

PREDATION, ENDEMISM, AND RELATED PROCESSES STRUCTURING SHALLOW-WATER REEF FISH ASSEMBLAGES OF THE NWHI

BY

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ABSTRACT

Data on distribution, abundance, and related patterns, reflecting key ecological processes such as predation, are herein summarized for the shallow-water (< 18-m) reef fishes of the Northwestern Hawaiian Islands (NWHI). This summary is based on the results of two complementary series of relatively recent underwater diver surveys conducted by the Pacific Islands Fisheries Science Center (PIFSC), National Marine Fisheries Service, National Oceanic and Atmospheric Administration (NOAA) and allied-agency personnel that began in the early 1990s and extended through 2004. The first series of surveys began in 1992 at French Frigate Shoals and 1993 at Midway Atoll as a re-characterization of a decade-prior baseline assessment conducted by the U.S. Fish and Wildlife Service (USFWS). These surveys were repeated yearly from 1995 through 2000. A second series of assessment surveys began in 2000 and extended through 2001 and 2002. The first series thus is an intensive long-term but spatially limited characterization that complements a spatially extensive but relatively short-term characterization for all ten emergent NWHI reefs in the second series. Among the more important patterns linked to predation and related processes that have been revealed recently are: a nearly three-fold greater standing biomass of shallow-water reef fishes in the NWHI (versus the Main Hawaiian Islands, MHI) that primarily reflects the near extirpation of apex predatory reef fishes in the MHI and a large reduction in secondary carnivores; the importance of wave-sheltered habitats as juvenile nurseries for many species and the value of atolls that provide disproportionate amounts of sheltered habitat; the heretofore unquantified extent of endemism (e.g., > 50% by numerical abundance) in NWHI reef fishes and its geographic increase with latitude-longitude to maxima at the three northernmost atolls; and the effects of apex predators on the body size distribution of prey reef fishes and the size-at-sex change in protogynous parrotfishes in the NWHI. These findings have identified the NWHI as one of the few remaining predator-dominated coral-reef ecosystems and an important part of an archipelago with a unique and strongly endemic fish fauna.

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INTRODUCTION

Predation is a keystone process in marine ecosystems (Hixon, 1991), especially in near-pristine systems like the NWHI that have been minimally impacted by humans. Many perceived patterns within an ecosystem represent responses at various scales—from individuals to population and assemblage levels of organization—to the fundamental ecological processes that structure it, and careful examination of patterns can provide insight into these processes. In this paper we identify conspicuous patterns related to the major structuring process of predation and several other processes indirectly related to predation. In so doing, we hope to broaden appreciation by fishery and coastal resource managers, and the general public, of the unique value of the NWHI as a natural, predation-structured ecosystem and the need to conserve, protect, and learn from it.

PATTERNS RELATED TO PREDATION

There are many phenomena whose patterns clearly attest, directly or indirectly, to predation as a major structuring agent. Among the most obvious are those related to the relative magnitude of conspicuous elements of the fish faunas (apparent to an *in situ* diver-observer) at shallow, conventional diving depths on NWHI and MHI reefs. Our observations of these patterns have provided insights into the population and community processes that structure the NWHI shallow coral-reef ecosystem.

Observations of NWHI reef fishes have been accrued over two series of partially overlapping monitoring and assessment-monitoring surveys during the periods 1992-2000 and 2000-2004. The first series of surveys was conducted by the PIFSC and began in 1992 at French Frigate Shoals (FFS) and 1993 at Midway Atoll. Its objective was to track the temporal dynamics of the shallow-reef fish forage base of monk seals (*Monachus schauinslandi*) at FFS and Midway by, first, re-characterizing and then subsequently monitoring the densities of fishes at stations established a decade prior during an initial baseline assessment conducted by the USFWS. These monitoring surveys were repeated yearly from 1995 through 2000. A second series of fish resource assessment surveys were initiated by the PIFSC, the NOAA National Ocean Survey (NOS) Coastal Oceans and National Marine Sanctuary Program, and other allied agencies (State of Hawaii Department of Land and Natural Resources, Division of Aquatic Resources) in 2000 and was extended through 2001 and 2002. These surveys were followed in 2003 and 2004 by the first two of a continuing series of annual surveys dedicated to monitoring a representative subset of stations. Briefly stated, a combination of quantitative (transect-delimited, stationary diver), and qualitative (Rapid Visual Assessment), nondestructive visual surveys have been conducted, with method linked to the type of estimate and to the size and mobility of different groups of fishes. Reef sites and survey methods are specified by DeMartini et al. (1996, 2002) and Friedlander and DeMartini (2002).

The most conspicuous of the patterns documented by these *in situ* observations is the strikingly higher numerical and biomass densities and greater average body sizes of reef fishes in the NWHI compared to the MHI, particularly for large jacks, reef

sharks, and other apex predators (Fig. 1). Also notable is the overall reduced numbers and biomass of lower trophic level fishes in the MHI, including lower-level carnivores (Fig. 2). The smaller proportion of lower-level carnivore (versus herbivore) biomass in the MHI is likely due to the greater extraction of the former by line fishing and selective gillnetting as well as spearfishing. The lesser abundance of apex predators as well as lower-trophic-level fishes in the MHI is likely the result of overexploitation by humans in the MHI (Friedlander & DeMartini, 2002). Were it not for extraction, reef-fish productivity in the MHI should be higher (not lower) than in the NWHI as a result of greater terrigenous nutrient input and more diverse juvenile nursery habitats at the vegetated, high windward islands; other anthropogenic stressors insufficiently explain the lower standing stocks of reef fishes in the MHI (Friedlander and DeMartini, 2002; Friedlander and Brown, 2004).

Perhaps the strongest evidence for the controlling influence of apex predation on the structure of fish assemblages in the NWHI is provided by data on the size, composition, and spatial distribution of prey species. In the early 1990s, differences were first noted between FFS and Midway in the relative abundance of herbivores and carnivores and in the distribution of fish numbers and biomass among barrier reef and lagoonal patch reef habitats—with large-bodied herbivores prevailing on barrier reefs and relatively small-bodied (< 10 cm Total Length) carnivores dominating numerically on patch reefs (DeMartini et al., 1996). Size structure data collected during re-assessment surveys in 2000-02 provided further insights into the effects of apex predators on their shallow-water reef fish prey: protogynous (female-to-male sex-changing) labroid fishes (primarily parrotfishes), the adult sexes of which conspicuously differ in body coloration, are preferred prey of the giant trevally (also called white ulua or ulua aukea, *Caranx ignobilis*; Sudekum et al., 1991). The giant trevally is the dominant apex predator in the NWHI, and the species is particularly abundant on exposed fringing and barrier reefs (Friedlander and DeMartini, 2002). Among the three northernmost atolls of the NWHI, body sizes at coloration (sex) change of labroids are larger (Fig. 3), and overall size distributions are skewed larger in labroids (Fig. 4) and other prey fishes (Fig. 5) at Midway Atoll (all $p < 0.001$), where giant trevally are fewer compared to Pearl and Hermes Atoll (PHR), where they are more abundant (Fig. 6; $p < 0.001$; DeMartini et al., 2005). Interestingly, prey size distributions are also skewed larger at Kure Atoll ($p < 0.001$), where giant trevally are even fewer than at Midway, likely reflecting over three decades (ending in 1992) of extraction and disturbance of trevally by resident Coast Guard tending Kure's Loran station (DeMartini et al., 2005). The differences in giant trevally abundance we observed among these three northernmost atolls in 2000-02 were similar to those observed between FFS and Midway during the 1990s (DeMartini et al., 2002), including the early 1990s when recreational extraction of trevally at Midway was not prohibited. Giant and bluefin trevally (or omilu, *Caranx melampygus*) were then more frequently encountered by divers (and hence likely more abundant) at FFS versus Midway, and the magnitude of this general difference increased (as ulua sightings decreased) subsequent to 1996 (Fig. 7). In 1996, a recreational catch-and-release fishery was begun at Midway after the Midway Naval Air Station was closed and the Atoll became a USFWS National Wildlife Refuge, and the observed further decrease in ulua sightings at Midway likely represent declines in the adult ulua populations, changes in ulua behavior (conditioned aversion to boats and divers), or both (DeMartini et al., 2002).

