative stations at each reef site during the time series through 2000. Analyses have been constrained to 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 (statistical power = $[1-\beta] < 0.80$ at $\alpha_2 = 0.10$: DeMartini et al., 1996; where β = Type 2 Error or the probability of failing to reject a false null hypothesis: Cohen, 1988). Relative densities and the species composition ("assemblage structure") of reef fishes were not explicitly reevaluated for the entire time series at each site because most previous evaluations (except for Midway in 1997—reflecting an atypically large recruitment of a single species—see DeMartini and Parrish, 1998) have indicated persistence in composition and relative abundances. Appendix Table B also provides mean densities for each habitat at each site (averaged over all 7 survey years) for each taxon in the time series, ranked by its weighted mean biomass density over both habitats at a site.

Spatial and temporal patterns of numerical densities were evaluated using factorial (2-, 3-way) ANOVAs (Model 1, all factors fixed). The spatial factors evaluated were habitat (2 levels: barrier reef, lagoonal patch reefs), nested within reef site (2 levels: FFS, Midway). A nested model was chosen because of differences between the FFS and Midway sites in nominally equivalent habitats, particularly differences in the three-dimensional structure of patch reefs. Lagoonal patch reefs at FFS are more complex, with greater live coral cover, and provide a greater range of shelter hole sizes; whereas, the more ancient and weathered patch reefs at Midway provide less relief and few large shelter holes. The temporal factor analyzed was survey-year (7 levels: 1992/93, 1995-2000). A Bonferroni correction ($P_{crit} = 0.1/m$, where m = number of tests within the series of evaluations; Manly, 1991) was used to adjust for multiple testing. For infrequent cases in which ANOVA results were marginal ($P_{0.1} > P_{obs} > P_{crit}$) or the estimated density differences were >50% but insignificant, we evaluated the power of the test at $P_{crit} = 0.1/m$.

The densities of size-classes within total fishes were estimated by apportioning numerical counts into yoy- and older- (larger-) sized fishes as follows. For each species in the database, a size-frequency distribution was generated for all FFS and Midway surveys pooled. Using these length distributions, a species-specific, yoy-to-older body length threshold was identified (Appendix Table B) based on the separation of yoy from older age-group modes. Biomass densities ($kg \cdot 10\ m^{-2}$) were calculated first for each taxon at each station as the cross product of mean body weight ($kg \cdot fish^{-1}$) and mean numerical density ($N\ fish \cdot 10\ m^{-2}$) in each survey year. These biomass estimates were then averaged over stations within habitat type (BR, PR) to provide a mean and a variance for each habitat and survey year. Biomass density estimates were apportioned for higher taxonomic levels after pooling species over the appropriate category. Large-bodied apex predators (all sharks; the three jacks *Caranx ignobilis*, *C. melampygus*, and kahala, *Seriola dumerili*; and the grey snapper or "uku" *Aprion virescens*) were excluded from the biomass estimates because they are very large, rare and patchily distributed, fast-swimming transients which are unlikely prey of monk seals; they were poorly quantified by the method used; and they inappropriately inflate resident fish biomass estimates.

ANOVAs were calculated using proc glm of PC SAS v. 6.12 (SAS Institute, Inc., 1990). A balanced design was retained in the analyses by estimating the lone missed data point (BR Station 10 on the 1996 survey at Midway) based on Station 10 estimates for the other survey years at Midway; error degrees of freedom were decremented after the fact by one (always with trivial effect because total sample size for the 7 survey years was 126). A parametric GLM analysis model was used because standard nonparametric ANOVAs were inappropriate for the nested model described above. Analyses used untransformed data to facilitate interpretation of a posteriori contrasts. Despite the use of raw data, the observed patterns were robust to the assumptions of homogeneous variances and normality because the design was balanced (Underwood, 1997). Trials using both log-transformed and raw data for several key test variates (yoy and older-stage fish densities) produced nearly identical, respective P-values, attesting to the robustness of the balanced design.

RESULTS

Shallow Reef Fish Surveys at FFS and Midway

Numerical Densities and Stage Composition

At FFS, total fish densities during the past several survey years averaged 17.1 ± 1.5(se) individual fish $\cdot 10\ m^{-2}$ in 1998, 17.9 ± 1.9 individuals $\cdot 10\ m^{-2}$ in 1999, and 20.1 ± 2.5 individuals $\cdot 10\ m^{-2}$ in 2000 (Table 1). At Midway, the respective estimates were 16.8 ± 1.8, 18.2 ± 4.7, and 9.1 ± 0.5 individuals $\cdot\ 10\ m^{-2}$ on the 1998, 1999, and 2000 surveys (Table 2). Numerical densities have thus far been indistinguishable between FFS and Midway (2-way ANOVA; site effect: $P >> 0.1$) for all fish taxa pooled (Table 3A; Fig. 1). Densities of component trophic levels and foraging guilds likewise have not differed between FFS and Midway (Tables 4, 5, 6). The effects of survey year also have been indetectable for numbers of all higher taxa at each site to date (Tables 3, 6). For total fishes (whose estimates are more precise than those of herbivores and carnivores), CVs of grand means were about 15% and 30% at FFS and Midway, respectively (Tables 1, 2). Based on data collected through 2000, the statistical power to detect temporal changes $\geq$ 50% as a survey year effect (at $\alpha = 0.1$) for numerical densities of total fishes using a nested 2-way (habitat within site, survey year) ANOVA model has been only about 45%. A survey year difference of at least half again as large (≈ 75%) would have been necessary for an 80% probability of detection.

The apparent site similarity for all taxa pooled conceals opposing differences for yoy- and older-stage fishes at FFS and Midway in recent years. Densities of yoy have been lower and those of older fishes higher at FFS, and vice versa at Midway (Tables 1,2; site effect: all $P < 0.001$: Table 3B,C). The significant site effect for yoy persists even after the data for one especially dynamic species, the endemic Hawaiian bigeye or "aweoweo" *Priacanthus meeki* (exceptionally present in huge numbers at only 2 of 5 patch reefs, only on the 1997 survey at Midway), are excluded (Table 3D; Fig. 1). Site differences in yoy are not dominated by at least one other major taxon--the numerical densities of yoy damselfishes (Pomacentridae), a family that contributed 34% and 20% of all yoy (26% excluding aweoweo) and represented 30% and 32% of total fishes at FFS and Midway, respectively, did not differ between sites (Tables 1, 2, 3E,F). Rather, the observed differences between FFS and Midway in yoy densities have been caused by differences between sites in recruitment by a variety of other species of reef fishes. There also has been no apparent temporal pattern to the fluctuations in yoy recruits at either site; at both FFS and Midway, yoy fish numbers have not varied monotonically or in any other predictable manner over time during 1992/93 and 1995-2000 (Fig. 2).

One generally significant spatial factor influencing numerical densities has been habitat type. For most compound taxa, the effect of habitat (nested within site–see Methods) has been consistent and highly significant at both FFS and Midway (Tables 3, 6). Overall, total numerical densities on lagoonal patch reefs have averaged nearly five- and threefold greater than on the barrier reef of the respective site since 1992/93 (Fig.1). At FFS, the densities of total fishes on patch reefs were an estimated 3.9, 5.5, and 8.5 times greater than on barrier reefs during 1998, 1999, and 2000 (Table 1). At Midway the corresponding estimates were 2.2, 3.8, and 2.0 times greater on patch reefs (Table 2).

Density contrasts have differed between trophic levels. Herbivorous (primary consumer) fishes in general have been denser at barrier reefs and carnivorous fishes (secondary consumers) have been denser at lagoonal patch reefs at both FFS and Midway (Table 6). Since 1992, herbivores at FFS have been only slightly less numerous (46% of total fishes) than carnivores on its barrier reef; conversely, carnivores have been much more numerous (73%) than herbivores on lagoonal patch reefs at FFS (Tables 1, 6). The benthic carnivore guild has dominated numerically in both barrier and patch reef habitats (55% and 54% of all carnivores, respectively) at FFS (Table 4). The distribution of trophic categories among habitats has been qualitatively consistent over the entire time series at FFS (Table 4). Likewise at Midway, herbivores have been a large minority (46% of total) on its barrier reef, whereas carnivores have dominated (79%) on patch reefs (Tables 2 and 5). The benthic carnivore guild has dominated numerically in both habitats at Midway as well (43-64% of all carnivores; Table 5).

One additional factor that might possibly be influencing fish densities differently at FFS (where the population of monk seals is relatively dense but declining) and at Midway (where the monk seal population is relatively sparse but increasing) is whether or not a particular taxon contributes significantly to the monk seal diet. For this reason, we evaluated whether site, survey year, or habitat factors might be influencing densities of top-ranked families of monk seal prey. Results were mixed: the densities of two fish families were lower at FFS, two were lower at Midway, and the densities of a fifth family were indistinguishable between FFS and Midway (Table 7; Fig. 3).

Body size composition.--At FFS low and variable proportions of yoy and other small-bodied fishes contributed to length-frequency tallies in 1998-2000; overall, yoy comprised 15, 8, and 7% of all fishes tallied on the 1998, 1999, and 2000 surveys (Table 1). The corresponding estimates at Midway were higher but less variable (34%, 32%, and 31%) in 1998, 1999, and 2000, respectively (Table 2). At both FFS and Midway, length-frequency distributions differed among the 1998, 1999, and 2000 surveys in each and both habitats pooled (K-S tests, all $P < 0.001$). If, for simplicity, all size-composition data are pooled over all survey years at each site, length-frequency distributions differed between FFS and Midway for fishes in each major habitat and both habitats pooled (2-sample K-S tests, all $P < 0.001$; Fig. 4A,B). This at least partly reflects fundamental site differences in the average magnitude of yoy recruitment between Midway (where yoy have averaged 37% of all fish [and 28% of all fish excluding *P. meeki*]) and FFS (mean = 12%)(Tables 1,2, and 3B,D).

Variations in yoy represent more than just site differences at the spatial scale of entire reefs, however. Yoy have been proportionately better represented on lagoonal patch reefs versus the barrier reef at Midway but better represented (although at indistinguishably low densities) on the barrier reef versus patch reefs at FFS (Fig. 1). During 1992 and 1995-2000 at FFS, yoy contributed an estimated average 10% to fish totals at patch reefs versus 27% in barrier reef habitat (Table 1). Yoy (excluding *P. meeki*) on average contributed 31 and 17% to patch reef and barrier reef totals, respectively, at Midway during 1993 and 1995-2000 (Table 2).

Length-frequency distributions also clearly illustrate some important differences between reef sites and trophic levels after data are pooled by habitat over survey years (Fig. 4). Mean body weight per fish individual has differed between FFS and Midway, and this has partly reflected the presence of relatively more, larger-bodied lower-trophic-level fishes at Midway (site effect: 2-way ANOVA, $P = 0.001$; Tables 8, 9). Excluding transient predatory sharks and jacks, the size of reef fish has averaged almost 40% larger at Midway (mean = 103 g · fish^{-1}) than at FFS (74 g · fish^{-1}; Table 9). If sharks and jacks (non-monk seal prey) are included, however, the mean body size of fishes at FFS (both habitats) inflates by over 40%, and the overall FFS estimate then becomes indistinguishable from that for Midway, where both sharks and large jacks have been much less frequently encountered (see Frequency Occurrence of Apex Predators, below).

The interrelations of fish body size with habitat and trophic level have been similar at FFS and Midway. Like the yoy-older stage dichotomy in numbers, the body size of resident non-apex predator reef fishes at each reef has averaged greater in barrier reef than patch reef habitat (Table 8). Individual fish weight at FFS averaged nearly 50% greater on the barrier reef (89 g · fish^{-1}) versus patch reefs (60 g · fish^{-1}) during 1992 and 1995-2000 (Table 9). At Midway, mean body weight estimates averaged over fivefold greater in barrier reef (172 g · fish^{-1}) versus patch reef habitats (33 g · fish^{-1}) during 1993 and 1995-2000 (Table 9). The mean body weights of herbivores (FFS: 120 g · fish^{-1}; Midway: 161 g · fish^{-1}) were greater than that of lower-level carnivores (55 and 66 g · fish-1, respectively) overall; herbivores have tended to particularly dominate in average size as well as numbers and biomass in barrier habitats at both sites (Tables 1,3, 9; Fig. 4). Lower-level carnivores have averaged over twofold smaller in body size (60 g · fish^{-1}) than herbivores (140 g · fish^{-1}) overall; lower-level carnivores were especially small-bodied on patch reefs at FFS (46 g · fish^{-1}) and at Midway (30 g · fish-1; Table 9) in particular.

Biomass Densities

During the past 3 years, the biomass densities of total resident (excluding apex predator) reef fishes have, as in the preceding survey-years, generally averaged around 1 kg ·10 m^{-2} at both reef sites (Fig. 5). Estimates on shallow reefs at FFS were 1.35, 1.0, and 0.9 kg ·10 m^{-2} in 1998, 1999, and 2000, respectively. Corresponding estimates were 1.2, 0.9, and 0.7 kg ·10 m^{-2} at Midway (Table 8). Like the numerical densities of total fishes, total fish biomass densities have varied imperceptibly over the entire time series (2-way ANOVA; site effect: $P >> 0.1$; Table 9). CVs of grand means estimated through the 2000 surveys were 32% and 27% at the respective site (Table 8). The statistical power to detect a survey year effect in a nested 2-way ANOVA for total biomass density has thus far been about 78%.

Unlike total fish numbers, however, total fish biomass at the reef-site scale has differed between habitat types at sites in several interesting ways. For example, total biomass densities have fluctuated around the same levels on the Midway barrier reef (1.42 kg ·10 m^{-2}) and on FFS patch reefs (1.55 kg ·10 m^{-2})--at levels more than twofold greater than on Midway patch reefs (0.62 kg ·10 m^{-2})) and on the FFS barrier reef (0.52 kg ·10 m^{-2}; Table 8). Overall values for habitats pooled differed little between FFS and Midway if transient apex predators are excluded from the estimates. However, if (for heuristic reasons not directly related to the issue of monk seal forage) these apex predators are included, biomass densities actually averaged about one-half higher at FFS (1.44 kg ·10 m^{-2}) versus Midway (0.99 kg ·10 m^{-2}) because of the relatively greater abundance of apex predators in both habitats at FFS.

Biomass densities partitioned by trophic levels show similar patterns at FFS and Midway: In 1998 at FFS, the biomass density of total fishes ranged from 0.5 to 2.2 kg ·10 m^{-2}, depending on habitat (Table 8). Herbivores comprised 70% and 49% of total fish biomass in barrier and patch reef habitats, respectively; the corresponding estimates for carnivores were 30% and 51% (Fig. 5). Total biomass density ranged from 0.4 to 1.7 kg ·10 m^{-2} in 1999, varying with habitat as in 1998. On the 1999 survey, about 25% of total biomass was represented by carnivores and 75% by herbivores at BR stations, and about 56% and 44% were carnivores and herbivores, respectively, at PR stations (Fig. 5). Biomass densities similarly ranged between habitats from 0.1 to 1.6 kg $\cdot 10\ m^{-2}$ in 2000 (Table 8). About 31% were carnivores and 69% herbivores on the barrier reef, and 74% and 26% were carnivores and herbivores, respectively, at patch reefs (Table 8). During all 3 recent years at FFS, biomass densities averaged about 1.1 kg $\cdot 10\ m^{-2}$ (59%) for carnivores and 0.7 kg $\cdot 10\ m^{-2}$ (41%) for herbivores on patch reefs. Analogous estimates at BR stations were 0.09 (29%) and about 0.2 kg $\cdot 10\ m^{-2}$ (71%) for carnivores and herbivores, respectively (Fig. 5).

Trophic partitioning of biomass between habitats at Midway during 1998-2000 was similar to that at FFS. Biomass density estimates at Midway in 1998 ranged from 0.5 to 1.8 kg $\cdot 10\ m^{-2}$, depending on habitat. Analogous biomass densities in 1999 and 2000 averaged 0.6 to 1.3 kg $\cdot 10\ m^{-2}$ and 0.4 to 1.1 kg $\cdot 10\ m^{-2}$, respectively (Table 8). On the 1998 survey, about 27% were carnivores and 73% were herbivores at BR stations; conversely, about 69% were carnivores and 31% were herbivores at PR stations. About 45% were carnivores and 55% were herbivores on the barrier reef on the 1999 survey, and 83% and 17% were carnivores and herbivores, respectively, at patch reefs (Fig. 5). On the 2000 survey, about 26% were carnivores and 74% were herbivores at BR stations, and about 61% and 39% were carnivores and herbivores, respectively, at PR stations (Fig. 5). During all 3 recent years at Midway, biomass densities averaged almost 0.4 kg $\cdot 10\ m^{-2}$ (75%) for carnivores and about 0.1 kg $\cdot 10\ m^{-2}$ (25%) for herbivores on patch reefs (Fig. 5); the corresponding estimates for carnivores and herbivores at BR stations were 0.45 (32%) and 0.94 kg $\cdot 10\ m^{-2}$ (68%), respectively (Table 8).

Yoy fishes consistently represented <1% of total biomass estimated on each annual survey at FFS and Midway on the 1998-2000 surveys. This was similar to patterns observed at both sites prior to the 1997 survey. Rather, biomass densities, body weight metrics, and numerical densities all support the observation that relatively large-bodied (mainly herbivorous) reef fishes predominate in barrier reef habitats at both FFS and Midway, and that relatively small (mostly micro-carnivorous) reef fishes comprise the majority of the fishes present on lagoonal patch reefs at both sites, especially Midway (Tables 8, 9).

Frequency Occurrence of Apex Predators

Transient apex predators (sensu Carr and Hixon, 1995) comprising reef sharks, large jacks, and uku are inadequately quantified by small-scale diver-transects because of the relative rarity and patchy spatial and temporal distributions of these fishes. For this reason, we used frequency of occurrence (presence-absence at survey-stations) as an index of their abundances. Sharks and uku in general were too rare (sharks in particular at Midway) for meaningful evaluation of possible site (FFS versus Midway) and temporal effects. Both of the two largest-bodied and most abundant species of large jacks (the giant trevally or white ulua, *Caranx ignobilis*, and the bluefin trevally or “omilu”, *C. melampygus*) were encountered sufficiently often to enable such an analysis. We were specifically interested in whether any change in encounter rate occurred beginning in 1996, when ecotourism was initiated at Midway. Overall, each species of jack has been encountered less frequently at Midway relative to FFS since surveys began in 1992/93 (Table 10); in addition, there has been a relative dearth of encounters at Midway since 1996 (Fig. 6). Results to date are consistent with one or more types of human impact at Midway that perhaps have been magnified since 1996 (see Discussion).

