SHARKS AND JACKS IN THE NORTHWESTERN HAWAIIAN ISLANDS FROM TOWED-DIVER SURVEYS 2000 - 2003

BY

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ABSTRACT

Sharks (Carcharhinidae) and jacks (Carangidae) were surveyed using towed divers at the atolls and banks of the Northwestern Hawaiian Islands (NWHI) during annual surveys from 2000 to 2003. We compared numerical and biomass densities of these predators among reefs, among habitats within atolls (forereef, backreef, channel, and lagoon) and banks (insular and exposed), and mapped the spatial distribution of predators at the reefs where they were most abundant. Shark and jack densities were both very high at two of the three pinnacles in the chain, Necker and Gardner Pinnacle. Otherwise, shark densities were highest at Maro Reef and Midway Atoll, and jack densities were highest at Pearl and Hermes Atoll and Lisianksi-Neva Shoals. Galapagos sharks (*Carcharhinus galapagensis*) and gray reef sharks (*C. amblyrhynchos*) were observed most frequently in forereef habitats within atolls, and on exposed reefs within banks. Whitetip reef sharks (*Triaenodon obesus*) showed no significant habitat preferences on either atolls or banks. Giant trevally (*Caranx ignobilis*), bluefin trevally (*C. melampygus*), and amberjack (*Seriola dumerili*) were most frequently observed in forereef habitats within atolls, although the difference was significant only for amberjack. Jack densities were similar on exposed and insular reefs within banks. Maps of the spatial distribution of Galapagos sharks at Maro Reef and Midway Atoll and giant and bluefin trevally at Pearl and Hermes and Lisianski Island-Neva Shoals showed localized hotspots (areas of high density) within these habitats. We conclude that towed-diver surveys provide an effective method to assess shark and jack populations at the remote, expansive atolls and banks of the NWHI. Continued tow surveys will enable us to monitor the status of these important apex predators in an ecosystem relatively undisturbed by humans.

INTRODUCTION

In the remote Northwestern Hawaiian Islands (NWHI), human impacts on the shallow coral reef ecosystems have been relatively minimal, and large mobile predators are abundant (Sudekum et al., 1991; Friedlander and DeMartini, 2002). Worldwide,

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many coral reefs currently have far fewer apex predators than were historically present (Jackson, 1997; Jennings and Kaiser, 1998; Pauly et al., 1998; Jackson et al., 2001). Reefs of the Main Hawaiian Islands (MHI) are a case in point (Shomura, 1987). Recent surveys found very few jacks or sharks in the MHI (Friedlander and DeMartini, 2002; Friedlander et al., 2003), in contrast to the impressive densities of predators encountered in the older, more remote, northwestern part of the Hawaiian Archipelago (Friedlander and DeMartini, 2002).

The objective of our study was to complete a comprehensive initial assessment of shark and jack populations at the 10 major reefs of the NWHI. We recorded numerical and biomass densities, as well as spatial distribution, using towed-diver surveys. Relative densities of apex predators were compared across several spatial scales to address the following questions:

1. Do median counts differ among reefs based on all relevant data for jacks and sharks?
2. Are shark and jack species equally represented in all of the habitats available at a reef?

Coral-reef ecosystems in remote areas such as the NWHI are in a more natural state than reefs subjected to significant fishing pressure, habitat degradation, pollution, runoff, and other anthropogenic stressors in the MHI. The NWHI reefs have the potential to provide insight into how a healthy ecosystem operates, especially concerning the role of predators on coral reefs. Mobile predators have a strong effect on the abundance, diversity, and behavior of other coral-reef residents (Parrish et al., 1985; Sudekum et al., 1991; Norris and Parrish, 1998; Stevens et al., 2000; Dulvy et al., 2004). Sharks and jacks prey on bony and cartilaginous fishes, cephalopods, crustaceans, and gastropods (Wass, 1971; Okamoto and Kawamoto, 1980; Randall, 1980; Sudekum et al., 1991; Weatherbee et al., 1997; Meyer et al, 2001). We initiated a comprehensive, quantitative documentation of predator abundance and distribution to provide necessary baseline data. These data will help decipher patterns of apex predator abundance and distribution, and could provide insight into the predation process structuring lower trophic levels (Friedlander and DeMartini, 2002; DeMartini and Friedlander, 2004; DeMartini et al., 2005).