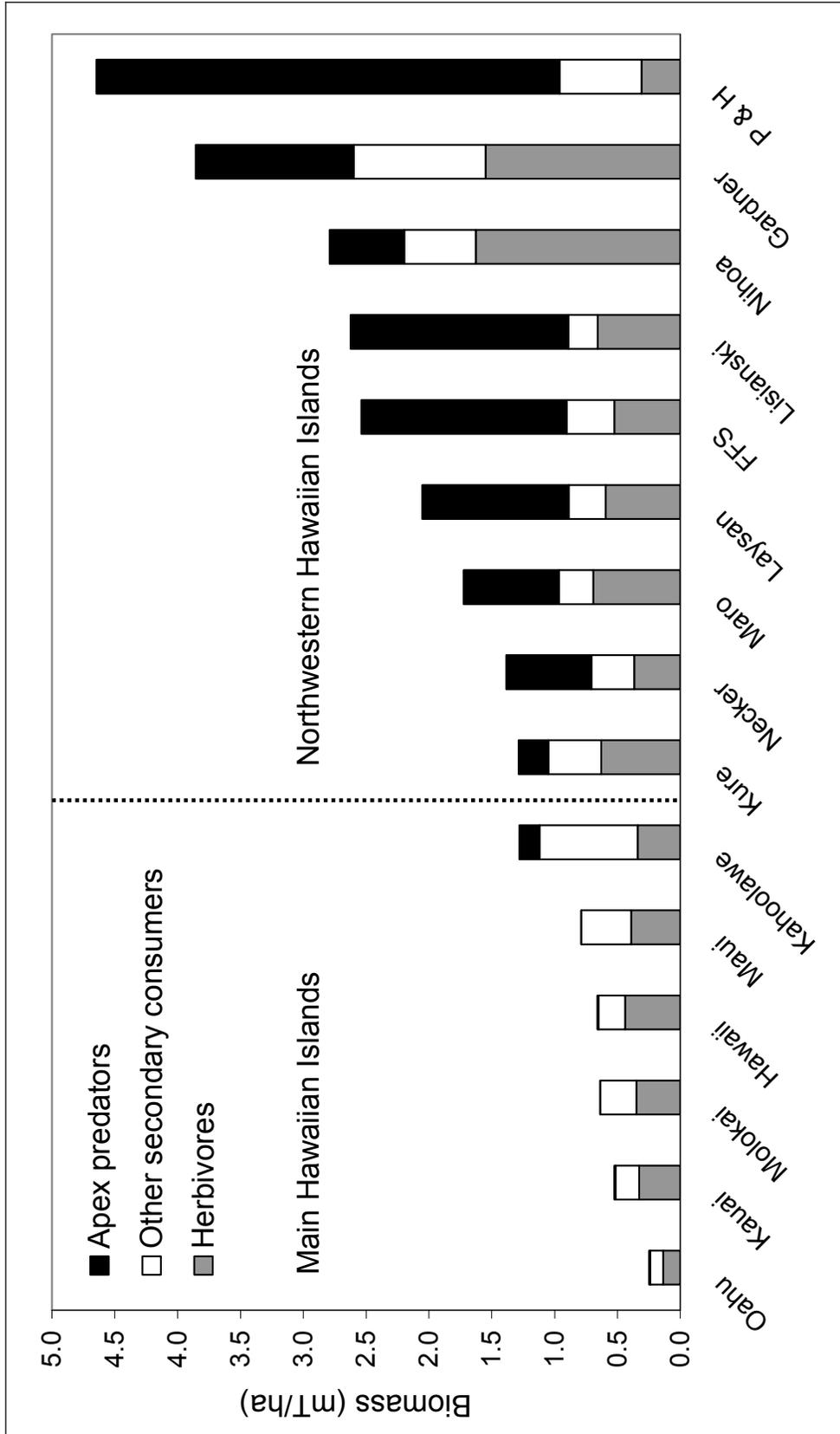


Figure 1. Histograms of ranked (from left to right, lowest to highest) total grand mean biomass density and grand mean reef fish biomass density by trophic level for all reefs in the MHI and the NWHI, based on belt transects made during initial surveys in the year 2000. Data collected at stations in similarly wave-exposed habitats (e.g., forereefs at atolls) only were compared. Protected areas were weighted by area of coverage. FFS = French Frigate Shoals; P&H = Pearl & Hermes. Source: Adapted from Figure 3 of Friedlander and DeMartini (2002).

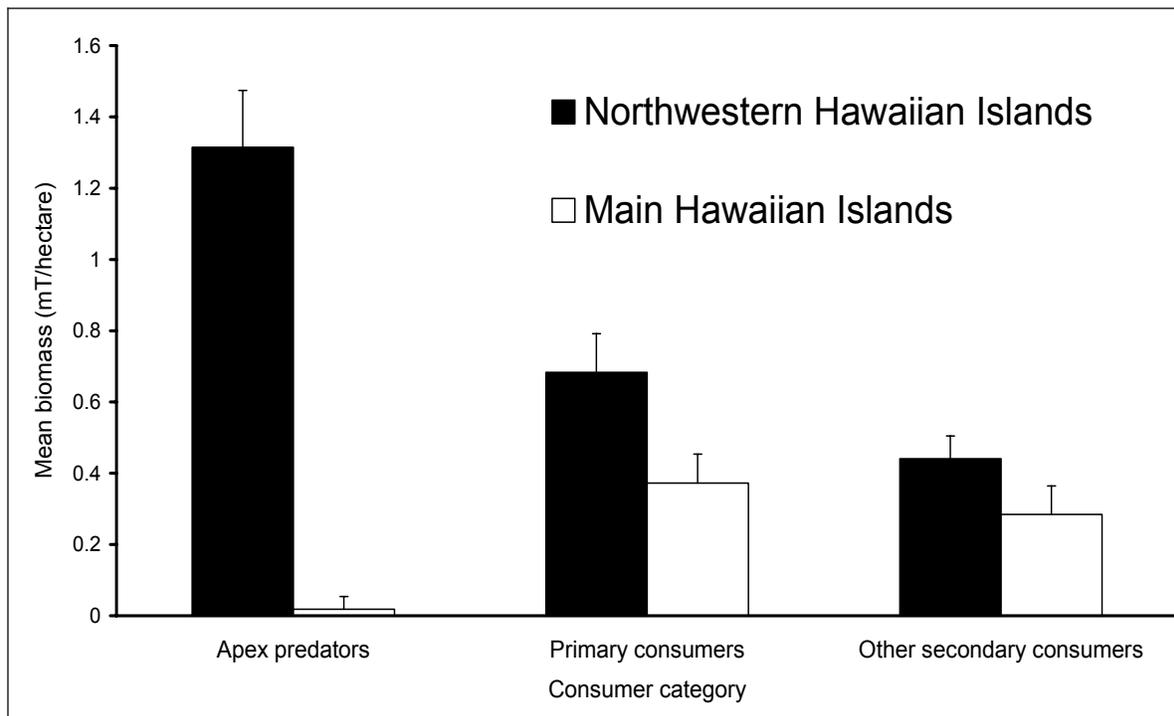


Figure 2. Trophic comparisons of fish assemblages in the NWHI and MHI. Source: Figure 17.5 of Sladek-Nowlis and Friedlander (2005); based on data in Table 1 of Friedlander and DeMartini (2002).