Deep Slope Survey at FFS in August 1998

In addition to the standard shallow-water survey, a diver visual observation survey was conducted on the lower talus slope of the northwestern (windward) barrier reef at FFS in August

1998. A total of 55 fish and conspicuous macroinvertebrate (e.g., lobster, octopus) taxa were encountered on eight, 20-min belt transects, each surveying a bottom area of approximately 150-m^2, conducted at two (52, 61 m) depths at each of four stations. Species richness was about twice as great (28.2± 4.6[se][n=4] taxa per transect) at the 52-m depth compared to the 61-m depth (14.8± 2.1 taxa per transect). A majority of the taxa encountered (58-59% at the two depths) were the same as those present at the FFS shallow stations. The remaining 48-49% of the organisms encountered were taxa (like zooplanktivorous anthiine basslets) representative of greater depths in the NWHI. *Octopus* sp., slipper lobster (*Scyllarides squammosus*), and muraenid and congrid eels together comprised a small minority ($<0.5\%$) of the organisms tallied, although a considerably greater (but inestimable) fraction of total biomass. A 2-way ANOVA of depth nested within station effects on the numbers of individual organisms (of all taxa pooled) encountered on transects was marginally ($P \approx 0.05$) significant for both depth and station (Table 11).

Methods-Calibration Study

Direct diver counts using the Old Method were predictably related to direct counts using the New Method; coefficients of determination (r^2) for numbers and biomass were 0.46-0.47. The New Method, however, produced numerical and biomass density estimates (an average of 16 fish weighing 1.0 $kg \cdot m^{-2}$), which were about threefold and twofold higher than the respective Old Method estimates (Table 12; Fig.7). Indirect fish counts from video were more strongly related ($r^2 =$ 0.97 and 0.83 for numbers and biomass, respectively) to New Method direct counts than were relations between the Old-New Method direct counts (Table 13; Fig. 8). Observations ancillary to the calibrations per se also provide interesting data pertinent to reef fish surveying methodologies (see Discussion).

DISCUSSION

Temporal Changes in Numerical Density

Previous reports in an Administrative Report series have attempted to interpret year-to-year similarities and differences in fish density estimates at FFS and Midway. The comprehensive analysis of temporal and spatial patterns provided in this report supercedes the evaluations provided by previous reports in the series. Prior-described patterns can be briefly summarized as follows: Numerical fish densities at shallow-reef stations were first characterized as having declined overall at FFS and Midway between the original 1980-83 baseline and the initial survey (1992/93) in the recent time series (DeMartini et al., 1993, 1994, 1996). Evaluations of subsequent temporal variation, starting with the first annual survey in 1995 and continuing through 1997 (DeMartini and Parrish, 1997, 1998), were qualitative only because of insufficient data.

Comprehensive analyses of the entire time series reported herein indicate that total resident reef fish stocks remained at “normal” low (relative to 1980-83) levels throughout the 1990s. The densities of yoy fishes have been more dynamic (see below) but have nonetheless varied without pattern (trend).

Temporal Patterns of Oceanic Productivity

The relation between oceanic (planktonic) productivity and biomass (as a proxy for production) of fishes on shallow NWHI reefs remains elusive. 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 typical lower productivity in the NWHI ecosystem (Polovina et al., 1994, 1995). Productivity since the mid 1990s has fluctuated both up and down with El Nino and La Nina episodes with as yet no conclusive evidence for long-term change over normally low levels (J. Polovina, pers. comm.). Thus the suggestions (insignificant) increases and decreases in fish densities observed at FFS and MW during the second half of the decade are consistent with other inconclusive measures of productivity.

Evaluating recruitment phenomena on finer taxonomic scales provides some limited insights. Pomacentrids, a reef fish family with an atypically brief (2- to 3-wk-long: Wellington and Victor, 1989) planktonic larval stage, only weakly influenced spatial and temporal patterns in fish counts even though they contributed a large minority to the total counts. Conversely, the observed fluctuations in total yoy did reflect those of a variety of taxa with more typical, several-month-long planktonic durations (DeMartini, ms under review). If recruitment variation is driven by advective losses, risk should be proportional to time spent in the plankton. The inconstancy of reef fish recruitment during 1995-2000 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.

Density estimates for yoy, as opposed to older life-stage fishes, arguably provide the most realistic measures of fluctuations in oceanic productivity experienced by planktonic larvae. By definition, yoy are present on reefs for less than a year, beginning immediately after larvae settle from the plankton onto reefs. Yoy therefore should be least influenced by post-settlement processes such as competitive and predatory interactions with reef-based stages of the same and other species. Fluctuations in the numbers and biomass of older-stage fish already resident on the reef (comprising many year-classes in most species) are buffered by population inertia. Resistance to short-term change in numbers is true collectively among species comprising trophic levels, foraging guilds, and the total reef-fish assemblage as well as within particular species (the latter has been referred to as the "storage effect" by Warner and Chesson, 1985). Assuming, then, that these yoy data provide the most sensitive measure of productivity fluctuation, there is scant evidence for temporal patterns in recruitment since the recent time series began in 1992/93. Neither monotone nor clearly cyclic fluctuations in recruitment are indicated by plots of yearly estimates across time (Fig. 2), despite the occurrence of major El Niños in 1992-93 and 1997-98, followed by a strong La Niña in 1999. Hence, the fluctuations in yoy fish densities that did in fact occur were not clearly related to the timing of El Niño/La Niña events in the central North Pacific. That yoy densities fluctuated independently of ENSO events contrasts with the observation that the body girth (somatic condition) of young monk seals at FFS and at Laysan Island appears to have increased during both the 1992 and 1998 El Niño years (J. Baker, NMFS, unpubl. data). Perhaps our yoy density estimates do not adequately represent actual year-class productivity or yoy fishes do not represent a meaningful measure of monk seal prey production.

Temporal Patterns of Fish Size Composition and Biomass

Although the average body size of fishes has varied with habitat and reef-site, average size in general has not fluctuated appreciably over time for particular habitats within sites. In part this reflects the lack of temporal pattern in the relative contribution of small-bodied yoy to total fish numbers for habitats within sites. Interannual variations in total fish biomass densities, moreover, have been indistinguishable and little influenced by fluctuations in yoy numbers because yoy contribute trivially to total fish biomass. Throughout the time series, yoy have consistently represented less than several percent of total standing biomass. Large yoy recruitments can potentially translate to substantial biomass following grow-out of established year-classes, especially if a series of good year-classes occurs in sequence. A possible example would have been the 1997 year-class of *P. meeki*, had it become established. However, this did not occur. The exceptional one-time recruitment of *P. meeki* (with densities of nearly 40 yoy ·10

m^{-2} at only 2 of 5 Midway patch reef stations) occurred only in 1997. Larger-than-yoy *P. meeki* were scarce, and yoy *P. meeki* were not observed present at historical stations or elsewhere at Midway in 1998-2000. We have never observed greater than trivial numbers of yoy *P. meeki* at FFS. Given the inconsistent pattern of yoy recruitment observed, it is not surprising that estimated biomass density at both Midway and FFS, averaged over both major (barrier, patch reef) habitats, have ranged indistinguishably around 1 kg·10 m^{-2} from 1992/3 through 2000 (DeMartini and Parrish, 1996, 1997, 1998; Fig. 5, this report).

Site Differences in Densities and Composition of Monk Seal Prey

Because of poorly understood specifics of the monk seal forage base, the densities of likely (Goodman-Lowe, 1998) monk seal prey have had to be evaluated at a gross taxonomic (family) level. Nonetheless, some interesting patterns have emerged. Two cases of lower prey densities at FFS are consistent with a higher level of monk seal predation there (Table 7A,B; Fig. 3A,B). Muraenid (moray) eels, which rank among the top 3 prey of monk seals, and synodontids (lizardfishes), a secondary prey of seals (Goodman-Lowe, 1998; Parrish et al., 2000), were observed to occur at ten- and sixfold lower densities at FFS, where the monk seal population, although perhaps still declining, is nonetheless large and surely must be reducing populations of major prey species.

Other significant site differences in the taxonomic composition of monk seal prey are best explained either in terms of biogeography or site-habitat interactions. Labrids (wrasses), for example, were also relatively less numerous at FFS, but this likely reflects differences in labrid species composition between sites (labrids are more diverse at Midway because of relatively high standing stocks of many endemic Hawaiian species such as *Anampses cuvier*, *Coris venusta*, *Macropharyngodon geoffroy*, and *Thalassoma ballieui*). Conversely, the relatively greater density of balistids (triggerfishes) at FFS reflects the contributions of *Melichthys vidua* and *Sufflamen bursa*, two strictly tropical Indo-West Pacific species that are rare to absent at subtropical high-latitude Midway. Densities of holocentrids (squirrelfishes) on the other hand have been consistently greater at FFS because the more complex, three-dimensional patch reefs there provide the greater amounts of daytime shelter resources necessary to support higher standing stocks. The densities of one other major prey taxon--scarids (parrotfishes)--were indistinguishable between sites. Scarids exhibit no biogeographic or habitat relations which might complicate site comparisons.

Observed patterns of variation among habitats in the size composition of reef fishes also might have important relations to monk seal foraging. Small-bodied reef fishes (comprising both yoy of small and large species and older-stages of small-bodied species) predominate in wave-sheltered lagoonal patch reef habitat (this study; DeMartini, ms under review). Lagoonal patch reefs at atolls may provide important foraging habitat for young monk seals learning to forage, particularly if they forage on smaller prey items.

Similarities and differences between FFS and Midway in the taxonomic and size composition of reef fishes also have important biogeographic implications. As Randall et al. (1993) noted previously for Midway, the percentage endemism of the reef fishes in the NWHI--at FFS as well as Midway--is particularly high (30% and 32% at the two respective sites; Appendix Table B) relative to the overall level of endemism in the shore fishes of Hawaii (23.1 %: Randall, 1998). We herein provide the first quantitative evidence that the shallow reef fish faunas of both FFS and Midway are also dominated in abundance by Hawaiian endemics, which comprised 41% and 57%, respectively, of total numerical densities. Endemic species represented 26% of the non-apex predator biomass at FFS; and the biomass represented by endemics (45%) was especially pronounced at Midway (Appendix Table B). Greater proportions of endemic species at Midway, farther northwest (upchain, downwind) in the archipelago, may be related to patterns of larval transport and distribution due to prevailing currents (DeMartini, ms under review).

Trophic Structure of the NWHI Reef Fish Assemblages

Both FFS and Midway Atoll, like other shallow reefs and atolls in the NWHI (Friedlander and DeMartini, 2002) are dominated by carnivorous rather than herbivorous fishes in terms of numbers and especially biomass. Biomass on tropical reefs is an inverted trophic pyramid because most of the carnivorous fish biomass is supported by invertebrate animal plankton and reef-based invertebrates, not by herbivorous fishes (Parrish, 1990). Fish numbers in particular are dominated by carnivores because the most numerous fishes in tropical reef ecosystems are small-bodied, plankton- and invertebrate-feeders that prey on small water column and reef invertebrates (Parrish, 1990). One apparent (at least partial) exception to this generality is represented by reef fish assemblages in the main Hawaiian Islands (MHI) that are presently much less carnivore dominated than analogous habitats in the NWHI, even after allowing for the virtual absence of apex predators in the MHI (Friedlander and DeMartini, 2002). The greater rate of extraction of carnivorous species (subject to removal by hook-and-line as well as spearfishing) likely provides at least part of the explanation for the relatively depressed lower-level carnivore stocks in the MHI (Friedlander and DeMartini, 2002). Were it not for human extraction of herbivores and lower-level carnivores, in addition to apex predators in the MHI, indirect ecosystem effects resulting from the near-extirpation of apex predators in the MHI might already have become evident. Plausible mechanisms include coral-algal shifts (McManus et al., 2000) resulting from predatory release of the herbivorous parrotfish prey preferred by *Caranx* spp (Sudekum et al., 1991).

Frequency Occurrence of Large Jacks

Frequency occurrence is an abundance proxy which is oftentimes necessary for assessing stocks of large rare fishes (Thresher and Gunn, 1986). *Caranx ignobilis* and *C. melampygus* are the two most abundant and frequently encountered species of large carangids in the NWHI (Hobson, 1984; DeMartini et al., 1996; Friedlander and DeMartini, 2002). The frequencies of encounter (abundances) of both of these species have been low at Midway, relative to FFS, since 1992/93 and, perhaps more significantly, since 1996 at Midway. It is likely that four decades of recreational fishing after WW II by Naval Air Station personnel and contractors prior to 1996, even if limited to incidental capture and extraction of nontargeted fish, has reduced the stocks of jacks at Midway. It is also likely that the apparent further declines observed subsequent to 1996, when jurisdiction of the Midway Naval Air Facility was transferred to the U.S. Fish and Wildlife Service, are related to one or several ecotourism activities (recreational catch-and-release fishing, sport diving), which were established shortly after base transfer. The ability to distinguish human-induced alterations in fish behavior (conditioned decrease in attaction to, or increased avoidance of, boats and divers; e.g., see Kulbicki, 1998) from actual declines in population size (for example, due to catch-and-release-induced mortality) would require more than continued diver-observer surveys of fish abundances, however. One or more experimental evaluations of population size and mortality would be necessary. These include a carefully designed and documented conventional tag-recapture program with an adequate evaluation of tag loss (which, if large and ignored, generates a bias for overestimation of population size). Also needed is an evaluation of the possible physiological impact of a lengthy capture process (i.e., when fish are played to exhaustion on light tackle for International Game Fish Association world records). The possibly deleterious effects of physiological stress should not be discounted even though these physically tough organisms can be “horsed” with impunity on heavy tackle. Blood samples could be analyzed for biochemical correlates of post-release survivability for uluas caught on light versus heavy tackle. Their post-release behavior and survival could perhaps be monitored by tagging a representative subset of the blood-analyzed fish with Pop-up Satellite Archival Tags.

Deep-Reef Survey at FFS

The numerical densities of fishes and macroinvertebrates at deep talus slope stations were considerably less than at the shallower reef stations in August 1998, conservatively averaging about 5% as dense as on the shallow reefs (where only finfishes were tallied). This was especially true at 62 m, where the organisms surveyed were < 2% as dense as fishes in shallow reef habitats. There was considerable overlap in the species composition of fishes encountered at 52- and 61-m depths on the windward talus slope of the barrier reef and those observed in shallow barrier and lagoonal patch habitats at FFS. Sizes of fish prey captured by monk seals in deep slope habitat at FFS (Parrish et al., 2000) broadly overlap with the sizes of fishes present on shallow reefs at FFS (Fig. 4, this report). The monk seal forage spectrum therefore differs more quantitatively than qualitatively between shallow and deep regions of the reef at FFS. Generally lower abundances seem characteristic of talus slopes, even though the limited data suggest that abundances vary by a factor of 3 between areas like stations 3 and 4 (offshore of Tern Island) with more and larger pieces of talus and areas like stations 1 and 2 (farther to the southwest off Shark Island) with smaller talus. Interestingly, CRITTERCAM and other activity data suggest that at least adult male monk seals commonly forage in the more developed talus fields off Tern Island during daylight hours (Parrish et al., 2000). Foraging on deep talus slopes rather than in shallow reef habitats may reflect greater prey availability in a shelter-limited environment. Prey availability, not prey abundance per se, could be the major factor influencing foraging habitat use by monk seals (Parrish et al., 2000), at least for some seal populations and habitats.

No information is presently available on interannual variations in the abundances of potential monk seal prey on deep talus slopes at FFS. A second diver-survey, conducted in July 1999 by FAP and RCB at the same station-areas, emphasized the tallying of organisms present under talus fragments (FAP, unpubl. data) and is not directly comparable to the 1998 survey. Additional deep survey work using technical dive gear is necessary to address temporal issues.

Methods-Calibration Study

The various matched samples differ in the nature as well as the strength of their relationships to one another, although all relationships, as logic dictates, were positive. The two types of direct (diver) counts were fairly strongly related to one another, with one count type explaining about one-half of the variance in the other type of count. Indirect counts (video records) and the New Method diver counts were more strongly related and explained over three-fourths of the variance in one another. We believe that these results demonstrate several important phenomena. First, the relatively rapid ($50\ m^2 \cdot 3\ min^{-1}$) visual scans required by the Old Method undersampled small cryptic fishes even though they perhaps better sampled larger-bodied, more mobile fishes, compared to the more methodical, slower ($50\text{-}100\ m^2 \cdot 10\ min^{-1}$) searches used in the New Method. Second, even a brief (half-hour) temporal lag has a greater effect on the reproducibility of direct diver counts than a small (5-m) spatial offset. This latter might be expected given the benefit of hindsight because much of the temporal variation in both fish numbers and biomass in barrier reef habitats is caused by the movements of roving, typically heterospecific, schools of large numbers of moderately large-bodied herbivores, primarily surgeonfish. (When present, these schools equivalently dominate counts separated by only several meters distance.) Last and most importantly, the various types of density estimates can be predicted from one another, even though the indirect (video) count appears less accurate than the others (see below). For example, the New Method of direct counts allows for a more careful tally of small-bodied, cryptic fishes and thereby provides a more thorough, hence accurate, characterization of fish diversity.

Our video records tended to greatly over-document the presence of fishes, especially some species such as the wrasses *Thalassoma ballieui*, *T. trilobatum*, and *T. purpureum* that are unavoidably attracted to moving (or stationary) divers. Several detailed comparisons (Epperly, 1983; Bortone et al., 1986; Greene and Alevizon, 1989) describe the relative abilities of video and direct diver tallies to characterize fish assemblages in terms of species composition, rank abundances, and frequency of occurrence. However, only Greene and Alevizon (1989) compared quantitative abundance estimates between these two methods. At unnaturally high total fish densities of nearly 100 fish · 10 m^{-2} , albeit in a controlled coral reef environment at the "Living Seas" exhibit at Walt Disney World, Epcot Center, video transects produced abundance (count) estimates which were about 27% higher (Greene and Alevizon, 1989) than estimates produced by direct-diver count transects. Our video overestimate for total fishes (on average nearly fourfold higher) was appreciably greater than this and may partly reflect the less-controlled field conditions of our study. The discrepancy between our and Greene and Alevizon's (1989) findings might also be due in part to the unnaturally high fish densities in the "Living Seas" tanks. The additional comparative data needed to quantify differences between methods are lacking. To our knowledge, no one else has compared quantitative fish density estimates using underwater video and direct diver observations. It would however appear, based on existing data, that video records likely provide a biased (inaccurate) although (if carefully standardized) precise and predictable index of actual fish densities.

The calibration study provides information useful for converting between the recent time series of fish density estimates (this study) and newly derived estimates using surveying protocols developed for the broad-scale Rapid Ecological Assessments conducted by the NOW-RAMP. The first NOW-RAMP survey overlapped the 2000 survey described herein, and this allows us to compare fish densities that were independently, and almost concurrently, estimated using two (test versus operational) applications of the New Method at one (FFS) of the two sites. If the NOW-RAMP data for FFS are limited to those collected by RCB (to control for some unavoidable variability among divers), the mean ± se densities ($N \cdot 10\ m^{-2}$) produced by the two New Method applications was 8.3±1.05 (test; 9 stations) and 9.7±3.10 (operational; 6 other stations) total fish ·10 m^{-2}. These two obviously indistinguishable estimates demonstrate the generality of the results of our Methods-Calibration Study. The New Method should estimate the density and biomass of resident reef fishes with accuracy and precision comparable to the Old Method. In addition, Stationary Point Counts (SPCs; Bohnsack and Bannerot, 1986) and Towed Diver Counts (both included in the NOW-RAMP sampling protocol) will provide new information on the density and biomass of apex predators (sharks and jacks). Thus the NOW-RAMP program should provide additional information on the potential competitors and predators of, as well as prey resources of, the monk seal over a larger geographic area.