MATERIALS AND METHODS

Survey Sites

A total of 331 towed-diver fish surveys were completed during annual NWHI cruises from 2000 to 2003 organized by the Coral Reef Ecosystem Division (CRED) of the Pacific Islands Fisheries Science Center (PIFSC), National Oceanic and Atmospheric Administration (NOAA), Honolulu, Hawaii. The towed-diver surveys covered 865 linear kilometers of reef habitat at 10 different locations (Fig. 1), generally during late summer or early fall. Surveys were conducted at four atolls (French Frigate Shoals, Pearl and Hermes Atoll, Midway Atoll, and Kure Atoll), three banks (Maro Reef, Laysan

Island, and Lisianski Island-Neva Shoals), and three pinnacles (Necker, Nihoa, and Gardner Pinnacles). Atolls and banks were designated according to geomorphological reef structure (NOAA, 2003). Atolls were characterized by a distinctive barrier reef and lagoon. Banks were characterized by a shelf of submerged reef without any of the classic barrier-reef-and-lagoon structure of an atoll. Pinnacles were considered separately from banks based on their unique geomorphological characteristic of basaltic rock elevated above sea level and to accommodate survey logistical limitations. We were constrained by diver physiology and survey protocol to the small area of relatively shallow reef (<30 m) directly surrounding the elevated basalt pinnacles.

Atolls and banks do not have the same habitats and were treated separately for the smaller-scale comparisons. To compare habitats within atolls, the following reef zone classifications were used: forereef, backreef, lagoon, and channel. Towed-diver surveys completed along the outward-facing part of the barrier reef, next to open ocean, were designated as forereef. Towed-diver surveys conducted along the inward-facing section of the barrier reef were designated as backreef. Tows along reefs and sand areas in the center of the atoll were considered lagoon surveys. Channel tows were those that primarily cut across openings or interruptions in the barrier reef. To compare habitats within banks, we designated reefs as exposed or insular. Tows along the outermost edge of the bank were called exposed and those on the interior (i.e., not directly adjacent to open ocean) as insular.

These remote reefs were accessed by the NOAA ships *Townsend Cromwell* and *Oscar Elton Sette*. The towed-diver surveys were part of CRED's comprehensive, multidisciplinary Pacific Reef Assessment and Monitoring Program (Pacific RAMP). Concurrent data were collected on corals, algae, reef fishes, invertebrates, oceanographic conditions, and benthic habitat.

Towed-Diver Fish Surveys

Surveys for large mobile predators were conducted using towed divers in order to search large areas of reef in a limited period. We used a modified version of the manta board (Done et al., 1981; Kenchington, 1984), modeled after prototypes used in the NWHI to classify spiny lobster habitat (Parrish and Polovina, 1994). Towboards were mounted with an underwater digital video camera, Seabird Electronics temperature depth recorders (a SBE39 set to record at 5-sec intervals), timing devices, and observer data sheets. In addition, the fish towboard carried a magnetic-switch telegraph for communication with personnel on the surface.

Towed-diver surveys covered an average of ~2.5 km linear distance per tow. Two divers were towed behind a skiff on a 60-m line at a speed of approximately 1.5 knots. One diver served as a fish observer and recorded all fish ≥ 50-cm total length (TL) (Zgliczynski et al., 2004). The second diver recorded benthic habitat characteristics and conspicuous, ecologically important macro-invertebrates (Hill and Wilkinson, 2004). Divers attempted to maneuver the towboards ~1 m off the bottom, avoiding obstacles and abrupt ascents as necessary. Surface support personnel located in the towing vessel used a handheld GPS unit to record waypoints at the beginning and end of each survey as well as a track throughout the tow (5-sec interval).