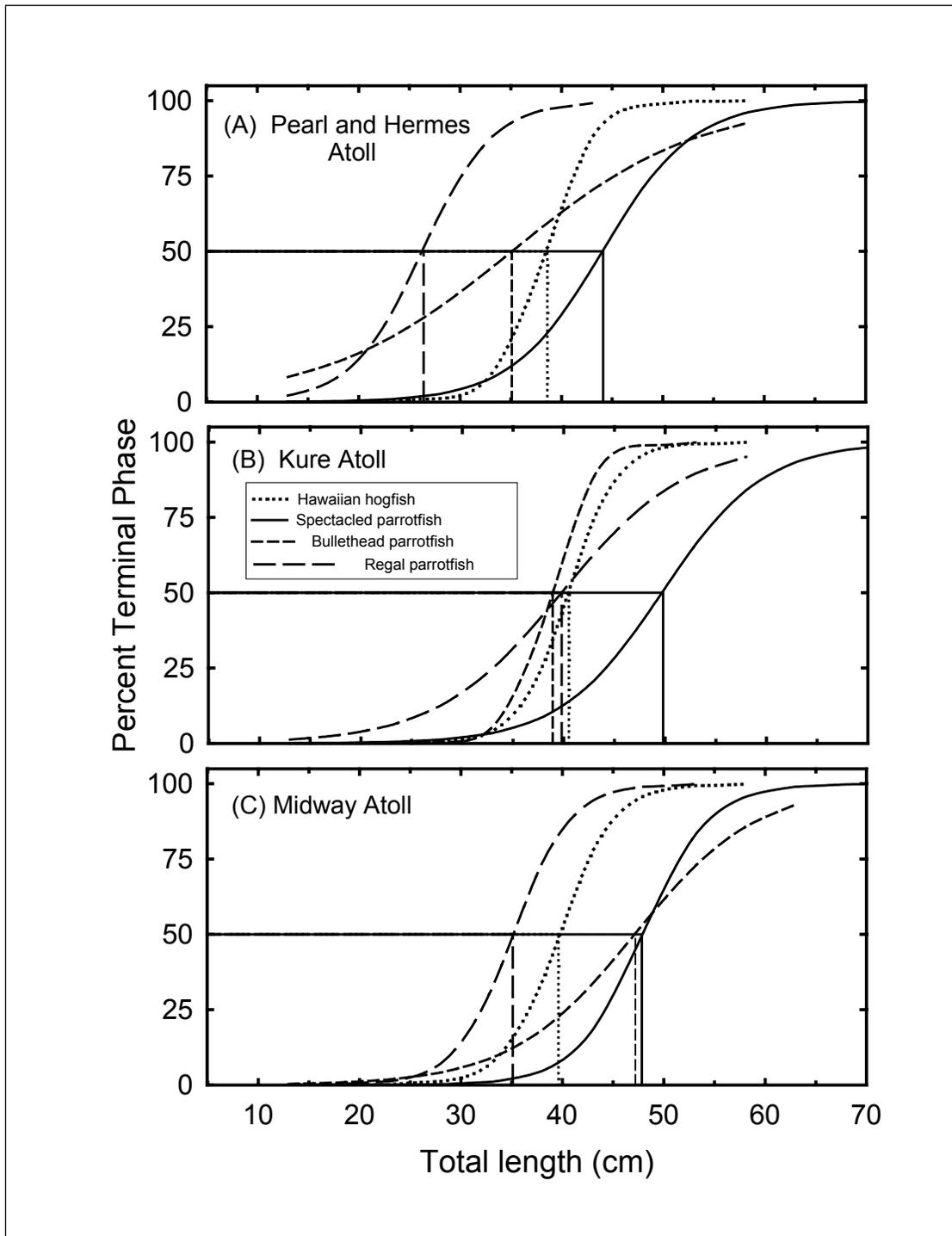


Figure 3. Logistic spline curves (predicted fits) of the percentage Terminal Phase (of all individuals observed—both Initial female and Terminal male phases) by 5-cm Total Length (TL) class, for each of four major species of labroids (one labrid plus three scarids), at (A) Pearl and Hermes, (B) Kure, and (C) Midway Atolls in the NWHI during September–October of 2000 and 2002. Vertical lines indicate estimated body length at which 50% of individuals are Terminal Phase. Source: Figure 1 of DeMartini et al. (2005).