SUMMARY

Comprehensive results are presented for an extensive series of multiyear surveys of shallow (< 15-m deep) reef fish populations at select reef sites. Data are summarized for 1998, 1999, and 2000 surveys and temporal and spatial patterns statistically evaluated for the entire 1992/93 and 1995-2000 time series of surveys at FFS and Midway Atoll, two atolls in the Northwestern Hawaiian Islands (NWHI) whose Hawaiian monk seal (*Monachus schauinslandii*) populations are of particular concern to protected species management. Two types of special diver-survey results are also provided: (1) a one-time (August 1998) survey of fishes and macroinvertebrates (potential monk seal prey) in deep (52, 61 m) talus slope habitat at FFS and (2) a methods-calibration survey conducted at the two sites in 2000.

Recent Survey Results

During July-August of 1998, 1999, and 2000, experienced diver-biologists visually resurveyed reef fishes at both sites. Surveys were repeated at the same station-areas at which fishes were surveyed in July 1992 (at FFS), in August 1993 (Midway), in September 1995 at both sites, in August (FFS) and September (Midway) 1996; and in August 1997 at both sites. 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 Midway. Either all three or two of the same three divers (EED, FAP, RCB) conducted all surveys using established protocols.

At FFS, the estimated mean total numerical density (all fish taxa except apex predators) was 17 ± 1.5(se), 18 ± 1.9, and 20 ± 2.5 fish$\cdot$10 m^{-2} in 1998, 1999, and 2000, respectively. The analogous 1998, 1999, and 2000 estimates at Midway were 17 ± 1.8, 18 ± 4.7, and 9 ± 1.5 fish$\cdot$10 m^{-2}. Yoy fishes comprised 15%, 8%, and 7% of total fish numbers at FFS, and the respective estimates were 34%, 32%, and 31% at Midway in 1998, 1999, and 2000. Standing biomass estimates at FFS during 1998-2000 ranged from 0.1-0.5 kg $\cdot$10 m^{-2} and from 1.6-2.2 kg $\cdot$10 m^{-2}, in barrier (BR) and patch reef (PR) habitats, respectively. The corresponding estimates for Midway were 1.1-1.8 kg $\cdot$10 m^{-2} and 0.4-0.6 kg $\cdot$10 m^{-2} in BR and PR habitats during 1998-2000.

Special Surveys

Additional diver-observation surveys were conducted in August 1998 in deep slope habitat of the windward barrier reef at FFS. Two divers (FAP, RCB), using technical dive gear and mixed gases, surveyed two (52, 61 m) depths at each of four stations. On each dive, all fishes and other conspicuous fauna (macroinvertebrates such as octopus and lobsters) encountered within a @ 2-m wide path during a 20-minute observation-swim were tallied by noncontiguous, 3-min interval to provide a mean count and variance estimate per depth at each station. Species richness was higher (28.2± 4.6[n=4] taxa per transect) at the 52-m depth compared to the 61-m depth (14.8± 2.1 taxa per transect). A majority of the taxa encountered (58-59% at the two depths) were the same as those present at FFS shallow stations. A 2-way ANOVA of depth nested within station on the numbers of individual organisms (all taxa pooled) encountered on transects suggested depth and station effects that each varied about threefold, with higher counts at the shallower of the two depths and at the pair of stations having more numerous and larger pieces of talus.

Two types of methods-calibration surveys were conducted in 2000. (1) Standard (50-m long by 5-m wide; 250-m^2 area, 15-min duration) fish counts conducted using historical protocols were matched with same-diver counts in a 2-m-wide (100 m^2, 10-min duration) strip centered on the wider lane but lagged by 30 minutes. The same diver (RCB) was used in all matched-pair surveys to remove the variance added by diver differences. (2) The latter 100-m^2 area diver-counts, developed for the NOW-RAMP, were matched with video records for a 2-m-wide strip, surveyed concurrently by a second diver, about 5-m to one side of the 2-m-wide strip in which RCB was counting fish. The two types of calibration thus included the effects of a brief (half hour) time lag and short (5-m) spatial separation, respectively, when comparing the two types of direct counts and comparing the newly developed counting method with the video record. Two series totaling 22 matched-pair surveys (9 at FFS, 13 at Midway) were completed at outer and inner barrier reef habitats. Both calibrations produced useful results. The two types of direct diver count methods were adequately correlated for both total fish density and total fish biomass (r ≈0.68). The new type of direct count was even better correlated with the video transect record (numbers: r = 0.98; biomass: r = 0.91), suggesting that replicability (precision) of fish estimates is more strongly influenced by a brief time lag than by a small spatial offset, when estimating numbers and biomass dominated by home-ranging, schooling species, in particular the mixed-species feeding flocks of herbivores that dominate biomass on barrier reefs. The excellent correlation observed between the indirect (video) and direct diver counts suggests that, in the future, it might be possible to collect useful fish counts on video transects using competent divers who need not be experienced in underwater identification of Hawaiian fishes and in specific data recording protocols. Twenty-minute video clips require an average 90 minutes to process by a trained observer in the laboratory, however; and this tradeoff is one important factor that must be considered when deciding whether video records should be used to replace direct diver counts.

Comprehensive Time Series Evaluation

The 2000 surveys at the shallow stations represented the seventh in an 8- to 9-yr series of annual surveys at Midway/FFS intended to estimate nonapex predator fish densities on shallow reefs with a precision capable of detecting 50% or greater changes over a decadal time scale. Data are as yet insufficient for meaningful evaluations of change; not surprisingly, total fish densities were indistinguishable between sites and among years at each site. Grand means for the entire time series were 17 ± 0.7 and 16 ± 1.3 fish $\cdot 10\ m^{-2}$ at FFS and Midway, respectively, and 16.5 ± 0.9 fish $\cdot 10\ m^{-2}$ for both sites pooled. Yoy representation did not differ among years within site but did differ between sites; on average, yoy have contributed 12% and 28-37% to total fish densities at FFS and Midway, respectively, since 1992/93. The biomass densities of resident reef fishes (excluding apex predators) were generally indistinguishable between sites and among all years at each site. Grand means for the entire time series were 1.03 ± 0.09 and 1.02 ± 0.07 kg $\cdot 10\ m^{-2}$ at FFS and Midway, respectively, and 1.03 ± 0.06 kg $\cdot 10\ m^{-2}$ for both sites pooled.

Although surveys are yet too few to expect many powerful evaluations, several interesting changes over time and spatial similarities and differences between the two sites have been detected. Namely, (1) persistently large differences in the numerical densities of two taxa of monk seal prey (muraenid eels: a tenfold difference; lizardfishes: a sixfold difference) exist between Midway (where monk seals are still relatively uncommon but increasing in numbers) and FFS (where the monk seal population, although declining in recent years, is still relatively numerous). No meaningful site differences were detected for four other families of reef fishes (Balistidae, Holocentridae, Labridae, Scaridae) considered to be major monk seal prey by Goodman-Lowe (1998), or for trophic levels (herbivores, carnivores) or major carnivore feeding guilds of fishes. (2) Although overall fish densities have been indistinguishable between FFS and Midway, the densities of yoy fishes have averaged at least twofold greater at Midway. Yoy densities at Midway have averaged >250% greater overall than at FFS (if the highly variable *Priacanthus meeki* is included) and 200% greater (excluding *P. meeki*). Conversely, the mean densities of older-sized fishes have been about one-third higher at FFS, indicating that if the pattern continues, the densities of biomass-dominant adults will eventually diverge at the two sites. (3) Compared to FFS, two species of large carangid jacks (giant trevally, *Caranx ignobilis*; bluefin trevally or omilu, *C. melampygus*) continue to be encountered in threefold to fivefold lower frequency at Midway, where they had been fished by US Naval Air personnel prior to 1996 and where they have been the target of a catch-and-release fishery since Midway was transferred to the USFWS in 1996. With the addition of the year 2000 survey data, we were able to detect a significant (P=0.02) decline in the relative frequency occurrence of each of the two species of large jacks at Midway fish-survey stations since 1996.

Several additional, fundamental patterns (common to both sites) have become apparent: (1) Larger-bodied fishes (both species and life-stages within species; and herbivorous parrotfishes and surgeonfishes in particular) dominate barrier reef habitats. Conversely, (2) smaller-bodied fishes, including the yoy of parrotfishes that are common on the barrier reef as adults, and the juveniles-adults of many smaller-bodied species of microcarnivores (wrasses in particular) are relatively abundant on lagoonal patch reefs. (3) Numerical densities are generally higher on patch reefs, whereas biomass densities are higher on barrier reefs. These observations suggest that sheltered lagoonal reefs provide essential habitat for the juveniles of many fishes at NWHI atolls, a factor that should be included in the site-selection criteria for no-take MPAs within the NWHI Coral Reef Ecosystem Reserve.

Finally, patterns of fish numbers and biomass at FFS and Midway are reevaluated relative to the possible current and future food limitation of monk seals at FFS. The most important observations in this regard are the opposite patterns of yoy and older fish density in shallow habitats at FFS and Midway despite similar overall standing stock fish numbers and biomass. Reef fish stocks at these two reef-sites, although presently comparable, appear to have different underlying dynamics. If the process (relatively lower recruitment at FFS) producing these patterns continues, the abundance of shallow-water reef fishes at FFS in time will decline sufficiently to enable detection of a general decrease in standing biomass of fishes at FFS. Such a decline would be consistent with Schmelzer's (2000) recent findings of sustained lower planktonic productivity at mid- versus high-latitude regions of the Hawaiian Archipelago based on remote imagery and the possibly continuing poor body condition of juvenile seals at FFS.

CONCLUSIONS AND RECOMMENDATIONS

The standing biomass of lower-trophic-level (excluding apex predator) fish populations in shallow reef habitats has remained indistinguishable at about 1 mt $\cdot$ha^{-1} at FFS and Midway Atoll during the period from 1992/93 through 2000. Despite the present similarities in stocks, resident reef fishes at FFS and Midway have different underlying dynamics. Possible future changes in reef fish abundance argue for extended monitoring at both sites because of the present evidence suggesting likely future declines in reef fish stocks at FFS and the importance of Midway as a potential translocation site for 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. The crucial assumptions–yet to be tested–linking fluctuations in oceanic productivity, reef fish abundance, and monk seal foraging biology are that shallow reef fishes are important to the forage base of female and juvenile monk seals and that the availabilities of these prey fishes are meaningfully related to their abundance. Testing the former assumption would require data on the prey consumed and habitats utilized by female and juvenile seals. Quantitative estimates of how the searching and capture efficiencies of monk seals of various ages and sexes might differ among prey types and habitats would be required to test the availability-abundance assumption. Both will be very difficult and costly, but their potential importance to monk seal conservation might justify the effort.

Reef sharks likely both compete with and prey upon monk seals to some extent, and carangids may be important competitors of monk seals–e.g., numerous CRITTERCAM observations have documented monk seals being kleptoparasitized by white ulua, kahala, and reef sharks (FAP, unpubl. data). It is therefore important that future surveys of fish stocks in the NWHI include quantitative assessments of sharks and jacks. The comprehensive sampling design developed for surveying fishes by the NOW-RAMP includes several estimators of apex predator densities. The more intensive as well as extensive sampling conducted on NOW-RAMP surveys could provide finer resolution of temporal patterns for apex predators and other reef fishes, depending on monitoring frequency after completion of initial baseline surveys in 2002. Experimental evaluations of the survivability of giant ulua following catch-and-release on light tackle also are needed to determine what, if any, effects catch-and-release has had on the ulua population at Midway and what effects on uluas (and indirectly on monk seals) therefore might be expected if catch-and-release programs were conducted elsewhere in the NWHI.

Possibly important differences in the prey consumed by monk seals at the various NWHI reefs and atolls (Goodman-Lowe, 1998) need further evaluation. One potentially valuable, as yet untapped, source of existing information might be a comparison between occurrence of prey taxa in scats and spews and relative abundance of these taxa at the respective site. Concurrent scat/spew-prey density data, in the past collected only at FFS and Midway, could be expanded in the future to include other NWHI sites as the NOW-RAMP develops. One complicating interpretative issue, however, will be whether to expect prey densities to be directly or inversely related to the incidence of prey in scats and spews. It all depends on whether monk seals continue to target heavily utilized prey after the stocks of these prey have been depressed by seal foraging at a site.

Patterns in our NWHI reef fish data also transcend issues directly related to monk seals. In the past we have characterized our long-term average estimates of fish biomass densities (about 1 kg $\cdot 10\ m^{-2}$) on relatively pristine, shallow NWHI reefs as 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). Based on recent complementary estimates of fish standing stocks in the MHI and throughout the NWHI (Friedlander and DeMartini, 2002), we now believe that our prior evaluations underestimated existing NWHI-MHI differences in fish standing stocks. If the biomass of apex predators, now virtually extirpated in the MHI, is added to that of other carnivorous and herbivorous fishes on NWHI reefs, the overall difference approaches a ratio of more than 3-to-1 (means of > 2 mt $\cdot$ ha^{-1} in the NWHI versus about 0.7 mt $\cdot$ ha^{-1} in the MHI; Friedlander and DeMartini, 2002). We reemphasize the importance of these differences as evidence for the continuing high levels of exploitation of reef fishes in the MHI and the pressing need for ecosystem-level management of reef systems in the MHI as well as NWHI.

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Table 1

French Frigate Shoals–Summary statistics for numerical density ($N \cdot 10\ m^{-2}$) estimates, during1992 and by survey-year within the period 1995-2000, for each habitat (barrier reef, BR, *n*=4 stations; lagoonal patch reef, PR, *n*=5) surveyed and for the grand mean of both habitats (*n*=2), for total fishes of all sizes; young-of-year (yoy) fishes of all taxa; older (non-yoy) fishes of all taxa; yoy fishes excluding the endemic Hawaiian bigeye, *Priacanthus meeki*; and damselfishes of all species and sizes pooled. Grand means over all years are based on *n*=7 surveys. Standard errors ($se = std \cdot n^{-1/2}$) of grand means treat the variances of all independent component means as additive.

	Numerical density (mean ± se $N \cdot 10\ m^{-2}$)							
	1992	1995	1996	1997	1998	1999	2000	All 7 yr
Total fishes (all sizes)								
BR	4.7±1.31	6.4±1.67	5.6±1.53	6.8±2.30	6.5±1.74	5.1±0.92	3.9±0.73	5.6±0.58
PR	18.0±0.94	30.3±3.71	25.8±3.31	21.1±1.83	25.5±2.41	28.1±3.64	33.1±4.95	26.0±1.22
Both	12.1±0.80	19.6±2.04	16.8±1.82	14.7±1.47	17.1±1.49	17.9±1.88	20.1±2.50	16.9±0.67
Yoy fishes (all taxa)								
BR	1.1±0.81	2.0±1.22	1.1±0.49	2.3±1.71	1.7±0.73	1.1±0.47	1.5±0.76	1.5±0.37
PR	1.0±0.26	3.3±0.93	4.4±2.54	3.0±0.52	3.4±0.74	1.8±0.46	1.5±0.23	2.6±0.42
Both	1.0±0.42	2.7±0.77	3.0±1.29	2.7±0.89	2.6±0.52	1.5±0.33	1.5±0.40	2.1±0.28
Older fishes (all taxa)								
BR	3.6±0.50	4.4±0.63	4.5±1.13	4.5±0.63	4.8±1.48	4.0±0.55	2.4±0.08	4.3±0.31
PR	17.0±1.17	27.0±3.12	21.3±3.26	18.1±1.71	22.1±2.64	26.3±3.48	31.5±5.12	23.3±1.20
Both	11.0±0.64	16.9±1.59	13.9±1.73	12.1±0.91	14.4±1.52	16.4±1.76	18.6±2.56	14.8±0.62
Yoy fishes minus *P. meeki*								
BR	1.1±0.81	2.0±1.22	1.1±0.49	2.3±1.71	1.7±0.72	1.1±0.47	1.5±0.76	1.5±0.37
PR	1.0±0.26	3.3±0.93	4.4±2.54	3.0±0.52	3.3±0.78	1.8±0.44	1.5±0.24	2.6±0.42
Both	1.0±0.42	2.7±0.77	3.0±1.29	2.7±0.89	2.6±0.53	1.5±0.32	1.5±0.40	2.1±0.28
Pooled damselfishes (all sizes of all species)								
BR	1.7±1.24	1.8±1.66	1.3±0.81	2.3±1.71	0.9±0.37	0.9±0.29	1.1±0.76	1.4±0.42
PR	4.2±0.36	7.4±1.00	9.1±1.43	9.7±1.08	9.8±1.09	9.3±1.18	10.2±1.46	8.5±0.43
Both	2.9±0.65	4.6±0.97	5.2±0.82	6.0±1.01	5.4±0.58	5.1±0.61	5.6±0.83	5.0±0.30

Table 2

Midway–Summary statistics for numerical density ($N \cdot 10\ m^{-2}$) estimates, during1993 and by survey year within the period 1995-2000, for each habitat (barrier reef, BR, *n*=4 stations; lagoonal patch reef, PR, *n*=5) surveyed and for the grand mean of both habitats (*n*=2), for total fishes of all sizes; young-of-year (yoy) fishes of all taxa; older (non-yoy) fishes of all taxa; yoy fishes excluding the endemic Hawaiian bigeye, *Priacanthus meeki*; and damselfishes of all sizes and species pooled. Grand means over all years are based on *n*=7 surveys. Standard errors ($se = std \cdot n^{-1/2}$) of grand means treat the variances of all independent component means as additive.