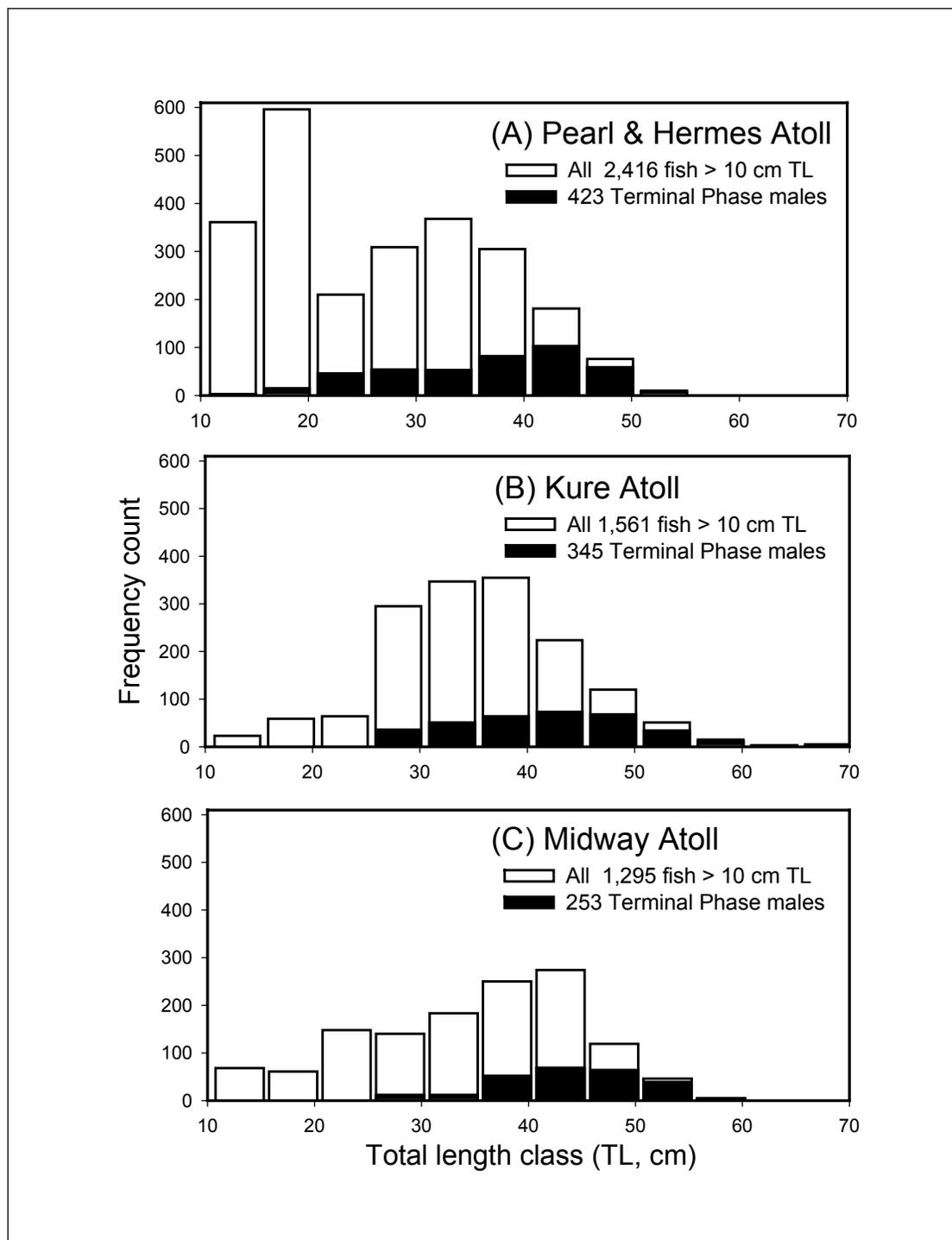


Figure 4. Body size (Total length, TL) frequency distributions of the aggregate of eight species of select (large-bodied, conspicuously dichromatic) labroids ≥ 10 cm TL, comprising four labrids and four scarids, observed by divers on Belt Transects and Stationary Point Count surveys at (A) Pearl and Hermes, (B) Kure, and (C) Midway Atolls in the NWHI during September–October of 2000 and 2002. Tallies are partitioned by Initial and Terminal phase individuals. Source: Figure 2 of DeMartini et al. (2005).

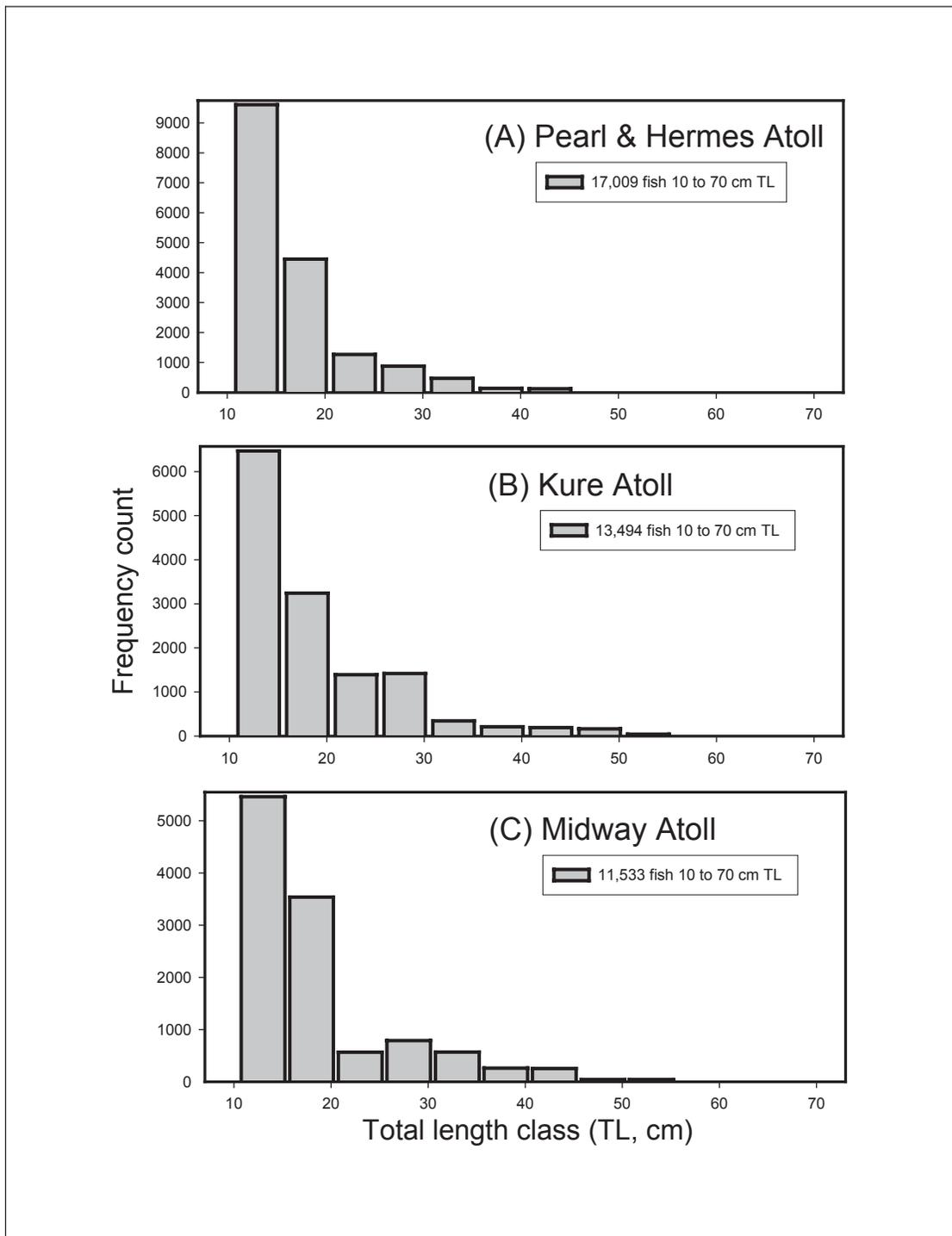


Figure 5. Body size (total length, TL) frequency distributions of the aggregate of all other taxa of prey reef fishes ≥ 10 cm TL observed by divers on belt transects at (A) Pearl and Hermes, (B) Kure, and (C) Midway Atolls in the NWHI during September–October of 2000 and 2002. Note different scales of y-axes in the various panels. Source: Figure 3 of DeMartini et al. (2005).