	Numerical density (mean ± se $N \cdot 10\ m^2$)							
	1993	1995	1996	1997	1998	1999	2000	All 7 yr
Total fishes (all sizes)								
BR	9.0±1.23	9.6±2.21	8.4±1.08	7.4±0.88	9.9±1.38	7.1±1.03	5.8±0.54	8.2±0.49
PR	16.7±1.77	23.7±6.35	26.0±5.16	29.3±12.0	22.3±3.40	27.1±9.36	11.7±0.86	22.4±2.53
Both	13.3±1.08	17.4±3.36	18.2±2.64	19.6±6.01	16.8±1.84	18.2±4.71	9.1±0.51	16.1±1.29
Yoy fishes (all taxa)								
BR	0.8±0.18	1.2±0.27	0.9±0.41	1.4±0.90	2.4±0.64	1.5±0.61	1.4±0.39	1.4±0.20
PR	4.6±1.31	8.9±4.42	8.6±4.45	23.1±12.2	8.3±1.11	9.2±3.23	3.9±0.44	9.5±2.03
Both	2.9±0.66	5.5±2.22	5.2±2.24	13.4±6.11	5.7±0.64	5.8±1.64	2.8±0.29	5.9±1.02
Older fishes (all taxa)								
BR	8.2±1.06	8.4±2.47	7.6±0.91	6.0±0.56	7.5±0.82	5.7±0.58	4.4±0.31	6.8±0.44
PR	12.1±2.48	14.8±2.57	17.4±4.46	6.2±1.78	14.0±3.30	17.9±8.19	7.8±0.59	12.9±1.53
Both	10.4±1.35	11.9±1.78	13.0±2.28	6.1±0.93	11.1±1.70	12.5±4.11	6.3±0.33	10.2±0.79
Yoy fishes minus *P. meeki*								
BR	0.8±0.18	1.2±0.27	1.0±0.62	1.4±0.90	2.4±0.64	1.5±0.61	1.4±0.39	1.4±0.21
PR	4.6±1.31	8.9±4.42	8.6±4.45	4.9±1.16	8.3±1.11	9.2±3.23	3.9±0.44	6.9±1.05
Both	2.9±0.66	5.5±2.22	5.2±2.24	3.3±0.73	5.7±0.64	5.8±1.64	2.8±0.29	4.5±0.54
Pooled damselfishes (all sizes of all species)								
BR	3.1±0.30	3.1±1.17	3.4±0.30	2.9±0.75	3.4±0.72	2.8±0.59	2.6±0.53	3.0±0.26
PR	7.2±1.21	6.5±1.58	7.0±0.79	4.7±0.96	8.9±1.50	9.5±3.00	6.4±0.39	7.2±0.59
Both	5.1±0.62	4.8±0.98	5.2±0.42	3.8±0.61	6.2±0.83	6.1±1.53	4.5±0.33	5.1±0.32

Table 3

French Frigate Shoals and Midway–Summary results of factorial ANOVAs testing the effects of habitat (2 levels: barrier, patch reef) nested within the two sites (FFS, Midway), and of survey year (7 levels: 1992/93, 1995-2000), on the numerical density ($N \cdot 10\ m^{-2}$) of (A) total fishes of all sizes and taxa (excluding apex predators); (B) young-of-year (yoy) fishes of all taxa; (C) older fishes of all taxa; and (D) yoy fishes of all taxa minus the endemic Hawaiian bigeye *Priacanthus meeki*; (E) all sizes of all taxa of damselfishes pooled; and (F) yoy of all damselfishes pooled. A survey year effect and all higher-order (interaction) terms were insignificant ($P > 0.05$) in all cases and are not listed. The results of Student-Newman-Keuls a posteriori tests are provided with their least squares means (underlined if not significantly different).

(A) Total fishes, all sizes of all taxa ($N \cdot 10\ m^{-2}$; model $r^2 = 0.488$):

Source	df	SS	MS	F-ratio	Prob>F
Model	3	9630.5	3210.2	38.75	0.0001
Habitat (Site)	3	9630.5	3210.2	38.75	0.0001
Error	122	10107.0	82.8		
Cor. Total	125	19737.5			

Habitat(Site): PR(FFS)=PR(MW)>BR(MW)=BR(FFS)
26.0=22.4>8.2=5.6

(B) Yoy fishes, all taxa ($N \cdot 10\ m^{-2}$; model $r^2 = 0.212$):

Source	df	SS	MS	F-ratio	Prob>F
Model	3	1498.5	499.5	10.93	0.0001
Site	1	350.2	350.2	7.66	0.0065
Habitat(Site)	2	1055.9	527.9	11.55	0.0001
Error	122	5576.9	45.7		
Cor. Total	125	7075.4			

Site: MW>FFS
5.4>2.1

Habitat(Site): PR(MW)>PR(FFS)=BR(FFS)=BR(MW)
9.5>2.6=1.5=1.4

Table 3.–Continued

(C) Older fishes, all taxa ($N \cdot 10\ m^{-2}$; model $r^2 = 0.568$):

Source	df	SS	MS	F-ratio	Prob>F
Model	3	7016.7	2338.9	53.43	0.0001
Site	1	453.5	453.5	10.36	0.0017
Habitat(Site)	2	6363.7	3181.9	72.68	0.0001
Error	122	5340.8	43.8		
Cor. Total	125	12357.5			

Site: FFS>MW
13.7>9.9
Habitat(Site): PR(FFS)>PR(MW)>BR(MW)=BR(FFS)
23.3>12.9>6.8=4.0

(D) Yoy fishes, all taxa minus *P. meeki* ($N \cdot 10\ m^{-2}$; model $r^2 = 0.296$):

Source	df	SS	MS	F-ratio	Prob>F
Model	3	665.8	221.9	17.12	0.0001
Site	1	134.7	134.7	10.39	0.0016
Habitat (Site)	2	494.9	247.5	19.09	0.0001
Error	122	1581.8	13.0		
Cor. Total	125	2247.6			

Site: MW>FFS
4.2>2.1
Habitat(Site): PR(MW)>PR(FFS)=BR(MW)=BR(FFS)
6.9>2.6=1.5=1.4

(E) Damselfishes, all sizes of all species ($N \cdot 10\ m^{-2}$; model $r^2 = 0.544$):

Source	df	SS	MS	F-ratio	Prob>F
Model	3	1056.17	352.06	48.51	0.0001
Habitat(Site)	3	1056.17	352.06	48.51	0.0001
Error	122	885.37	7.26		
Cor. Total	125	1941.54			

Habitat(Site): PR(FFS)=PR(MW)>BR(MW)=BR(FFS)
53=7.17>3.02=1.41

Table 3.–Continued

(F) Yoy damselfishes, all species (N · 10 m^{-2}; model $r^2 = 0.155$):

Source	df	SS	MS	F-ratio	Prob>F
Model	3	38.17	12.72	7.46	0.0001
Habitat (Site)	3	38.17	12.72	7.46	0.0001
Error	122	208.05	1.71		
Cor. Total	12	246.22			

Habitat(Site): PR(MW)>BR(FFS)=BR(MW)=PR(FFS)
1.8>1.0=0.5=0.5

Table 4

French Frigate Shoals–Summary statistics for numerical density (N ·10 m^{-2}) estimates, during1992 and by survey year within the period 1995-2000, for each habitat (barrier reef, BR, and lagoonal patch reef, PR) surveyed and for the grand mean (*n*=2) of both habitats, for major trophic levels and foraging guilds comprising herbivores (primary consumers), total carnivores (secondary consumers), and, within carnivores: benthic carnivores, corallivores, piscivores, and planktivores. Large transient predators (sharks and carangid jacks) are excluded from the piscivore foraging guild. Standard errors (se = std · $n^{-1/2}$) of grand means treat the variances of all independent component means as additive.

	Numerical density (mean ± se N ·10 m^2)							
	1992	1995	1996	1997	1998	1999	2000	All 7 yr
Herbivores								
BR	1.6±0.44	2.8±0.25	2.5±0.30	3.2±0.57	3.9±1.95	2.6±0.52	1.3±0.16	2.6±0.33
PR	7.5±0.58	8.4±2.24	8.0±0.61	6.1±0.85	8.2±0.95	7.6±0.68	5.6±0.26	7.3±0.40
Both	4.8±2.93	5.9±2.78	5.6±2.76	4.8±1.47	6.2±2.13	5.4±2.50	3.7±2.12	5.2±0.32
Total carnivores								
BR	3.2±1.55	3.7±1.84	3.2±1.37	3.7±1.82	2.7±0.74	2.6±0.52	2.6±0.77	3.1±0.19
PR	10.6±0.45	23.7±3.93	17.7±2.78	15.0±1.37	17.4±2.16	20.6±3.21	27.5±5.05	18.9±2.11
Both	7.3±3.69	14.8±9.93	11.2±7.23	10.0±5.60	10.9±7.33	12.6±8.94	6.4±12.4	11.9±1.15
benthic carnivores								
BR	1.6±0.32	1.7±0.28	1.8±0.25	1.5±0.25	2.0±0.34	1.9±0.29	1.6±0.13	1.7±0.08
PR	6.0±0.60	14.5±2.85	9.0±1.88	5.8±0.90	7.3±1.14	11.7±2.27	17.4±4.49	10.3±1.68
Both	4.1±2.21	8.8±6.37	5.8±3.58	3.9±2.18	5.0±2.64	7.3±4.84	10.4±7.83	6.5±0.93
corallivores								
BR	0.07±0.03	0.10±0.05	0.06±0.02	0.08±0.02	0.08±0.03	0.12±0.03	0.06±0.02	0.08±0.01
PR	0.14±0.06	0.23±0.06	0.27±0.04	0.39±0.06	0.34±0.02	0.31±0.07	0.34±0.07	0.29±0.03
Both	0.11±0.03	0.17±0.06	0.18±0.11	0.26±0.15	0.23±0.13	0.23±0.10	0.22±0.14	0.20±0.02
piscivores								
BR	0.05±0.02	0.12±0.08	0.12±0.11	0.17±0.09	0.03±0.01	0.09±0.04	0.00±0.00	0.08±0.02
PR	0.28±0.06	0.68±0.35	0.59± 0.40	0.62±0.39	0.87±0.62	0.60±0.21	0.25±0.09	0.56±0.08
Both	0.18±0.12	0.43±0.28	0.38±0.23	0.42±0.22	0.50±0.42	0.37±0.25	0.14±0.13	0.35±0.05
planktivores								
BR	1.5±1.30	1.8±1.67	1.1±1.03	2.0±1.85	0.5±0.44	0.5±0.33	0.9±0.82	1.2±0.23
PR	4.1±0.35	8.3±1.62	7.8±1.51	8.2±0.80	8.9±1.15	8.0±1.26	9.5±1.42	7.8±0.65
Both	2.9±1.33	5.4±3.22	4.8±3.32	5.4±3.04	5.2±4.15	4.6±3.74	5.6±4.27	4.9±0.35

Table 5

Midway–Summary statistics for numerical density (N ·10 m^{-2}) estimates, during1993 and by survey year within the period 1995-2000, for each habitat (barrier reef, BR, and lagoonal patch reef, PR) surveyed and for the grand mean (*n*=2) of both habitats, for major trophic levels and foraging guilds comprising total herbivores (primary consumers), total carnivores (secondary consumers), and (within carnivores): benthic carnivores, corallivores, piscivores, and planktivores. Large transient predatory sharks and carangid jacks are excluded from the piscivore foraging guild. Standard errors (se = std · n$^{-1/2}$) of grand means treat the variances of all independent component means as additive.

	Numerical density (mean ± se N ·10 m^2)							
	1993	1995	1996	1997	1998	1999	2000	All 7 yr
Herbivores								
BR	3.8±0.74	5.8±2.68	4.1±0.50	3.3±0.51	4.6±0.47	2.0±0.21	2.3±0.49	3.7±0.49
PR	5.0±0.52	3.7±0.65	7.2±1.68	3.3±0.92	5.0±0.89	5.6±0.97	3.5±0.73	4.8±0.54
Both	4.5±0.59	4.6±1.05	5.8±1.56	3.2±0.02	4.8±0.18	4.0±1.78	3.0±0.56	4.3±0.37
Total carnivores								
BR	5.2±0.65	3.8±1.32	4.4±0.79	4.1±1.12	5.4±0.93	5.1±1.09	3.5±0.49	4.5±0.27
PR	11.7±1.59	20.0±5.98	18.8±4.86	26.1±12.2	17.4±3.21	21.5±9.88	8.2±0.71	17.7±2.27
Both	8.8±3.24	12.8±8.03	12.4±7.14	16.3±10.9	12.0±5.96	14.2±8.15	6.1±2.36	11.8±1.28
benthic carnivores								
BR	4.1±0.50	1.7±0.19	2.8±0.62	2.6±0.18	3.9±0.59	3.0±0.17	2.5±0.13	2.9±0.31
PR	6.0±0.94	9.6±2.35	10.7±4.60	4.4±1.21	8.3±1.34	10.6±5.56	3.7±0.78	7.6±1.11
Both	5.1±0.97	6.1±3.91	7.2±3.91	3.6±0.90	6.3±2.20	7.3±3.78	3.2±0.59	5.5±0.62
corallivores								
BR	0.29±0.07	0.12±0.05	0.07±0.04	0.06±0.04	0.08±0.03	0.09±0.06	0.03±0.01	0.10±0.03
PR	0.09±0.05	0.12±0.05	0.07±0.04	0.18±0.08	0.26±0.10	0.31±0.13	0.10±0.06	0.16±0.03
Both	0.18±0.10	0.12±0.01	0.07±0.00	0.13±0.06	0.18±0.09	0.21±0.11	0.07±0.03	0.14±0.02
piscivores								
BR	0.00±0.00	0.01±0.01	0.06±0.02	0.01±0.00	0.12±0.09	0.03±0.01	0.04±0.04	0.04±0.01
PR	0.22±0.10	0.40±0.23	0.55±0.13	0.27±0.09	0.85±0.32	0.79±0.42	0.26±0.17	0.48±0.10
Both	0.12±0.11	0.23±0.19	0.33±0.24	0.15±0.13	0.52±0.37	0.45±0.38	0.16±0.10	0.28±0.06

Table 5.–Continued

		Numerical density (mean ± se N ·10 m^2)							
		1993	1995	1996	1997	1998	1999	2000	All 7 yr
planktivores									
	BR	0.8±0.52	2.0±1.50	1.5±0.86	1.5±1.06	1.3±1.07	2.0±1.10	0.9±0.61	1.4±0.17
	PR	5.3±1.13	9.9±3.94	7.5±2.76	21.2±11.9	8.0±2.58	9.8±4.33	4.2±0.93	9.4±2.12
	Both	3.3±2.26	6.4±3.93	4.8±2.98	12.4±9.81	5.0±3.30	6.3±3.89	2.8±1.64	5.9±1.21

Table 6

French Frigate Shoals and Midway–Summary results of factorial ANOVAs testing the effects of habitat (2 levels: barrier, patch reefs), nested within the two sites (2 levels: FFS, Midway), and of survey year (7 levels: 1992/93, 1995-2000) on the numerical densities ($N \cdot 10\ m^{-2}$) of (A) herbivores, (B) carnivores, and, within carnivores, (C) benthic carnivores, (D) corallivores, (E) piscivores (excluding sharks and jacks), and (F) planktivores. Site-by-survey interaction terms were insignificant ($P >> 0.05$) in all cases and are not listed. The results of Student-Newman-Keuls a posteriori tests of least squares means are provided (underlined if not significantly different). P_{crit} set at $\approx 0.1/m$, where m=6, so $P_{crit} \approx 0.016$.

(A) Herbivores ($N \cdot 10\ m^{-2}$; model $r^2 = 0.398$):

Source	df	SS	MS	F-ratio	Prob>F
Model	3	401.6	133.9	26.92	0.0001
Habitat (Site)	3	401.6	133.9	26.92	0.0001
Error	122	606.7	5.0		
Cor. Total	125	1008.3			

Habitat(Site): PR(FFS)>PR(MW)>BR(MW)=BR(FFS)
7.3>4.8>3.7=2.6

(B) Total carnivores ($N \cdot 10\ m^{-2}$; model $r^2 = 0.398$):

Source	df	SS	MS	F-ratio	Prob>F
Model	3	6597.5	2199.2	26.91	0.0001
Habitat (Site)	3	6597.5	2199.2	26.91	0.0001
Error	122	9970.1	81.7		
Cor. Total	125	16567.6			

Habitat (Site): PR(FFS)=PR(MW)>BR(MW)=BR(FFS)
18.9=17.7>4.5=3.1

(C) Benthic carnivores ($N \cdot 10\ m^{-2}$; model $r^2 = 0.339$):

Source	df	SS	MS	F-ratio	Prob>F
Model	3	1497.41	499.14	20.86	0.0001
Habitat(Site)	3	1497.41	499.14	20.86	0.0001
Error	122	2919.78	23.93		
Cor. Total	125	4417.18			

Habitat(Site): PR(FFS)=PR(MW)>BR(MW)=BR(FFS)
10.3=7.6>2.9=1.7

Table 6.–Continued

(D) (Corallivores (N · 10 m^{-2}; model $r^2 = 0.270$):

Source	df	SS	MS	F-ratio	Prob>F
Model	3	0.84	0.28	15.08	0.0001
Habitat (Site)	3	0.84	0.28	15.08	0.0001
Error	122	2.26	0.02		
Cor. Total	125	3.09			

Habitat(Site): PR(FFS)>PR(MW)=BR(MW)=BR(FFS)
0.29>0.16=0.10=0.08

(E) Piscivores (N · 10 m^{-2}; model $r^2 = 0.184$):

Source	df	SS	MS	F-ratio	Prob>F
Model	3	6.61	2.20	9.16	0.0001
Habitat (Site)	3	6.61	2.20	9.16	0.0001
Error	122	29.33	0.24		
Cor. Total	125	35.94			

Habitat(Site): PR(FFS)=PR(MW)>BR(FFS)=BR(MW)
0.56=0.48>0.08=0.04

(F) Planktivores (N · 10 m^{-2}; model $r^2 = 0.243$):

Source	df	SS	MS	F-ratio	Prob>F
Model	3	1710.20	570.07	13.05	0.0001
Habitat (Site)	3	1710.20	570.07	13.05	0.0001
Error	122	5043.49	43.68		
Cor. Total	125	6642.48			

Habitat(Site): PR(MW)=PR(FFS)>BR(MW)=BR(FFS)
9.4=7.8>1.4=1.2

Table 7

French Frigate Shoals and Midway–Summary results of factorial ANOVAs testing the effects of habitat (2 levels: barrier, patch reefs), nested within sites (2 levels: FFS, Midway=MW), and of survey year (7 levels: 1992/93, 1995-2000) on the numerical densities ($N \cdot 10\ m^{-2}$) of families of reef fishes reported by Goodman-Lowe (1998) to include the top 3 most important diurnal and nocturnal monk seal prey: (A) pooled muraenid (moray) eels, (B) pooled synodontids (lizardfishes), (C) pooled balistids (triggerfishes), (D) pooled holocentrids (squirrelfishes), (E) pooled labrids (wrasses), and pooled scarids (parrotfishes). Survey year main effects and all higher-order terms were insignificant ($P >> 0.05$) for all taxa and are not listed. The results of Student-Newman-Keuls a posteriori tests are provided with their least squares means (underlined if insignificantly different).