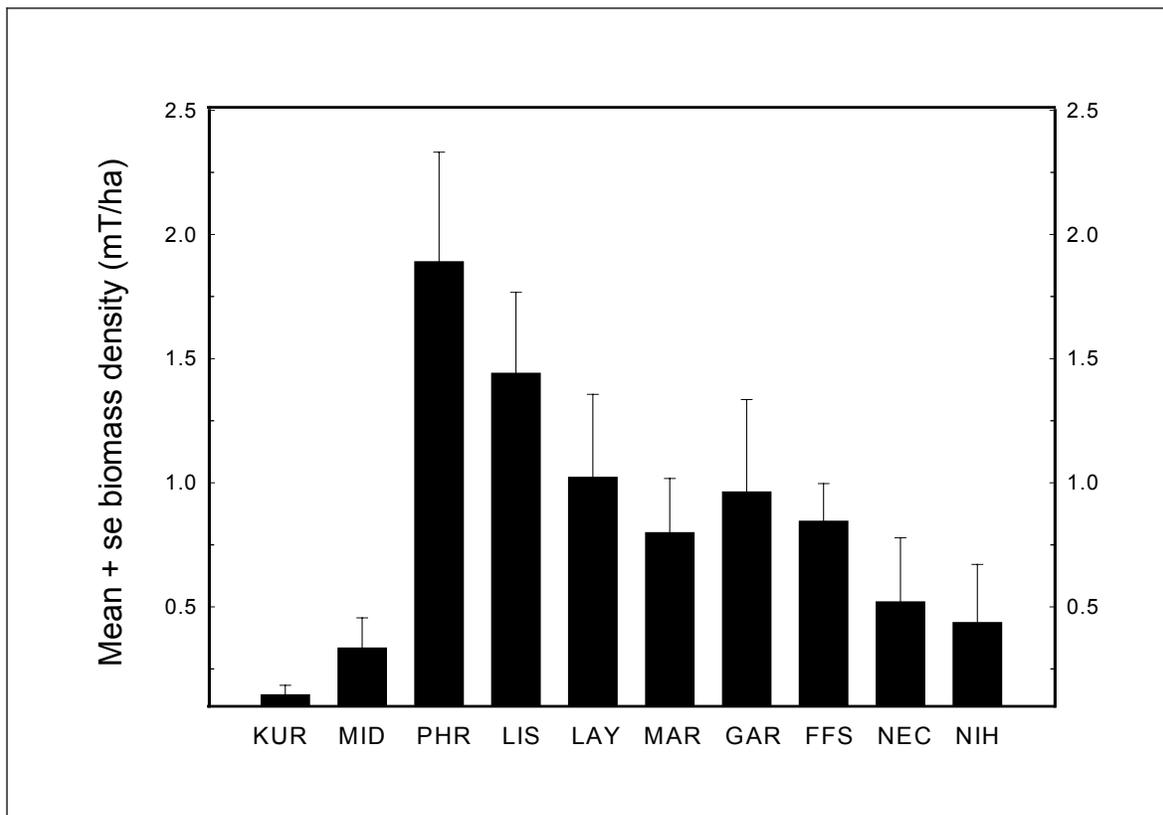


Figure 6. Geographic pattern of apex predator biomass density (averaging 70% giant trevally) at the 10 emergent NWHI reefs surveyed during September–October of 2000 and 2002. Estimates for these comprehensive surveys, based on standard belt transects (described by DeMartini and Friedlander, 2004) were sufficiently precise to justify presentation of standard error (se) bars. Source: Figure 8 of DeMartini and Friedlander (2004).

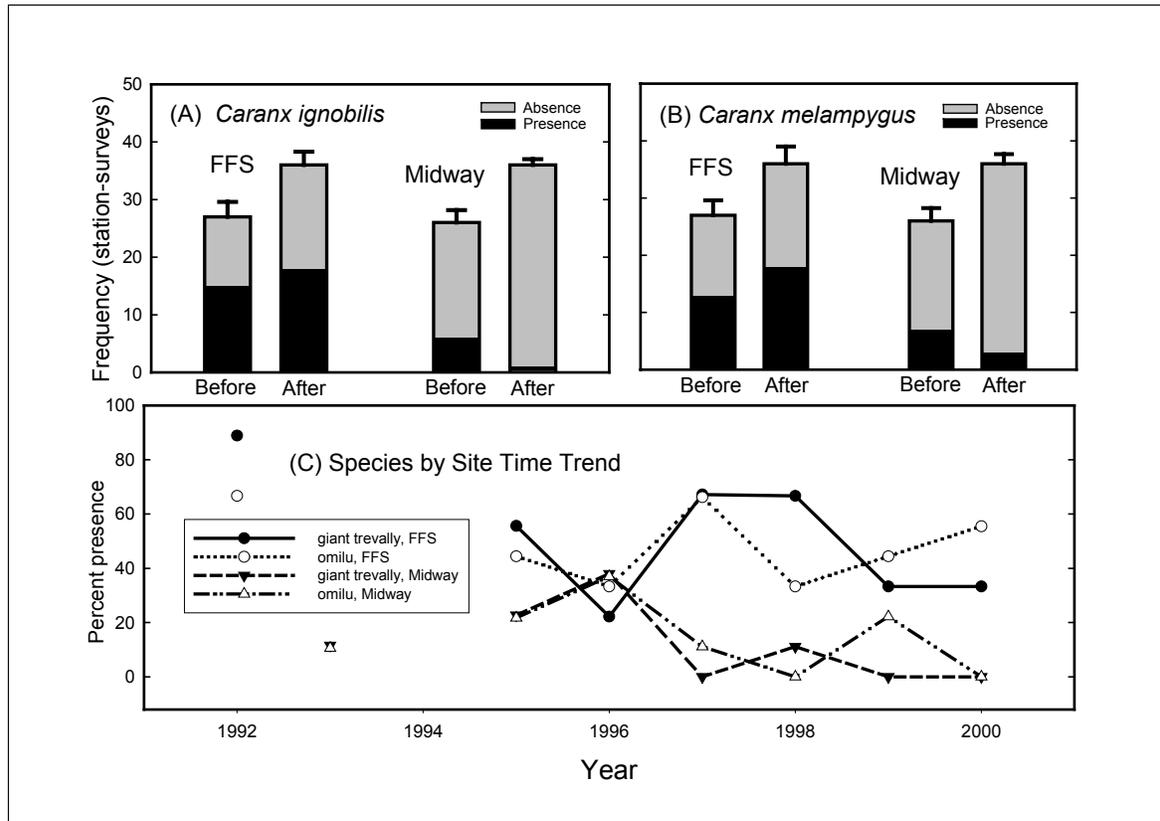


Figure 7. Relative presence-absence of (A) giant trevally (*Caranx ignobilis*) and (B) bluefin trevally (*C. melampygyus*) at FFS and Midway stations during 1992 (FFS) or 1993 (Midway) through 1995-2000 pooled. The stacked presence-absence bars indicate species subtotals up to and including 1996 (“Before”) versus after 1996 (“After”) at each site. Panel C plots percent presence at stations on each survey. Vertical lines atop histograms are 1 se. Source: Figure 6 of DeMartini et al. (2002).

Most likely, the difference between FFS and Midway in the abundance of jacks is primarily the result of persistent fishing-associated mortality and disturbance at the latter and minimal extraction at the former (DeMartini et al., 2005).

Our observations of predator effects on prey size composition and life history have several significant implications for an ecosystem-based approach to fishery management in the Hawaiian Archipelago. First, *in situ* observations instead of destructive sacrifice (necessary for gonadal examination) might prove useful for estimating size at sex change in labroids, one important parameter in stock assessment for this major group of reef fishes. Second, size spectra and related metrics (Graham et al., 2005; DeMartini et al., 2005) may be used to assess functional change on NWHI reefs. In particular, indices of exploitation based on prey size frequency distributions have the potential to be developed as an effective proxy for predation intensity (predator abundance).

Several other major patterns (shelter use and the planktonic dispersal of organisms

among reefs), indirectly related to predation, are also clearly evident in the NWHI fish assemblage data. Refuging behavior and the use of habitat for shelter are major anti-predator adaptations of reef fishes (Hixon and Beets, 1993; Friedlander and Parrish, 1998). DeMartini (2004) documented the habitat-specific spatial distributions of juvenile and other small-bodied fishes particularly susceptible to predation and recognized the importance of backreef, lagoonal patch reef, and other sheltered (wave-protected) habitats as nursery areas for juvenile reef fishes in the NWHI (Fig. 8). This study, based on re-analyses of data collected at FFS and Midway Atoll during the 1990s, has contributed substantially to development of both “essential fish habitat” (EFH) and “habitat areas of particular concern” (HAPC) concepts in recognizing the greater per-unit-area value of atolls due to their larger proportion of sheltered juvenile nursery habitats (DeMartini, 2004).

The planktonic dispersal of reef fishes is an important process linked to the persistence of benthic reef populations besieged by continuing sources of natural mortality that include predation and physical disturbances like habitat-destructive hurricanes and other major storm events. Endemism must be importantly related to the dispersal and connectivity of reef-fish populations in Hawaii and is remarkably high for shallow reef fishes throughout the Archipelago, particularly in the NWHI (DeMartini and Friedlander, 2004). Percentage endemism based on a typical species-presence criterion is about one-fifth higher (30% versus 25%) in the NWHI versus MHI (DeMartini and Friedlander, 2004). The latter MHI value, also based on *in situ* diver observations, is indistinguishable from the best present estimate of 23% for Hawaiian fishes based on comprehensive specimen sources including market sampling, poison stations, and other sources for museum collections (Randall, 1998). Endemism is even more strongly expressed in terms of standing stock per unit area in the NWHI—both biomass (mean 37%) and especially numerical (mean 52%) densities increase with latitude throughout the islands even though species-presence-based measures of endemism lack latitudinal pattern in the NWHI (Fig. 9; DeMartini and Friedlander, 2004). These recent observations of a latitudinal effect on standing stock-based endemism were foreshadowed by an analogous pattern observed previously at FFS and Midway Atoll (Fig. 10; DeMartini, 2004).

Greater endemism upchain in the NWHI may be related to consistently higher rates of replenishment by young-of-the-year (recruitment of benthic “yoy”) upchain following dispersal as pelagic larvae and/or juveniles (DeMartini and Friedlander, 2004). This was first indicated by survey data collected during the 1990s at FFS and Midway (DeMartini et al., 2002; DeMartini, 2004). During this period, there was consistently higher recruitment of young-of-the-year (yoy) life stages of fishes at Midway Atoll versus FFS despite the generally greater densities of older-stage fishes at FFS (Fig. 11). During 2000-02, recruit fish densities were generally greater upchain to the northwest (versus downchain) and a larger number of endemic (versus non-endemic) species recruited to a greater extent upchain in the NWHI (Table 1; DeMartini and Friedlander, 2004). The observed greater abundance and recruitment of endemics upchain were not importantly complicated by species composition or within-species adult body size differences (DeMartini and Friedlander, 2004).

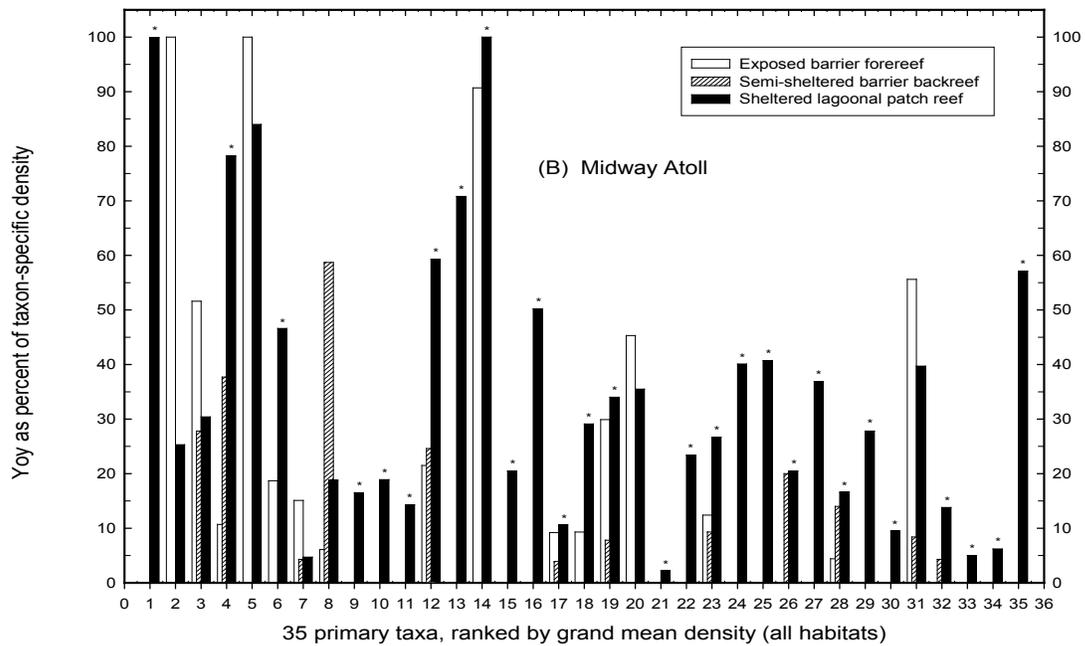
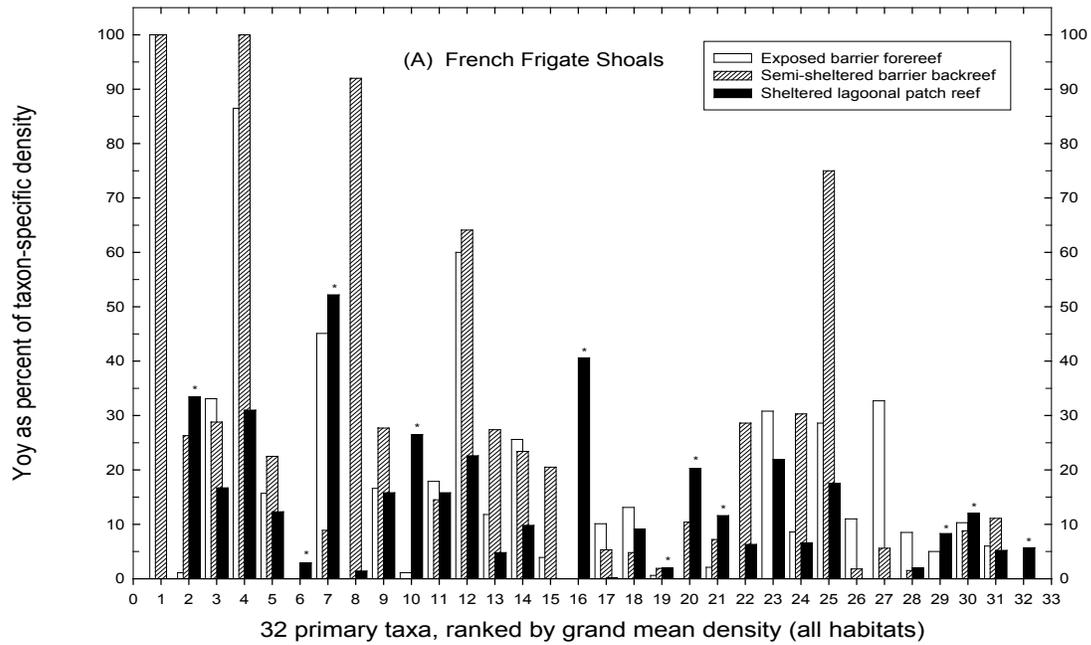


Figure 8. Bar histograms of the percentage contribution of yoy to overall yoy plus older-stage densities for each primary (common and abundant) taxon at (A) FFS and (B) Midway Atoll. Estimates are numbered, ordered, and partitioned by habitat. Taxa with nominally highest yoy percentages at sheltered patch reefs are noted by asterisk; see DeMartini (2004) for names of taxa. Source: Figure 3 of DeMartini (2004).