(A) Pooled moray eels ($N \cdot 10\ m^{-2}$; model $r^2 = 0.200$):

Source	df	SS	MS	F-ratio	Prob>F
Model	3	0.0992	0.0331	10.16	0.0001
Site	1	0.0289	0.0289	8.87	0.0035
Habitat (Site)	2	0.0629	0.0315	9.67	0.0001
Error	122	0.3971	0.0033		
Cor. Total	125	0.4963			

Site: MW>FFS
0.033>0.002

Habitat(Site): PR(MW)>PR(FFS)=BR(FFS)=BR(MW)
0.065>0.003=0.002=0.001

(B) Pooled lizardfishes ($N \cdot 10\ m^{-2}$; model $r^2 = 0.231$):

Source	df	SS	MS	F-ratio	Prob>F
Model	3	2.375	0.792	12.22	0.0001
Site	1	0.536	0.536	8.28	0.0047
Habitat(Site)	2	1.704	0.852	13.15	0.0001
Error	122	7.903	0.065		
Cor. Total	125	10.279			

Site: MW>FFS
0.165>0.033

Habitat(Site): PR(MW)>PR(FFS)=BR(FFS)=BR(MW)
0.327>0.064=0.003=0.002

Table 7.–Continued

(C) pooled triggerfishes ($N \cdot 10\ m^{-2}$; model $r^2 = 0.126$):

Source	df	SS	MS	F-ratio	Prob>F
Model	3	0.031	0.010	5.84	0.0009
Habitat (Site)	3	0.031	0.010	5.84	0.0009
Error	122	0.218	0.002		
Cor. Total	125	0.249			

Habitat(Site): BR(FFS)>BR(MW)=PR(FFS)=PR(MW)
0.039>0.003=0.0=0.0

(D) pooled squirrelfishes ($N \cdot 10\ m^{-2}$; model $r^2 = 0.314$):

Source	df	SS	MS	F-ratio	Prob>F
Model	3	13.11	4.37	18.64	0.0001
Site	1	2.77	2.77	11.81	0.0008
Habitat (Site)	2	9.49	4.74	20.24	0.0001
Error	122	28.61	0.23		
Cor. Total	25	41.72			

Site: FFS>MW
0.43>0.13
Habitat(Site): PR(FFS)>PR(MW)=BR(MW)=BR(FFS)
0.82>0.16=0.11=0.04

(E) pooled wrasses ($N \cdot 10\ m^{-2}$; model $r^2 = 0.344$):

Source	df	SS	MS	F-ratio	Prob>F
Model	3	80.10	26.70	21.36	0.0001
Site	1	20.36	20.36	16.29	0.0001
Habitat (Site)	2	62.31	31.16	24.93	0.0001
Error	122	152.49	1.25		
Cor. Total	125	232.59			

Site: MW>FFS
3.06>2.26
Habitat(Site): PR(MW)=PR(FFS)>=BR(MW)>BR(FFS)
3.46=3.17>=2.66>1.34

Table 7.–Continued

(F) pooled parrotfishes ($N \cdot 10\ m^{-2}$; model $r^2 = 0.215$):

Source	df	SS	MS	F-ratio	Prob>F
Model	3	95.90	31.97	11.16	0.0001
Habitat (Site)	3	95.90	31.97	11.16	0.0001
Error	122	349.47	2.86		
Cor.Total	125	445.37			

Habitat(Site): PR(FFS)=PR(MW)>BR(FFS)=BR(MW)
$\underline{2.34=1.98}>\underline{0.47=0.38}$

Table 8

French Frigate Shoals and Midway–Summary statistics for mean body weight (g · fish^{-1}) and biomass density (g ·10 m^{-2}) at (A) FFS and (B) Midway, during1992/93 and by survey year within the period 1995-2000, for each habitat (barrier reef, BR, *n*=4 stations; lagoonal patch reef, PR, *n*=5) surveyed and for the grand mean of both habitats (*n*=2), for total fishes, comprising herbivores and carnivores (excluding apex predators--all sharks, large carangid jacks, and uku snapper). Grand means over all years are based on *n*=7 surveys. Standard errors (se = std·n$^{-1/2}$) of grand means treat the variances of all independent component means as additive. Biomass densities are expressed in grams to improve readability.

		Mean ± se body weight (g · fish^{-1}) or biomass density (g ·10 m^{-2})							
		1992/93	1995	1996	1997	1998	1999	2000	All 7 yr
(A) FFS: Individual body weight									
Total fishes	BR	145±25	123±43	77±38	74±22	96±36	77±10	29±11	89±11
	PR	60±5	87±12	21±7	54±5	90±28	61±7	46±7	60±5
	Both	102±13	105±23	49±19	64±11	93±23	69±6	38±6	74±6
Herbivores	BR	247±85	181±59	94±50	128±67	177±63	114±12	56±19	142±21
	PR	74±13	171±45	23±5	90±11	143±66	98±27	78±18	97±13
	Both	160±43	176±37	58±25	109±34	160±46	106±15	67±13	120±12
Total carnivores	BR	84±16	104±40	67±31	67±39	73±38	43±12	14±3	65±11
	PR	51±1	58±9	20±7	39±6	63±12	47±4	42±6	46±3
	Both	67±8	81±20	44±16	53±20	68±20	45±6	28±3	55±6
Biomass density									
Total fishes	BR	729±308	767±254	597±438	611±371	474±130	367±35	102±29	521±102
	PR	1,063±689	2,531±406	569±214	1,137±168	2,229±727	1,660±198	1,630±414	1,546±142
	Both	896±158	1,649±240	583±244	874±204	1,351±369	1,013±100	866±207	1,033±87

Table 8.--Continued

		Mean ± se body weight (g · fish^{-1}) or biomass density (g · 10 m^{-2})							
		1992/93	1995	1996	1997	1998	1999	2000	All 7 yr
Herbivores	BR	293±48	506±182	250±157	498±346	373±109	283±44	73±26	325±63
	PR	536±68	1,108±202	195±51	584±142	1,074±521	751±203	442±117	670±90
	Both	414±42	807±136	222±83	541±187	723±266	517±104	257±60	498±55
Total carnivores	BR	206±62	260±70	336±271	187±93	160±54	94±15	33±6	182±44
	PR	538±28	1,286±283	381±161	555±71	1,120±257	950±140	1,226±340	865±80
	Both	372±34	773±146	358±158	371±59	640±131	522±70	629±169	524±46
Older stages (all taxa)	BR	712±307	660±239	552±410	548±318	396±119	324±25	94±25	469±126
	PR	1,051±68	2,383±385	562±215	1,101±154	2,125±713	1,620±192	1,689±457	1,504±113
	Both	881±157	1,522±227	557±231	824±177	1,261±361	972±97	892±229	987±76
(B) Midway: Individual body weight									
Total fishes	BR	152±12	184±23	226±54	132±44	177±23	165±32	182±26	174±13
	PR	76±21	30±9	27±12	28±10	23±5	20±6	30±6	33±4
	Both	114±12	107±12	127±27	80±23	100±12	92±16	106±13	104±7
Herbivores	BR	274±69	255±52	332±123	199±54	292±88	299±79	342±64	285±30
	PR	93±35	36±18	30±18	38±21	25±7	17±8	33±12	39±7
	Both	184±38	146±28	181±62	119±29	158±44	158±40	187±33	162±15
Total carnivores	BR	109±8	123±26	120±29	68±17	113±42	96±14	76±8	101±9
	PR	68±17	27±5	26±9	25±10	22±5	19±5	26±4	30±3
	Both	89±9	75±13	73±15	47±10	68±21	58±7	51±4	66±5

Table 8.--Continued

		Mean ± se body weight (g · fish^{-1}) or biomass density (g ·10 m^{-2})							
		1992/93	1995	1996	1997	1998	1999	2000	All 7 yr
<u>Biomass density</u>									
Total fishes	BR	1,378±225	1,746±367	1,687±363	978±332	1,841±446	1,253±330	1,067±180	1,422±125
	PR	1,272±337	572±103	568±170	432±68	506±129	637±346	356±77	621±78
	Both	1,325±203	1,159±191	1,128±200	705±169	1,174±232	945±239	711±98	1,021±74
Herbivores	BR	1,129±414	1,185±318	1,205±323	727±272	1,469±571	610±161	751±130	1,011±129
	PR	418±151	135±88	151±94	150±87	135±34	110±54	136±63	176±33
	Both	773±220	660±164	678±168	439±143	802±286	360±85	444±72	594±67
Total carnivores	BR	550±51	457±170	415±14	254±50	546±162	506±136	267±42	428±41
	PR	838±232	461±97	412±125	317±73	375±111	531±361	215±44	450±68
	Both	694±119	459±98	413±63	285±44	461±98	519±193	241±30	439±40
Older stages (all taxa)	BR	1,293±195	1,611±384	1,618±369	942±317	1,481±316	1,030±257	912±158	1,270±128
	PR	1,121±291	507±88	544±168	298±96	426±110	582±305	346±67	546±113
	Both	1,207±175	1,059±197	1,081±203	620±166	953±167	806±199	629±86	908±68

Table 9

French Frigate Shoals and Midway–Summary results of factorial ANOVAs testing the effects of habitat (2 levels: barrier, patch reefs), nested within sites (2 levels: FFS, Midway=MW), and survey year (7 levels: 1992/93, 1995-2000) on mean body weight (kg · fish^{-1}) for (A) total fishes, comprising (B) herbivores and (C) carnivores and biomass density (kg ·10 m^{-2}) for (D) total fishes comprising (E) herbivores, and (F) carnivores, and for (G) older-stage fishes (of all taxa pooled). Total fishes, carnivores, and older stages exclude apex predatory sharks, jacks, and uku. Higher-order terms are specified only if significant ($P < 0.05$). The results of Student-Newman-Keuls a posteriori tests are provided with their least squares (LS) means (underlined if insignificantly different). LS means in A-C are expressed in grams for readability.

(A) Total fishes, body weight (kg · fish^{-1}; model $r^2 = 0.546$):

Source	df	SS	MS	F-ratio	Prob>F
Model	3	0.3194	0.1065	48.59	0.0001
Site	1	0.0249	0.0249	11.38	0.0010
Habitat (Site)	2	0.3055	0.1527	69.69	0.0001
Error	122	0.2652	0.0022		
Cor. Total	125	0.5846			

Site: MW>FFS
103>74

Habitat(Site): BR(MW)>BR(FFS)>PR(FFS)>PR(MW)
172>89>60>33

(B) Herbivores, body weight (kg · fish^{-1}; model $r^2 = 0.457$):

Source	df	SS	MS	F-ratio	Prob>F
Model	3	0.9666	0.3222	34.01	0.0001
Site	1	0.0528	0.0528	5.57	0.0199
Habitat (Site)	2	0.9418	0.4709	49.70	0.0001
Error	122	1.1464	0.0095		
Cor. Total	125	2.1130			

Site: MW=FFS
161=120

Habitat(Site): BR(MW)>BR(FFS)=PR(FFS)>=PR(MW)
283>142=97>=39

Table 9.–Continued

(C) Carnivores, body weight (kg · fish^{-1}; model $r^2 = 0.399$):

Source	df	SS	MS	F-ratio	Prob>F
Model	9	0.1024	0.0114	8.48	0.0001
Survey year	6	0.0214	0.0036	2.66	0.0186
Habitat (Site)	3	0.0804	0.0268	19.98	0.0001
Error	116	0.1543	0.0013		
Cor. Total	125	0.2566			

Survey year: 1992/93>=all other>=1997
78>=....>=41

Habitat(Site): BR(MW)>BR(FFS)=PR(FFS)>=PR(MW)
100>65>46>=30

(D) Total fishes, biomass density (kg ·10 m^{-2}; model $r^2 = 0.380$):

Source	df	SS	MS	F-ratio	Prob>F
Model	9	33.17	3.69	7.82	0.0001
Survey year	6	6.82	1.14	2.41	0.0312
Habitat (Site)	3	26.17	8.72	18.52	0.0001
Error	115	54.18	0.47		
Cor. Total	125	87.35			

Survey year: 1995=1998=1992/93=1999=2000=1996=1997
1.41=1.27=1.11=0.99=0.80=0.79=0.78

Habitat (Site): PR(FFS)=BR(MW)>PR(MW)=BR(FFS)
1.55=1.40>0.62=0.52

(E) Herbivores, biomass density (kg ·10 m^{-2}; model $r^2 = 0.312$):

Source	df	SS	MS	F-ratio	Prob>F
Model	3	12.30	4.10	18.29	0.0001
Habitat (Site)	3	12.30	4.10	18.29	0.0001
Error	122	27.11	0.22		
Cor. Total	125	39.41			

Habitat(Site): BR(MW)>PR(FFS)>BR(FFS)=PR(MW)
1.00>0.67>0.32=0.18

Table 9.–Continued

(F) Carnivores, biomass density (kg ·10 m^{-2}; model $r^2 = 0.291$):

Source	df	SS	MS	F-ratio	Prob>F
Model	3	7.72	2.57	16.55	0.0001
Habitat (Site)	3	7.72	2.57	16.55	0.0001
Error	122	18.81	0.16		
Cor. Total	125	26.52			

Habitat(Site): PR(FFS)>PR(MW)=BR(MW)>BR(FFS)
0.86>0.45=0.43>0.18

(G) Older-stage fishes (all taxa) , biomass density (kg ·10 m^{-2}; model $r^2 = 0.321$):

Source	df	SS	MS	F-ratio	Prob>F
Model	3	25.46	8.49	19.05	0.0001
Habitat(Site)	3	25.46	8.49	19.05	0.0001
Error	122	53.92	0.45		
Cor. Total	125	79.38			

Habitat(Site): PR(FFS)=BR(MW)>PR(MW)=BR(FFS)
1.50=1.26>0.55=0.47

Table 10

Frequency occurrence of jacks. Summary statistics for a 3x2 (species x site x survey period) G-test comparison of relative frequency occurrence of two species of jacks (white ulua, *Caranx ignobilis*; omilu, *C. melampygus*) at the two sites (FFS, Midway), during two survey periods--“before”a recreational catch-and-release (C&R) fishing program was begun (prior to and during 1996) versus “after” (in 1997 and subsequent years) establishment of a C&R fishing program. Occurrence was scored based on presence-absence at each of the 9 historical monitoring stations during each of the 7 survey years at FFS (63 station-surveys) and at Midway (62 station-surveys). Note: the significant* Site x Survey period interaction term indicates the difference in relative frequency occurrence at FFS and Midway between “Before” and “After” survey periods.

Maximum-Likelihood Analysis-of-Variance Table

Source	df	Chi-square	Probability
Specis (ulua, omilu)	1	0.01	0.91
Site (FFS, Midway = MW	1	22.51	<0.0001
Survey period (Before-After)	1	2.20	0.14
Site x Survey period	1	5.24	0.022*
Likelihood ratio (= Error)	3	1.25	0.74

Species: omilu=white ulua
(41/125)=(40/125)

Site: FFS>MW
(32/63)>(9/62)

Site x Survey period: FFS, Before=FFS, After>MW, Before>MW, After
white ulua: (15/27)=(18/36)>(6/26)>(1/36)
omilu: (13/27)=(18/36)>(7/26)>(3/36)

Table 11

French Frigate Shoals–Summary results of 2-Way Nested ANOVA testing the effects of four stations (#1: at 23° 49.601' N, 166° 22.631' W ; #2: 23° 52.528' N, 166° 19.612' W ; #3: 23° 53.113' N, 166° 16.801' W; #4: 23° 53.350' N, 166° 14.290' W) and two depths (Shallow=S=52 m, Deep=D= 61 m) on the numbers of individual organisms (of all fish and macroinvertebrate taxa pooled) encountered on timed (20-min), 150 m^2 area, belt transects conducted on windward lower talus slopes of the barrier reef on August 24-27, 1998. Total counts were $\log_{10}(x+1)$-transformed to remove marked heterogeneity of variances. The results of Student-Newman-Keuls a posteriori tests on least squares means are provided.

Total numbers of all taxa					
Source	df	SS	MS	F-ratio	Prob>F
Model	7	4.51	0.65	2.78	0.02
Station	3	1.97	0.66	2.84	0.054
Depth (station)	4	2.54	0.64	2.74	0.046
Error	32	7.42	0.23		
Cor. Total	39	11.93			

Station: $\dfrac{1.518 = 1.458 = 1.166 = 0.971}{\text{Sta 3} = \text{Sta 4} = \text{Sta 1} = \text{Sta 2}}$

Depth (station): $\dfrac{1.88 = 1.80 = 1.18 = 1.16 = 1.15 = 1.12 = 1.03 = 0.91}{S(3) = S(4) = D(1) = S(1) = D(3) = D(4) = S(2) = D(2)}$

Table 12

Methods-calibration survey. Summary regression statistics for relations between the "Old Method"of direct (diver-survey) fish counts and the "New Method" of direct counts, for (A) numerical density ($N \cdot 10\ m^{-2}$) and (B) biomass density ($kg \cdot 10\ m^{-2}$), for total fishes of all taxa. Based on a total of 22 (FFS: 9; Midway:13) matched transect counts made during July-October 2000 at the two sites. Best-fit least-square nonlinear regressions rather than functional regressions were used because, despite the assumed equivalent estimation errors for y and x, the objective was prediction (of both y from x and x from y) rather than description of functional relationships.

(A) Numerical densities (general model: $y = ax^b$; $r = 0.680$):

Specific Model	se of a	se of b	r^2	Prob>F
Old Method = 2.530 · New Method $^{0.2905}$	0.5208	0.0714	0.463	< 0.001
New Method = 1.1225 · Old Method $^{1.5533}$	0.8766	0.4155		

where both counts are expressed as N fish $\cdot 10\ m^{-2}$.

(B) Biomass densities (general model: $y = ax^b$; $r = 0.685$):

Specific Model	se of a	se of b	r^2	Prob>F
Old Method = 0.564 · New Method $^{0.3805}$	0.0778	0.0902	0.470	< 0.001
New Method = 3.232 · Old Method $^{1.6471}$	0.6622	0.4655		

where both counts are expressed as kg $\cdot 10\ m^{-2}$.

Table 13

Methods-calibration survey. Summary regression statistics for relations between the "New Method" of direct fish counts and an indirect (video transect) record of counts for (A) numerical density ($N \cdot 10\ m^2$) and (B) biomass density ($kg \cdot 10\ m^2$), for total fishes of all taxa. Based on a total of 22 (FFS: 9; Midway:13) matched transect counts made during July-October 2000 at the two sites. Curves are best-fit least-square (linear and nonlinear) regressions rather than functional regression because, despite the assumed equivalent estimation errors for y and x, the objective was prediction (of both y from x and x from y) rather than description of functional relationships.

(A) Numerical densities (general model: $y = ax$ [no intercept]; $r = 0.982$):

Specific Model	se of a	se of b	r^2	Prob>F
New Method = 0.450 · Video	0.0186	n/a	0.966	< 0.001
Video = 2.1442 · New Method	0.0885	n/a		

where both counts are expressed as N fish $\cdot 10\ m^{-2}$.

(B) Biomass densities (general model: $y = ax^b$; $r = 0.911$):

Specific Model	se of a	se of b	r^2	Prob>F
New Method = 0.139 · Video $^{1.3142}$	0.0740	0.1784	0.830	< 0.001
Video = 4.5763 · New Method $^{0.7053}$	0.6841	0.0785		

where both counts are expressed as $kg \cdot 10\ m^{-2}$.