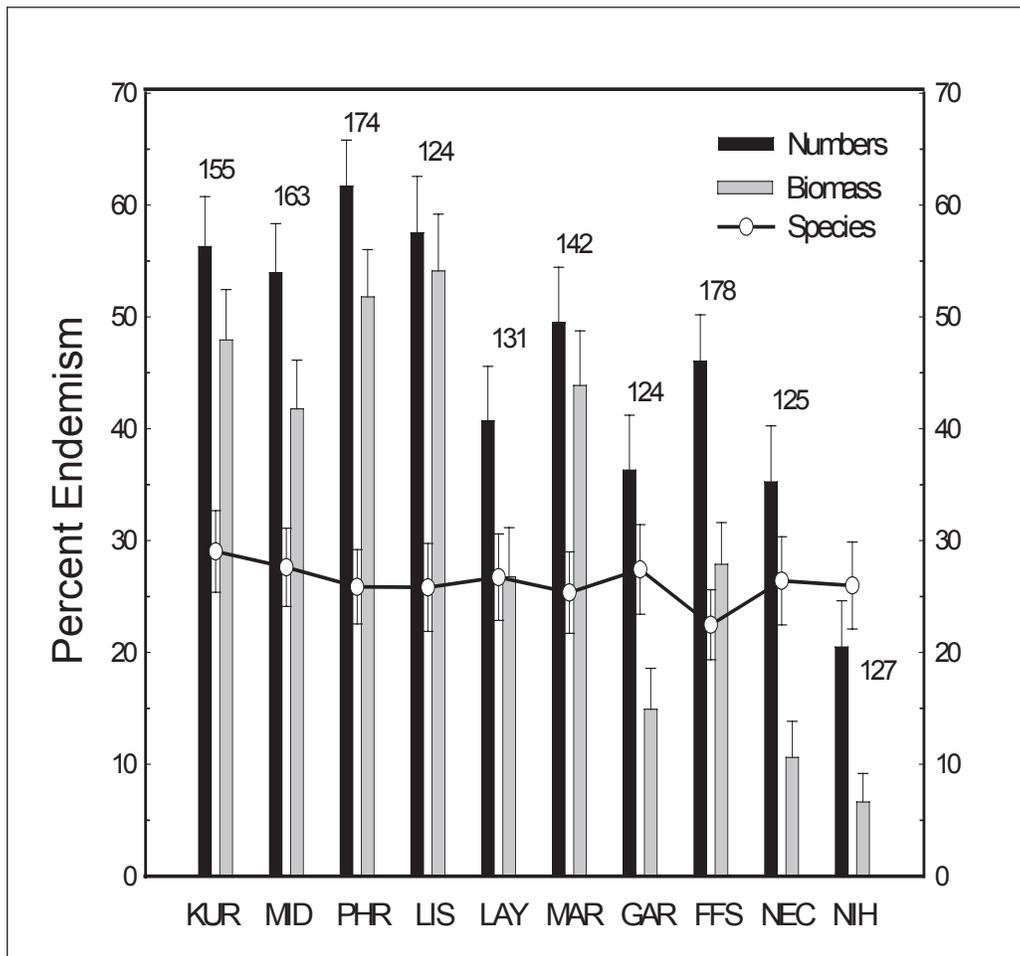


Figure 9. Various measures of percentage endemism (based on species occurrence, and on numerical and biomass densities) at each of ten emergent NWHI reefs, illustrating patterns of endemism with latitude-longitude. Occurrence data are indicated by line graph and density data by histograms. Vertical lines indicate se of estimates. Species richness (number of species) is noted by a number atop each set of histograms. Source: Figure 2 of DeMartini & Friedlander (2004).

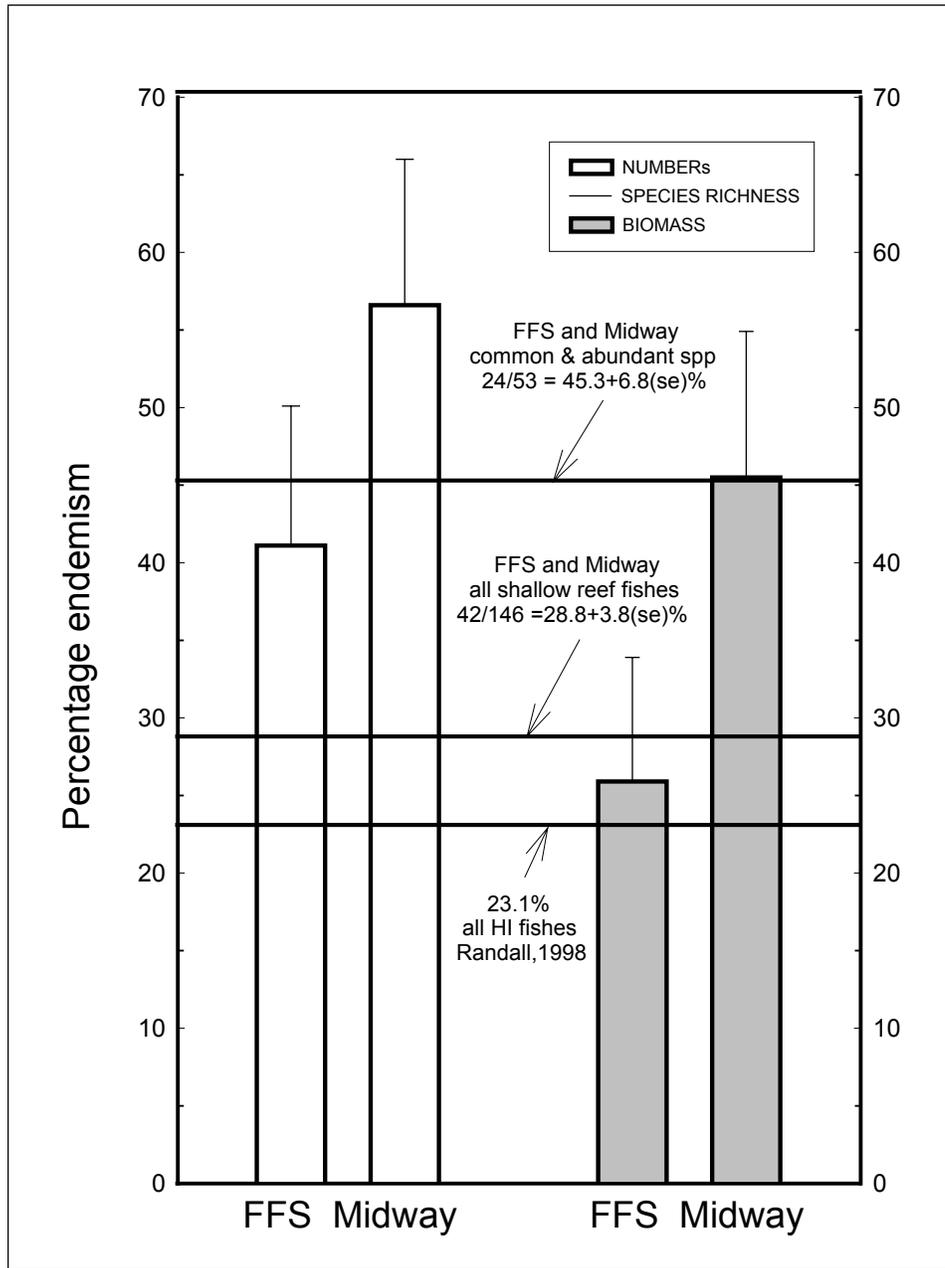


Figure 10. Bar histograms depicting percentage endemism based on numerical and biomass densities estimated on yearly diver surveys at FFS and Midway Atoll during the period from 1992/93-2000, inclusive. Arrows indicate three lines referring to species diversity (richness): for all Hawaiian fishes (Randall 1998), for all shallow reef fishes surveyed by DeMartini et al. (2002), and for only the most common and abundant fishes surveyed by DeMartini et al. (2002). Source: Figure 4 of DeMartini (2004).

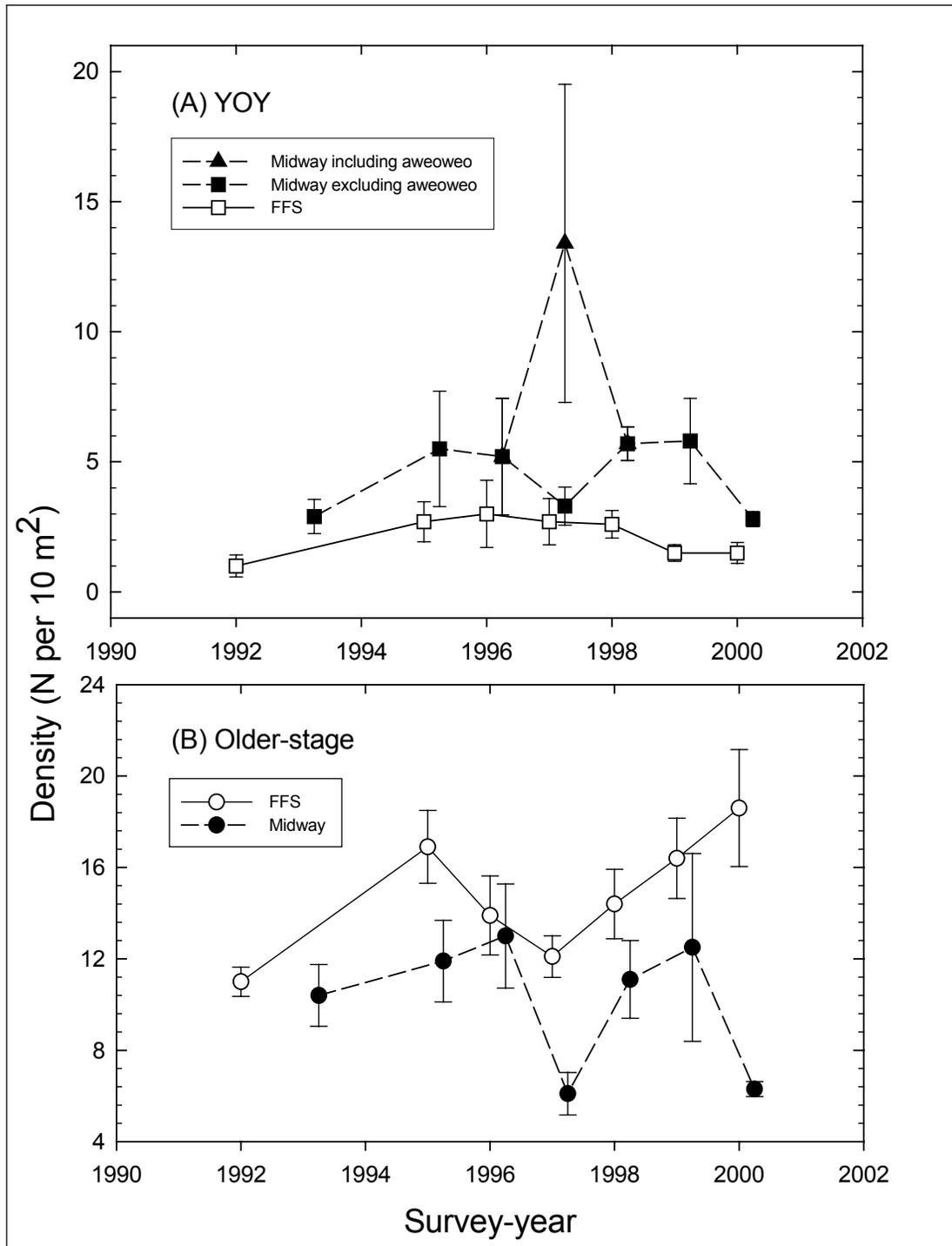


Figure 11. Time series of the estimated mean numerical density of (A) yoy and (B) older-stage fishes of all taxa at FFS and Midway during each survey year. Aweoweo = *Priacanthus meeki*. Each vertical bar represents 1 se of the estimated survey year grand mean for both major habitats. Source: Figure 1 of DeMartini (2004).

Table 1. Data classification and Chi-square test results evaluating signed (positive, negative) correlations and trends in a recruit index (numerical density ratio of yoy to larger-sized, older individuals comprising a species' reef-population) versus latitude for component species of endemic and non-endemic taxa. Source: Table 4 of DeMartini and Friedlander (2004).

Distribution of correlations/trends			Chi-square statistics	
	Pos	Neg	Both	
Endemic	13	2	15	$\chi^2 = 4.08$
Non-Endemic	9	10	19	df = 1
Both	22	12	34	$0.05 > p > 0.02$

THE SIGNIFICANCE OF PREDATION IN THE NWHI ECOSYSTEM

That predation is a major structuring agent in marine ecosystems is not a novel conclusion, and the shallow reef ecosystem of the NWHI is no exception. Our recent observations confirm and extend those made by Hobson (1984) and J.D. Parrish and USFWS co-workers (Norris and Parrish, 1988; Parrish et al., 1985, 1986) on the first NWHI diver surveys during the late 1970s and early to mid-1980s. Characterizing the extent and magnitude of piscivory on shallow NWHI reefs was a major focus of the USFWS studies, and these included a series of field experiments for assessing the effects of lower-level piscivores on patch-reef fish assemblages in the lagoon at Midway Atoll (Schroeder, 1989). An allied study (Schroeder, 1987) evaluated the effects of several shelter resource variables on the recruitment of fishes at these patch reefs.

Predation as a structuring process, of course, is not limited to shallow-reef areas, or just to fish assemblages in the NWHI. Parrish and Boland (2004), for example, recently described the over-arching influence that apex predators have on the distribution and abundance of substrate-associated fishes atop the summits (30-40 m) of deeper banks in the NWHI. Studies of the foraging habitat, feeding behavior, and diet of monk seals (Parrish et al., 2000; Goodman-Lowe, 1998) attest to the historical (if not present—due to depressed population level) importance of monk seals as predators that interact competitively with predatory fishes such as jacks and sharks and, to some extent, that serve as the prey of some larger sharks. Huge seabird populations exist in the NWHI, and the effects of seabird predation on the population dynamics of squid and small fishes, including the near-surface planktonic stages of many reef fishes, may be considerable (Harrison et al., 1983).

CONCLUSIONS AND SUGGESTED FUTURE RESEARCH

Clearly, coral reef fish assemblage structure is routinely controlled by so-called “top-down” predation in the NWHI, even if a “bottom-up” (nutrient input) process is sometimes responsible for regime shifts in overall ecosystem productivity (Polovina et al., 1994). The effects of apex predation, primarily by giant trevally, are pervasive: they structure prey population sizes and age distributions and strongly influence the reproductive and growth dynamics of harvestable fishes (such as parrotfish) as well as smaller-bodied, lower-trophic-level fishes on shallow NWHI reefs. Habitat utilization is related to refuging from predation, and the important nursery function of predator-inaccessible shallows and other wave-protected, finely structured regions at atolls cannot be overemphasized, especially when selecting sites for the establishment of no-take marine protected areas (MPAs). Finally, the inter-related processes of dispersal and recruitment cannot be overlooked because they represent the mechanisms used to counter local extirpation resulting from predation and physical disturbance. All of these processes—dispersal, recruitment, and predation—are linked, importantly if indirectly, to the present structure and function of the strongly endemic fish fauna of the NWHI.

The fish assemblages of oceanic islands such as the NWHI, like the ecosystems in which they are imbedded, are sensitive to human perturbations of the predatory hierarchy (DeMartini et al., 1999). Our appreciation of the pervasive influence of predation on the structure and behavior of reef fish and other assemblages within the NWHI ecosystem is, in a trivial sense, an “artifact” of the near-pristine nature of the NWHI. In the MHI, as in other human-impacted reef ecosystems, we no longer have an intact, naturally functioning system left to observe. We must continue to promote good stewardship of the NWHI ecosystem. In part this will require persistent dedication to responsible research that, to the extent possible, minimizes human disturbance while increasing our understanding of the functional structure of reef ecosystems.

Some logical suggestions for further research involving NWHI reef fishes include: (1) characterizing the strength of coral and other habitat linkages among reef fishes and other key fauna and flora; (2) obtaining extended time series describing the inter-annual variations in population replenishment for fish (as well as corals, algae, and key macroinvertebrates); (3) pursuing studies of genetics and trace element markers present in reef-fish otoliths that together can provide complementary insights into the evolutionary and present-day structure of their stocks; (4) conducting controlled field experiments (if such can be accomplished while maintaining responsible stewardship) that further quantify the influence of apex predators, especially giant trevally, on prey assemblage structure and function; and (5) comparative evaluations of the spatial and temporal dynamics of primary productivity and nutrient and detrital flux on NWHI and MHI reefs.

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