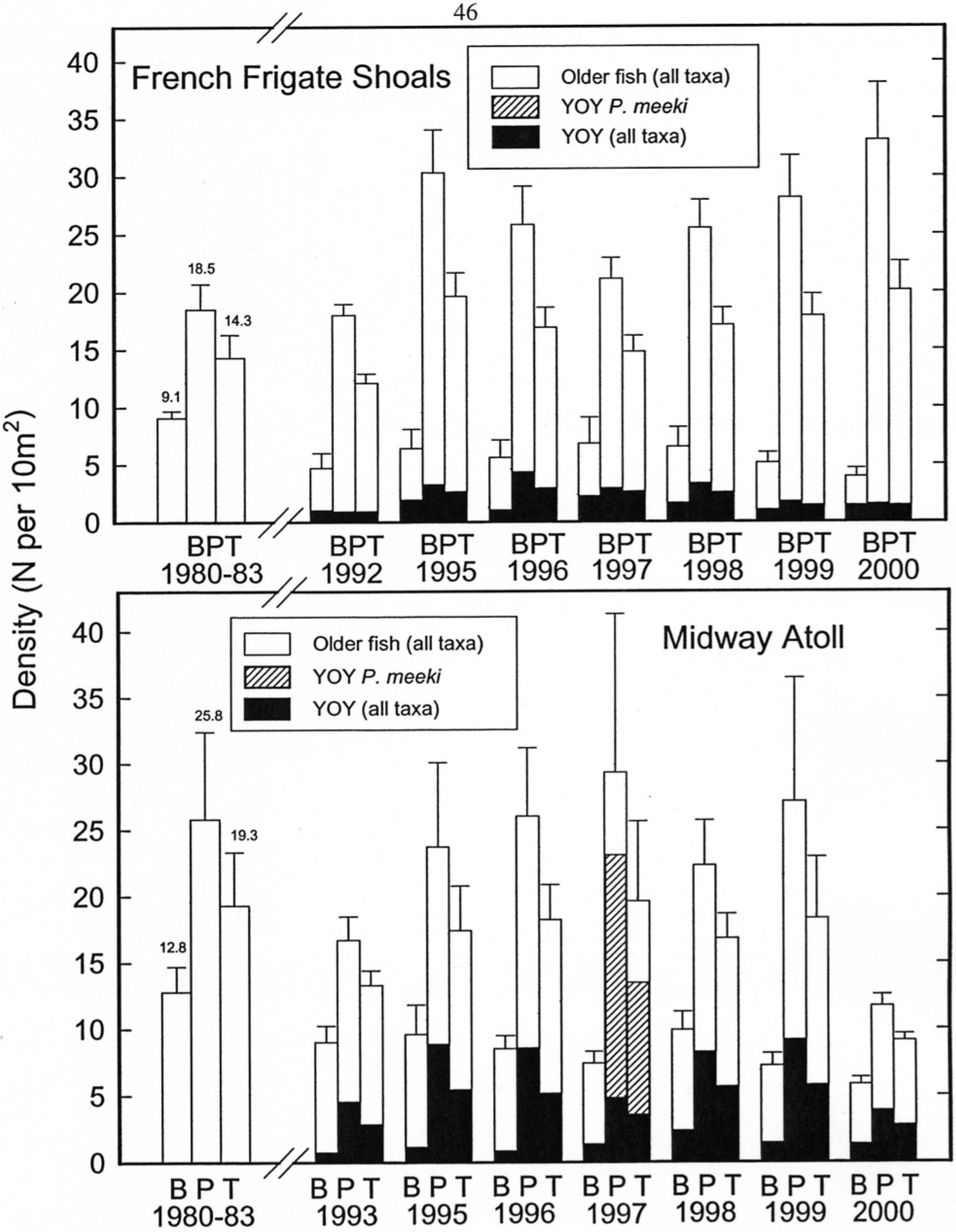

Fig. 1. Numerical densities of total fishes on the barrier` (B) reef, patch (P) reefs, and both habitats (T), at French Frigate Shoals (FFS) and Midway Atoll (MA), during initial baseline surveys and in 1992 (at FFS only), 1993 (MA only), and 1995-2000 (both sites). Vertical lines indicate 1 se for total fishes.

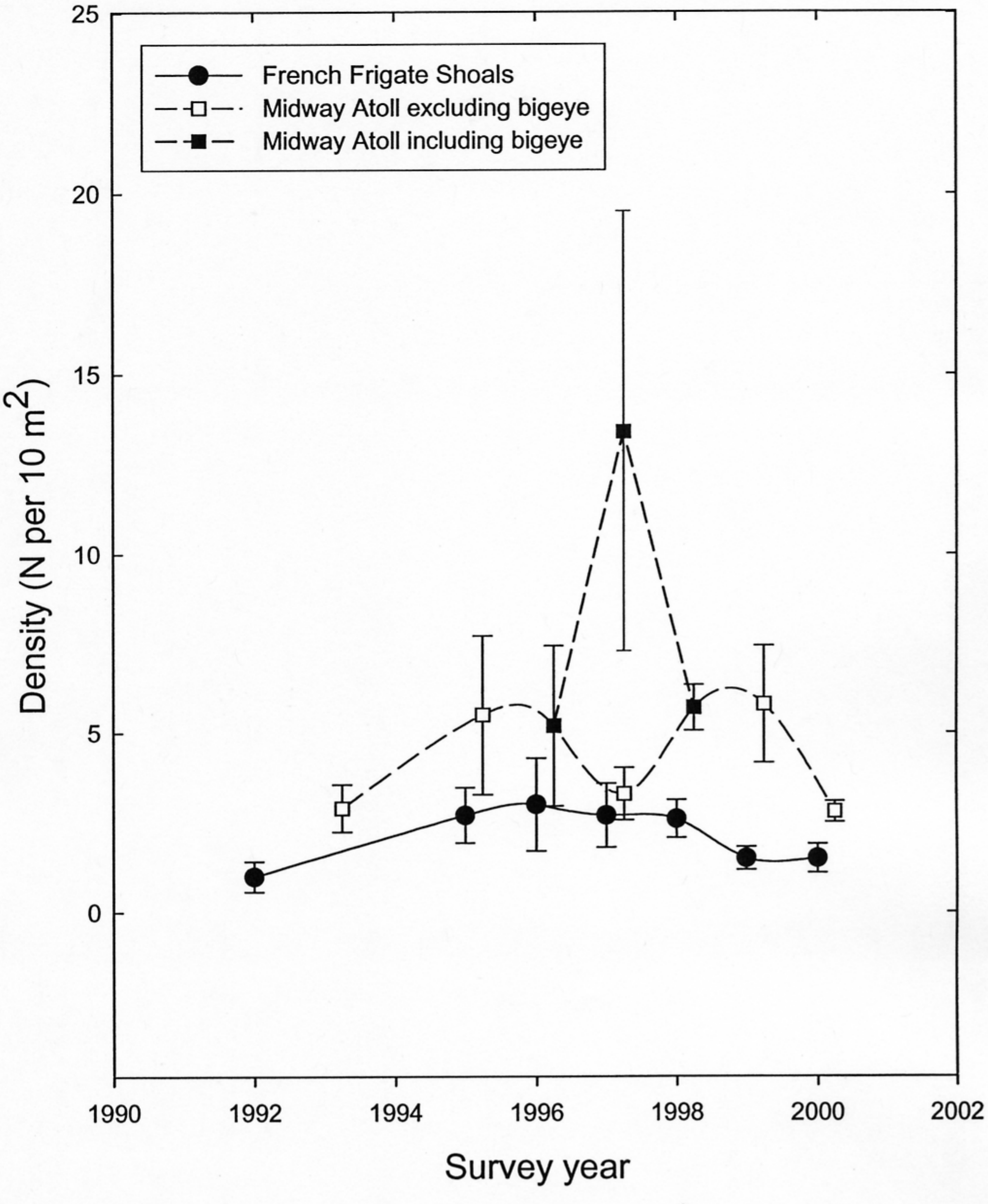

Fig. 2. Time-series plot of numerical densities (N per 10 m^2) for young-of-year (yoy) fishes of all taxa (either including or excluding Hawaiian bigeye, *Priacanthus meeki*) at French Frigate Shoals and Midway Atoll. Spline curves are fit to survey-year means; vertical lines indicate +/- 1 se.

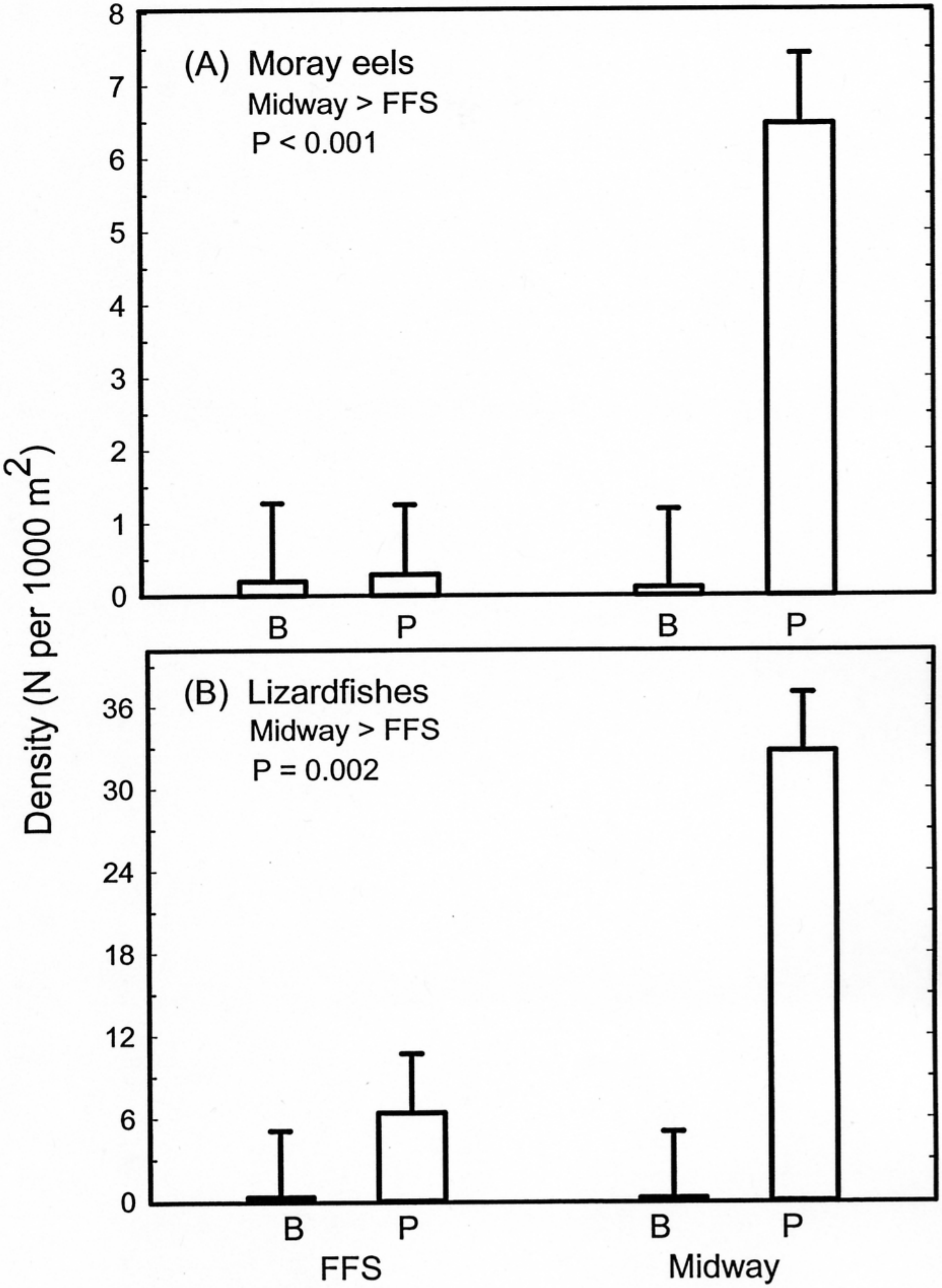

Fig. 3.-- Mean numerical densities (N/1000 m^2) of (A) muraenid eels (a top-ranked prey) and (B) synodontid lizardfishes (a secondary prey) at French Frigate Shoals (FFS) and Midway Atoll during 1992 (at FFS only), 1993 (Midway only), and 1995-2000 (both sites).

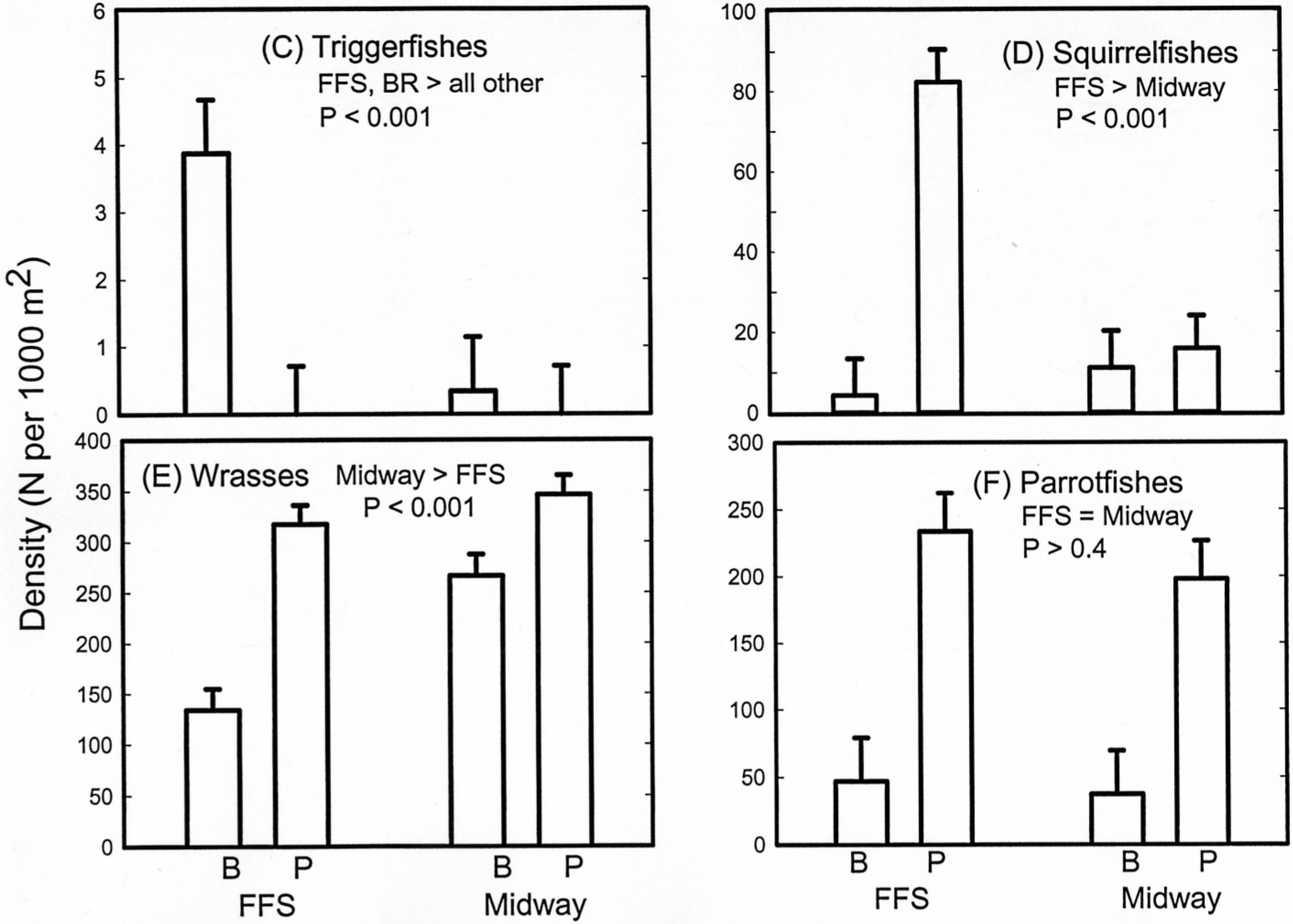

Fig. 3 (cont'd).-- Mean (+ 1se) numerical densities (N per 1000 m^2) of four other prey taxa of the Hawaiian monk seal contrasted between FFS and Midway Atoll. Note differences in density scale among taxa.

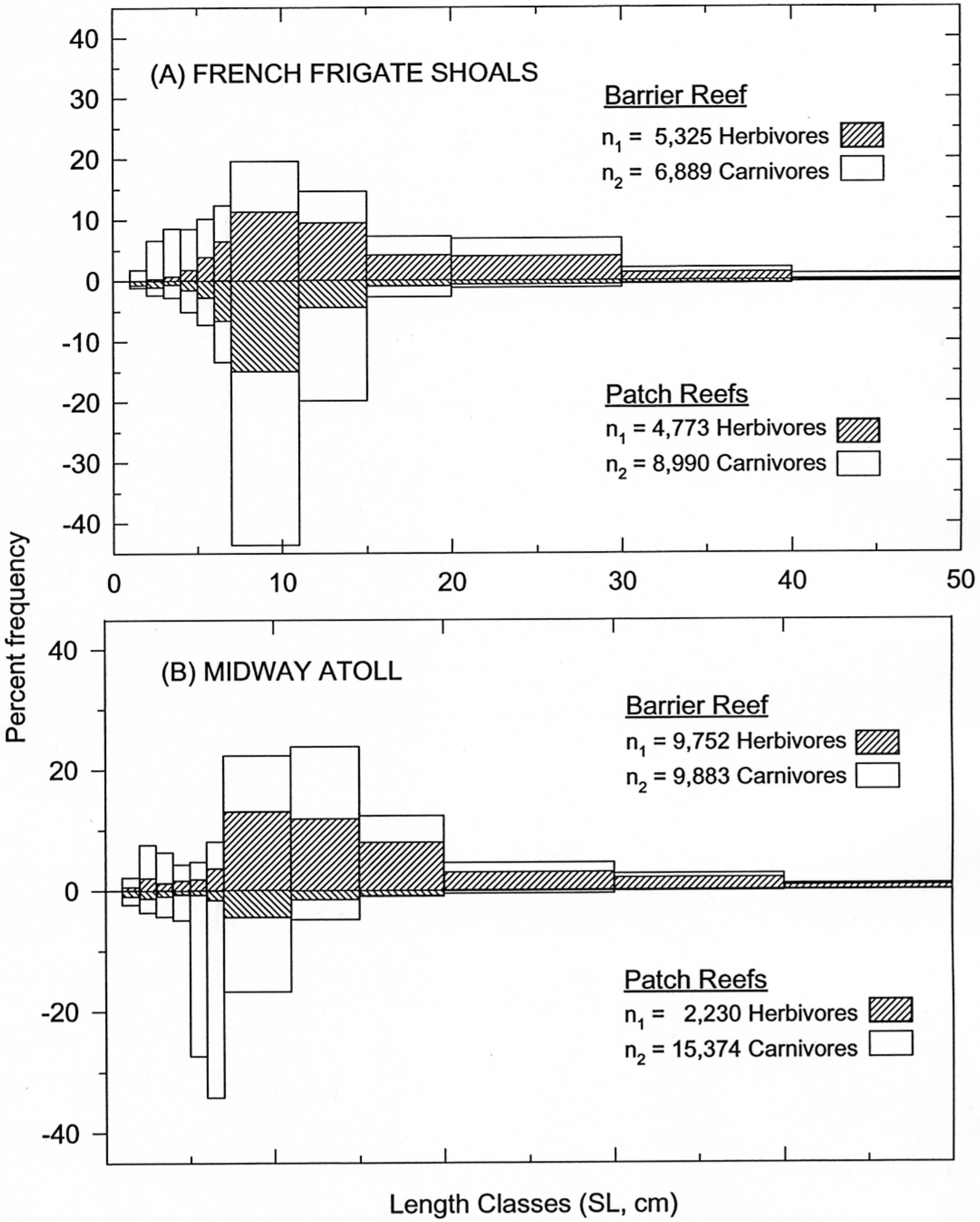

Fig. 4.--Percent frequency body size (Standard Length, SL) distributions for French Frigate Shoals and Midway Atoll, 1992/93 and 1995-2000 surveys pooled.

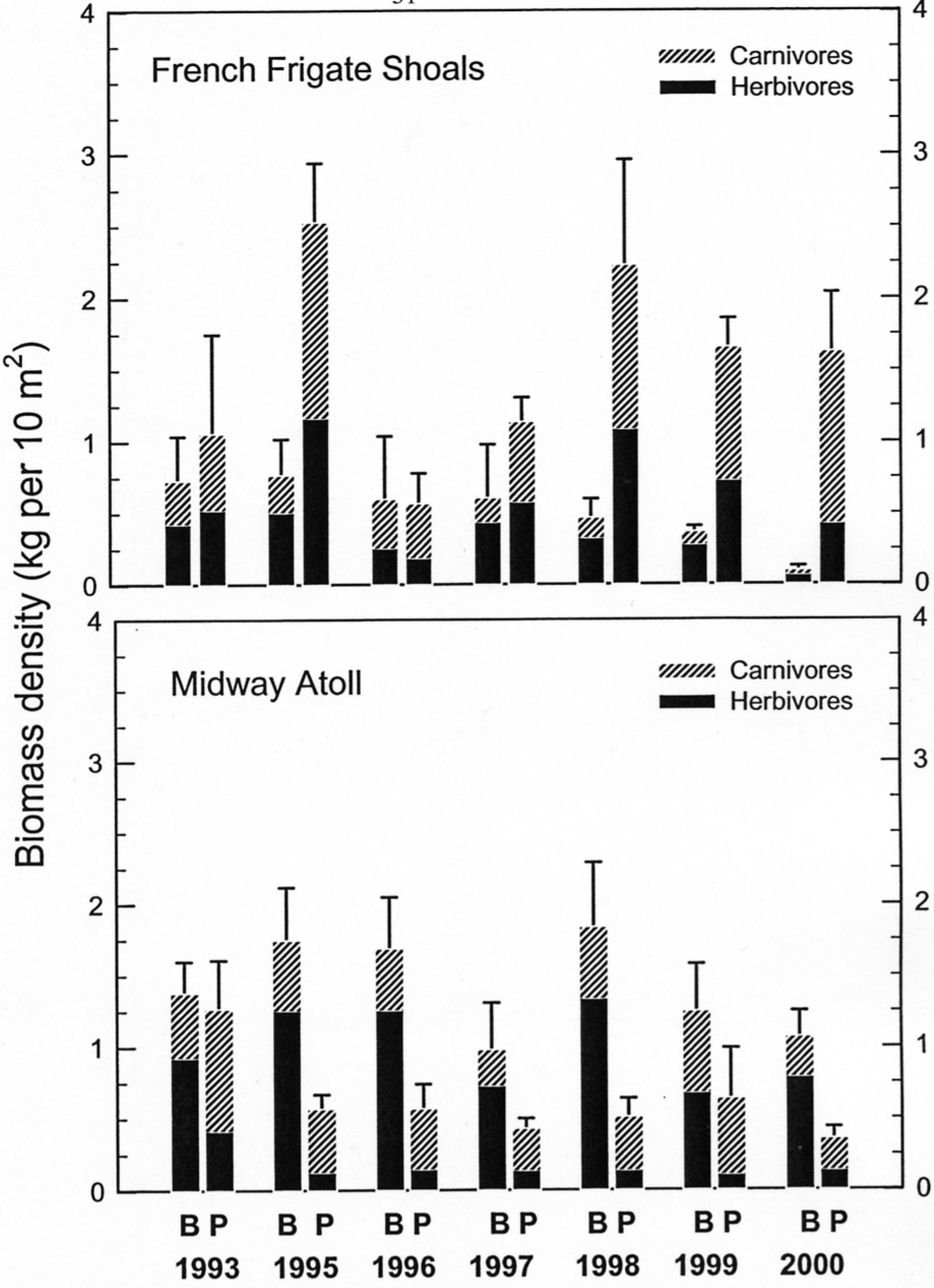

Fig. 5.--Biomass densities of herbivores (solid histograms) and carnivores (diagonals) at FFS and Midway in 1992 (FFS only), 1993 (Midway only), and 1995-2000 (both sites), in barrier (B) and patch (P) reef habitats. Standard errors are noted for total (herbivore plus carnivore) fishes.

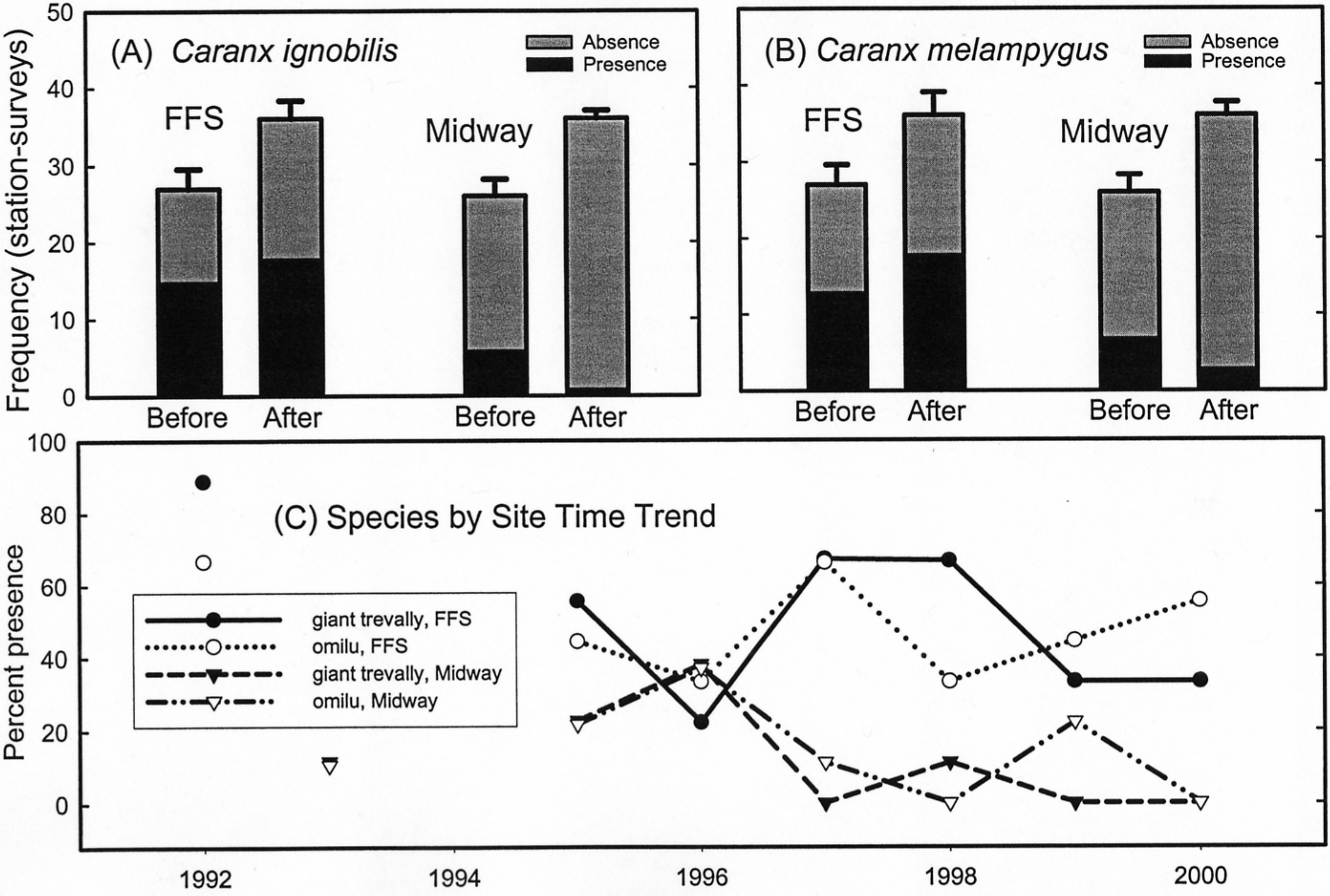

Fig. 6.--Relative presence-absence of (A) giant trevally (*Caranx ignobilis*) and (B) omilu *(C. melampygus)* at FFS and Midway stations during 1992 (FFS) or 1993 (Midway) through 1995-2000 pooled. The stacked presence-absence bars indicate species subtotals up to and including 1996 ("Before") versus after 1996 ("After") at each site. Panel C plots percent presence at stations on each survey. See Table 10 for results of 3 x 2 G-tests. Vertical lines atop histogram bars are 1 se.

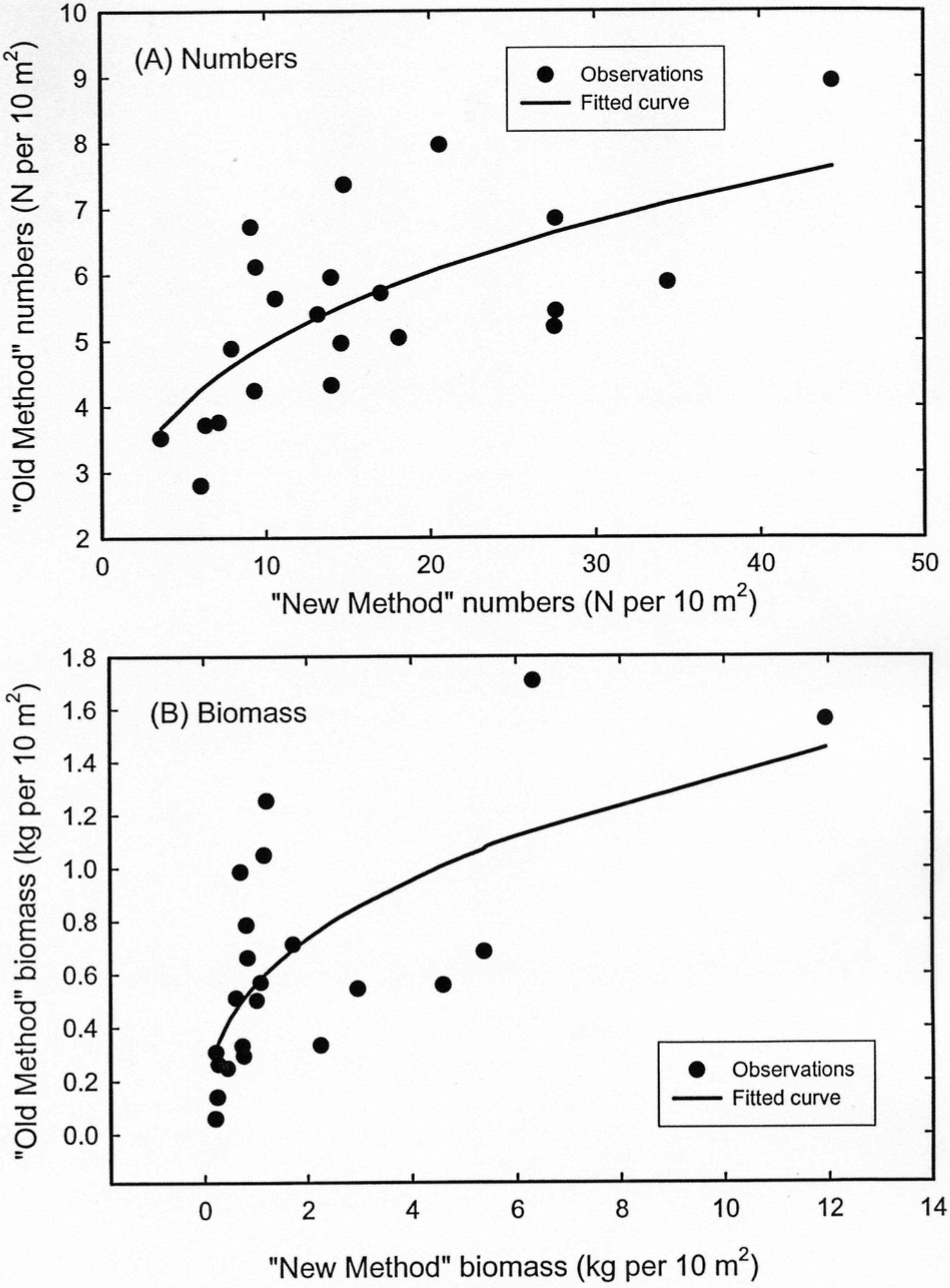

Fig. 7.--Scatterplot and fitted curves for (A) numerical (N per 10 m^2) and (B) biomass densities (kg per 10 m^2) relations for total fishes, for the "Old Method" versus the "New Method" of direct counts.

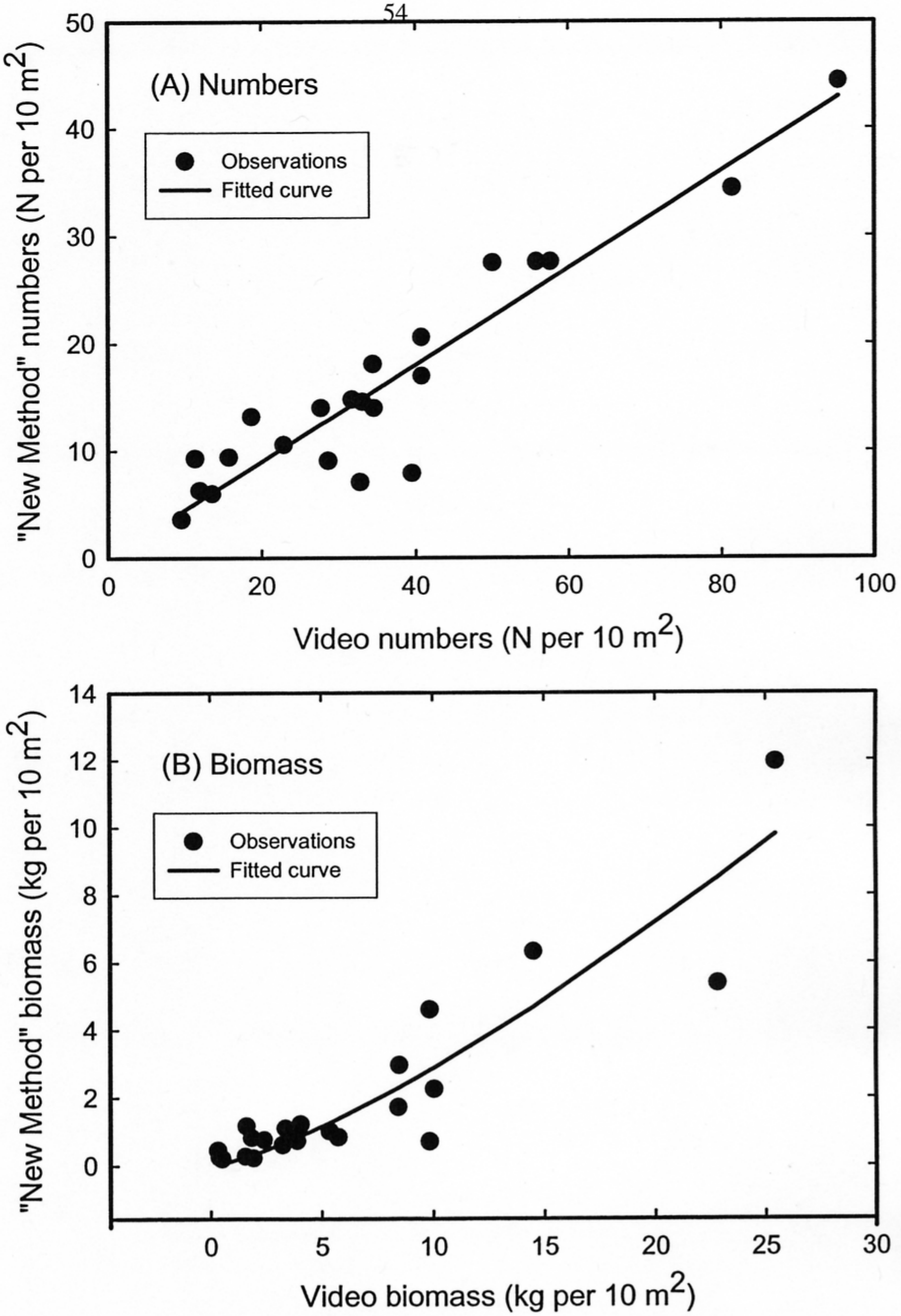

Fig. 8.--Scatterplot and fitted curves for (A) numerical (N per 10 m^2) and (B) biomass density (kg per 10 m^2) relations for total fishes, for the "New Method" of direct counts versus the indirect method (video record).

Appendix Table A

List of P-coded GPS locations of historical monitoring stations used in the1992/93, 1995-2000 study at French Frigate Shoals and Midway Atoll. Habitat code: BR = barrier reef; PR = lagoonal patch reef.

	Station number	Habitat type	Latitude (°N)	Longitude (°W)
FFS	4	BR	23° 51.970'	166° 13.069'
	6	BR	23° 52.810'	166° 16.392'
	7	BR	23° 51.169'	166° 17.871'
	8	BR	23° 51.292'	166° 16.149'
	5c	PR	23° 51.745'	166° 13.766'
	5d	PR	23° 51.748'	166° 13.800'
	5e	PR	23° 51.677'	166° 13.693'
	5f	PR	23° 51.635'	166° 13.765'
	23	PR	23° 51.241'	166° 13.354'
Midway	10	BR	28° 12.882'	177° 25.457'
	14	BR	28° 12.930'	177° 25.330'
	19	BR	28° 16.815'	177° 22.011'
	21	BR	28° 16.660'	177° 22.070'
	5	PR	28° 13.089'	177° 23.987'
	6	PR	28° 12.776'	177° 23.883'
	11	PR	28° 13.000'	177° 24.230'
	17	PR	28° 12.940'	177° 24.190'
	18	PR	28° 12.960'	177° 24.290'

Appendix Table B

List of fishes, by species or lowest taxon, recorded on quantitative diver-observation surveys conducted at historical survey stations at FFS and Midway during 1992/93 and 1995-2000. Taxa are ranked in descending order by 7-yr grand mean biomass density (kg · hectare^{-1}), pooled over both (barrier reef, lagoonal patch reef) habitats at each (FFS, Midway) site. Grand mean numerical density (N · hectare^{-1}) estimates (and their ranks) are also provided; each taxon is categorized by trophic level (primary or secondary consumer) and feeding guild. Included are the 4-digit numerical codes used to identify taxa on computer files and in all analyses. Also noted are the threshold body length (SL, in mm) used to distinguish between yoy and older individuals of each taxon; apex predators indicated by "n/a"; dashes (–) indicate taxon lacks presence of yoy stage on quantitative database. Hawaiian endemic species are indicated by **bold** type.

I. FFS (101 quantitative + 12 non-quantitative = 113 total taxa):	idno	Trophic level	Feeding guild	Density (N/ha)	Rank N	Biomass (kg/ha)	Rank bio	Yoy SL
Taxon								
Caranx ignobilis	201	secondary	piscivore	37	39	145	1	n/a
Dascyllus albisella	2406	secondary	planktivore	2753	1	116	2	4
Mulloidichthys vanicolensis	1103	secondary	ben. carnivore	1271	5	110	3	6
Mulloidichthys flavolineatus	1102	secondary	ben.carnivore	1824	2	94	4	6
Naso unicornis	2712	primary	herbivore	91	26	75	5	6
Chlorurus sordidus, juvenile scarids	2603	primary	herbivore	1396	3	75	6	6
Ctenochaetus strigosus	2710	primary	herbivore	1013	7	56	7	6
Bodianus bilunulatus	1203	secondary	ben.carnivore	97	25	55	8	5
Acanthurus triostegus	2708	primary	herbivore	585	10	50	9	5
Caranx melampygus	202	secondary	piscivore	30	44	47	10	n/a
Stegastes fasciolatus	2410	primary	herbivore	1217	6	41	11	4

Chlorurus perspicillatus	2602	primary	herbivore	71	27	32	12	6
Acanthurus nigroris	2706	primary	herbivore	166	19	25	13	5
Lutjanus kasmira	603	secondary	piscivore	184	17	23	14	6
Chaetodon miliaris	2203	secondary	planktivore	598	9	23	15	5
Thalassoma duperrey	1220	secondary	ben. carnivore	1314	4	23	16	5
Thalassoma ballieui	1219	secondary	ben. carnivore	114	24	22	17	5
Neoniphon sammara	802	secondary	ben. carnivore	382	11	21	18	5
Chromis ovalis	2403	secondary	planktivore	721	8	18	19	5
Acanthurus dussumieri	2714	primary	herbivore	60	32	14	20	6
Triaenodon obesus	104	secondary	piscivore	1	95	13	21	n/a
Carcharhinus amblyrhynchos	102	secondary	piscivore	0	97	11	22	n/a
Naso lituratus	2711	primary	herbivore	31	41	11	23	6
Sargocentron spiniferum	809	secondary	ben. carnivore	14	55	11	24	5
Kyphosus spp (*bigibbus, cinersacens, vaigiensis*)	2501	primary	herbivore	27	46	10	25	7
Zebrasoma flavescens	2713	primary	herbivore	182	18	9	26	6
Acanthurus olivaceus	2707	primary	herbivore	27	45	9	27	6
Scarus dubius	2601	primary	herbivore	26	48	9	28	6
Parupeneus multifasciatus	1107	secondary	ben. carnivore	189	15	9	29	6
Diodon hystrix	2902	secondary	ben. carnivore	2	81	8	30	6

Oxycheilinus unifasciatus	1228	secondary	ben. carnivore	47	34	8	31	7
Coris flavovittata	1205	secondary	ben. carnivore	26	47	8	32	7
Scarus spp	2604	primary	herbivore	9	60	7	33	6
Centropyge potteri	2101	primary	herbivore	236	13	7	34	4
Acanthurus spp	2701	primary	herbivore	12	57	7	35	6
Myripristis spp (*amaena, berndti, kuntee*)	803	secondary	planktivore	46	35	7	36	5
Epibulus insidiator	1209	secondary	ben. carnivore	45	36	7	37	5
Parupeneus pleurostigma	1108	secondary	ben. carnivore	59	33	6	38	6
Acanthurus xanthopterus	2709	primary	herbivore	4	74	6	39	6
Chaetodon ornatisssimus	2205	secondary	corallivore	36	40	5	40	5
Stethojulis balteata	1218	secondary	ben. carnivore	232	14	4	41	5
Acanthurus achilles	2702	primary	herbivore	20	52	4	42	6
Melichthys niger	1701	secondary	planktivore	6	69	3	43	7
Acanthurus nigrofuscus	2705	primary	herbivore	22	50	3	44	5
Macropharyngodon geoffroy	1223	secondary	ben. carnivore	135	22	2	45	5
Chaetodon fremblii	2202	secondary	ben. carnivore	64	29	2	46	5
Chaetodon auriga	2201	secondary	ben. carnivore	7	67	2	47	6
Coris venusta	1208	secondary	ben. carnivore	64	30	2	48	5
Zanclus cornutus	2801	secondary	ben. carnivore	30	43	2	49	7
Synodontidae	701	secondary	piscivore	37	38	2	50	6

Aprion virescens	602	secondary	piscivore	1	91	2	51	n/a
Calotomus spp (*carolinensis*, ***zonarchus***)	2607	primary	herbivore	4	75	2	52	6
Plectroglyphidodon johnstonianus	2408	secondary	corallivore	121	23	1	53	3
Adioryx spp (*diadema*, ***xantherythrum***)	801	secondary	ben. carnivore	30	42	1	54	5
Anampses cuvieri	1202	secondary	ben. carnivore	10	59	1	55	5
Chromis hanui	2402	secondary	planktivore	189	16	1	56	3
Monotaxis grandoculis	1001	secondary	ben. carnivore	1	87	1	57	7
Canthigaster jactator	1801	secondary	ben. carnivore	163	20	1	58	3
Gomphosus varius	1210	secondary	ben. carnivore	68	28	1	59	5
Sufflamen bursa	1704	secondary	ben. carnivore	8	65	1	60	7
Acanthurus blochii	2703	primary	herbivore	8	63	1	61	6
Chromis vanderbilti	2404	secondary	planktivore	358	12	1	62	6
Parupeneus cyclostomus	1105	secondary	ben. carnivore	10	58	1	63	6
Pseudocheilinus octotaenia	1222	secondary	ben. carnivore	42	37	1	64	5
Chaetodon multicinctus	2204	secondary	corallivore	22	51	1	65	5
Priacanthus meeki	1501	secondary	planktivore	24	49	1	66	7
Cheilodactylus vittata	1601	secondary	ben. carnivore	5	72	1	67	7
Naso brevirostris	2723	secondary	planktivore	13	56	1	68	6
Melichthys vidua	1702	secondary	ben. carnivore	2	82	1	69	7
Exallias brevis	2304	secondary	corallivore	5	70	1	70	5

Apogon spp (*kallopterus*, ***maculiferus***, *menesemus*)	901	secondary	planktivore	19	53	0	71	5
Paracirrhites arcatus	1303	secondary	ben. carnivore	15	54	0	72	5
Aulostomus chinensis	401	secondary	piscivore	62	31	0	73	7
Parupeneus porphyreus	1109	secondary	ben. carnivore	3	77	0	74	6
Forcipiger flavissimus	2211	secondary	ben. carnivore	9	62	0	75	5
Anampses chrysocephalus	1201	secondary	ben. carnivore	7	68	0	76	5
Labroides phthirophagus	1213	secondary	ben. carnivore	141	21	0	77	4
Gymnothorax spp (5 incl ***steindachneri***)	302	secondary	piscivore	2	80	0	78	--
Chaetodon lunulatus	2209	secondary	corallivore	3	78	0	79	5
Pervagor spilosoma	2002	secondary	corallivore	8	66	0	80	5
Aphareus furca	604	secondary	piscivore	0	99	0	81	7
Paracirrhites forsteri	1304	secondary	ben. carnivore	2	83	0	82	5
Chaetodon lunula	2212	secondary	ben. carnivore	1	92	0	83	5
Cirrhitops fasciatus	1301	secondary	ben. carnivore	9	61	0	84	5
Chaetodon trifascialis	2208	secondary	corallivore	2	86	0	85	5
Abudefduf abdominalis	2401	secondary	planktivore	2	85	0	86	6
Pseudocheilinus evanidus	1226	secondary	ben. carnivore	8	64	0	87	5
Rhinecanthus rectangulus	1705	secondary	ben.carnivore	1	93	0	88	7
Cirripectes vanderbilti	2303	primary	herbivore	5	71	0	89	5

Novaculichthys taeniourus	1216	secondary	ben. carnivore	2	84	0	90	7
Halichoeres ornatissimus	1221	secondary	ben. carnivore	4	76	0	91	5
Chromis verater	2411	secondary	planktivore	0	99	0	92	5
Dendrochirus barberi	1401	secondary	ben. carnivore	1	89	0	93	4
Coris gaimard	1206	secondary	ben. carnivore	0	97	0	94	5
Plectroglyphidodon imparipennis	2407	secondary	ben. carnivore	4	73	0	95	3
Ostracion meleagris	1901	secondary	ben. carnivore	1	94	0	96	4
Fistularia commersoni	501	secondary	piscivore	1	89	0	97	7
Taenianotus triacanthus	1404	secondary	ben. carnivore	1	96	0	98	4
Acanthurus leucopareius	2717	primary	herbivore	0	101	0	99	6
Plagiotremus ewaensis, goslinei	2307	secondary	ben. carnivore	3	79	0	100	4
Pseudocheilinus tetrataenia	1225	secondary	ben. carnivore	1	89	0	101	5

FFS, non-quantitative taxa (n=12, alphabetized):	idno	Trophic level	Feeding guild
Abudefduf vaigiensis	2414	secondary	planktivore
Bothus mancus	3501	secondary	piscivore
Calotomus zonarchus	2612	primary	herbivore
Cantherhines verecundus	2007	primary	herbivore
Cirrhitus pinnulatus	1305	secondary	ben. carnivore
Forcipiger longirostris	2213	secondary	ben. carnivore

Galeocerdo cuvier	103	secondary	piscivore					
Manta birostris	4502	secondary	planktivore					
Pterois sphex	1402	secondary	ben. carnivore					
Scarus rubroviolaceus	2611	primary	herbivore					
Scarus psittacus	2610	primary	herbivore					
Scorpaenopsis diabolus	1409	secondary	piscivore					
II. Midway (93 quantitative + 16 non-quantitative = 109 total taxa):	idno	Trophic level	Feeding guild	Density (N/ha)	Rank N	Biomass (Bio/ha)	Rank Bio	Yoy SL
Chlorurus perspicillatus	2602	primary	herbivore	75	30	152	1	6
Kyphosus spp (*bigibbus, cinerascens, vaigiensis*)	2501	primary	herbivore	204	15	132	2	7
Stegastes fasciolatus	2410	primary	herbivore	2087	1	81	3	4
Bodianus bilunulatus	1203	secondary	ben. carnivore	80	29	71	4	5
Dascyllus albisella	2406	secondary	planktivore	1916	2	54	5	4
Chlorurus sordidus/juvenile scarids	2603	primary	herbivore	1136	5	47	6	6
Thalassoma ballieui	1219	secondary	ben. carnivore	298	12	44	7	5
Parupeneus pleurostigma	1108	secondary	ben. carnivore	590	10	35	8	6
Acanthurus triostegus	2708	primary	herbivore	312	11	34	9	5
Calotomus spp (*carolinus*, ***zonarchus***)	2607	primary	herbivore	50	38	33	10	6
Thalassoma duperrey	1220	secondary	ben. carnivore	1539	3	33	11	5
Chromis ovalis	2403	secondary	planktivore	912	7	30	12	5

Abudefduf abdominalis	2401	secondary	planktivore	202	16	26	13	6
Acanthurus leucopareius	2717	primary	herbivore	74	31	22	14	6
Mulloidichthys flavolineatus	1102	secondary	ben. carnivore	995	6	22	15	6
Coris flavovittata	1205	secondary	ben. carnivore	35	43	21	16	7
Chaetodon miliaris	2203	secondary	planktivore	669	8	20	17	5
Caranx ignobilis	201	secondary	piscivore	4	70	17	18	n/a
Naso unicornis	2712	primary	herbivore	10	58	15	19	6
Ctenochaetus strigosus	2710	primary	herbivore	127	21	11	20	6
Epinephelus quernus	3202	secondary	ben. carnivore	2	74	11	21	--
Acanthurus nigroris	2706	primary	herbivore	88	27	11	22	5
Priacanthus meeki	1501	secondary	planktivore	1366	4	11	23	7
Myripristis spp (*amaena, berndti, kuntee*)	803	secondary	planktivore	59	36	11	24	5
Synodontidae	701	secondary	piscivore	186	17	10	25	6
Scarus dubius	2601	primary	herbivore	23	52	8	26	6
Paracirrhites forsteri	1304	secondary	ben. carnivore	66	32	8	27	5
Oxycheilinus unifasciatus	1228	secondary	ben. carnivore	24	50	7	28	7
Oxycheilinus bimaculatus	1227	secondary	ben. carnivore	297	13	6	29	4
Chaetodon fremblii	2202	secondary	ben. carnivore	117	22	6	30	5
Coris venusta	1208	secondary	ben. carnivore	161	18	6	31	5
Mulloidichthys vanicolensis	1103	secondary	ben. carnivore	61	35	6	32	6

Anampses cuvier	1202	secondary	ben. carnivore	64	33	5	33	5
Chaetodon auriga	2201	secondary	ben. carnivore	24	49	5	34	6
Carangoides orthogrammus	208	secondary	piscivore	1	82	4	35	n/a
Zebrasoma veliferum	2722	primary	herbivore	12	56	4	36	6
Neoniphon sammara	802	secondary	ben. carnivore	47	39	4	37	5
Thalassoma trilobatum	1229	secondary	ben. carnivore	18	54	3	38	5
Stethojulis balteata	1218	secondary	ben. carnivore	294	14	3	39	5
Parupeneus porphyreus	1109	secondary	ben. carnivore	62	34	3	40	6
Zebrasoma flavescens	2713	primary	herbivore	35	44	3	41	6
Parupeneus multifasciatus	1107	secondary	ben. carnivore	56	37	3	42	6
Arothron hispidus	3102	secondary	ben. carnivore	9	60	2	43	6
Gymnothorax (5 spp incl. ***steindachneri***)	302	secondary	piscivore	36	42	2	44	--
Chaetodon ornatissimus	2205	secondary	corallivore	11	57	2	45	5
Acanthurus nigrofuscus	2705	primary	herbivore	23	51	2	46	5
Caranx melampygus	202	secondary	piscivore	1	79	2	47	n/a
Scorpaenidae	1408	secondary	ben. carnivore	143	20	2	48	4
Apogon spp (*kallopterus*, ***maculiferus***, *menesemus*)	901	secondary	planktivore	645	9	2	49	5
Oplegnathus punctatus	3902	secondary	ben. carnivore	1	80	2	50	--
Diodon hystrix	2902	secondary	ben. carnivore	1	86	2	51	6

Macropharyngodon geoffroy	1223	secondary	ben. carnivore	85	28	2	52	5
Adioryx spp	801	secondary	ben. carnivore	28	47	1	53	5
Cirrhitus pinnulatus	1305	secondary	ben. carnivore	7	63	1	54	5
Aprion virescens	602	secondary	piscivore	1	82	1	55	--
Dendrochirus barberi	1401	secondary	ben. carnivore	89	26	1	56	4
Zanclus cornutus	2801	secondary	ben. carnivore	9	61	1	57	7
Cirrhitops fasciatus	1301	secondary	ben. carnivore	39	40	1	58	5
Scorpaenopsis diabolus	1409	secondary	piscivore	4	68	1	59	5
Plectroglyphidodon johnstonianus	2408	secondary	corallivore	94	24	1	60	3
Aulostomus chinensis	401	secondary	piscivore	37	41	1	61	7
Melichthys niger	1701	secondary	planktivore	1	79	1	62	11
Centropyge potteri	2101	primary	herbivore	10	59	1	63	4
Chaetodon lunulatus	2209	secondary	corallivore	6	64	1	64	5
Pervagor spilosoma	2002	secondary	corallivore	25	48	1	65	5
Thalassoma purpureum	1231	secondary	ben. carnivore	1	87	1	66	5
Cheilodactylus vittata	1601	secondary	ben. carnivore	6	65	1	67	7
Canthigaster jactator	1801	secondary	ben. carnivore	94	25	0	68	3
Sargocentron spiniferum	809	secondary	ben. carnivore	0	91	0	69	5
Chromis hanui	2402	secondary	planktivore	108	23	0	70	3
Decapterus macarellus	203	secondary	planktivore	6	66	0	71	--

Pseudocheilinus octotaenia	1222	secondary	ben. carnivore	21	53	0	72	5
Paracirrhites arcatus	1303	secondary	ben. carnivore	8	62	0	73	5
Gomphosus varius	1210	secondary	ben. carnivore	14	55	0	74	5
Exallias brevis	2304	secondary	corallivore	2	76	0	75	5
Labroides phthirophagus	1213	secondary	ben. carnivore	145	19	0	76	4
Fistularia commersonii	501	secondary	piscivore	5	67	0	77	7
Anampses chrysocephalus	1201	secondary	ben. carnivore	30	45	0	78	5
Parupeneus cyclostomus	1105	secondary	ben. carnivore	1	83	0	79	6
Conger cinereus	4101	secondary	piscivore	3	73	0	80	--
Pterois sphex	1402	secondary	ben. carnivore	3	72	0	81	4
Chromis vanderbilti	2404	secondary	planktivore	29	46	0	82	6
Halichoeres ornatissimus	1221	secondary	ben. carnivore	4	69	0	83	5
Enchelychore pardalis	315	secondary	piscivore	1	84	0	84	--
Brotula multibarbata	3701	secondary	ben. carnivore	0	90	0	85	--
Cheilio inermis	1234	secondary	ben. carnivore	0	93	0	86	5
Ostracion meleagris	1901	secondary	ben. carnivore	2	77	0	87	4
Epibulus insidiator	1209	secondary	ben. carnivore	0	89	0	88	5
Taenianotus triacanthus	1404	secondary	ben. carnivore	1	88	0	89	4
Forcipiger flavissimus	2211	secondary	ben. carnivore	1	85	0	90	5
Desmoholocanthus arcuatus	2102	secondary	ben. carnivore	0	93	0	91	5

Cirripectes vanderbilti	2303	primary	herbivore	2	75	0	92	5
Novaculichthys taeniourus	1216	secondary	ben. carnivore	4	71	0	93	7
Midway, non-quantitative taxa (n=16, alphabetized):	idno	Trophic level	Feeding guild					
Acanthurus dussumieri	2714	primary	herbivore					
Bothus mancus	3501	secondary	piscivore					
Calotomus zonarchus	2612	primary	herbivore					
Caracanthus typicus	3801	secondary	ben. carnivore					
Carangoides ferdau	204	secondary	piscivore					
Chaetodon unimaculatus	2210	secondary	corallivore					
Coris ballieui	1235	secondary	ben. carnivore					
Cymolutes lecluse	1233	secondary	ben. carnivore					
Forcipiger longirostris	2213	secondary	ben. carnivore					
Gnatholepis anjerensis	3402	secondary	ben. carnivore					
Lactoria fornasini	1902	secondary	ben. carnivore					
Manta birostris	4502	secondary	planktivore					
Oplegnathus fasciatus	3901	secondary	ben. carnivore					
Pseudocheilinus tetrataenia	1225	secondary	ben. carnivore					
Scarus psittacus	2610	primary	herbivore					
Seriola dumerili	205	secondary	piscivore					

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