The towed-diver fish survey protocol was designed specifically for quantifying large mobile predators. The fish observer recorded all fishes ≥ 50-cm TL that occurred within a 10-m swath in front of the diver (5-m to either side of the diver and 10-m forward). Fishes were identified to species level, and the number present was recorded in size bins of 50 to 75-cm TL, 75 to 100-cm TL, 100 to 150-cm TL, 150 to 200-cm TL, 200 to 250-cm TL, and >250-cm TL. The standard survey was composed of ten 5-min segments. During each 5-min segment, fishes within the 10-m swath were recorded for 4 min, followed by a 1-min count of all fishes ≥ 50-cm TL observed within the limits of visibility in a 360˚ arc. Data analyzed for this paper included only the quantitative 4-min transect data. The 1-min counts were not amenable to density estimates as the survey area was not as easily quantified. These data will be analyzed later for information on maximum numbers of predators encountered per tow survey.

Analyses

Data on individual fish sightings were used to calculate numerical and biomass densities, which were the basis of all statistical comparisons. Numerical density was calculated by dividing the number of fish by the transect area (tow length x 10-m width). Biomass was calculated using length-weight conversion formulas with species-specific values derived from studies in the tropical Pacific (Kulbicki et al, 1993; Letourneur et al., 1998; Hawaii Cooperative Fishery Unit, unpublished data; www.fishbase.org). Tow length was accurately computed in ArcView using the track recorded during the tow with a layback model applied (R. Hoeke, unpublished data).

Nonparametric statistics were used to test for differences in numerical and biomass densities among groups because all datasets failed tests for normality. We used Kruskal-Wallis (K-W) one-way analysis of variance (ANOVA) on ranks to compare large-scale differences among reefs, mesoscale differences among habitats within atolls (forereef vs. backreef vs. lagoon vs. channel) and within banks (exposed vs. insular reefs). When K-W ANOVA showed a significant difference, we used a K-W multiple comparison z-value test to detect which groups were different from each other. The effects of reef and habitat were tested separately with two one-way ANOVAs on rank. We did not use a Friedman's 2-way ANOVA because the dataset was doubly unbalanced, with habitats not represented at all reefs and unequal numbers of tow surveys in each habitat. To account for multiple testing of the dataset, an adjusted significance level of $\alpha=0.025$ was applied for statistical tests of higher-order taxa (i.e., at the family level), and $\alpha=0.016$ for tests at the species level.

For comparisons among reefs, only exposed habitats were included to make the comparison equitable among atolls, banks, and pinnacles. For comparisons among habitats, only those habitats specific to atolls or banks were used, depending on the group of reefs being tested. Reefs were pooled for the habitat analysis by geomorphology (atoll or bank) with the condition that densities not differ significantly among pooled reefs in the *post-hoc* multiple comparison test (K-W z-test) performed after the inter-reef K-W ANOVA.

Maps of the spatial distribution of biomass were created in ArcView 3.3. The biomass calculations for each species were geo-referenced using the aforementioned layback model. Biomass values were linked to the geographic midpoint of each 5-min tow segment. These values were displayed on the IKONOS image of the atoll or bank using a size-graduated scale of symbols to visually represent comparative biomass of shark and jack species across the areas surveyed.

RESULTS

Fish Assemblage

Five species of sharks were observed during towed-diver surveys in the NWHI (Table 1). Sharks were exclusively from the Family Carcharhinidae and included midwater reef-associated sharks such as Galapagos (*Carcharhinus galapagensis*), gray reef (*C. amblyrhynchos*), and tiger sharks (*Galeocerdo cuvier*), as well as a benthic species, the whitetip reef shark (*Triaenodon obesus*). In addition, blackfin reef sharks (*C. limbatus*) were recorded during non-quantitative surveys in low-visibility lagoon areas at Pearl and Hermes. The three most common sharks (Galapagos, gray reef, and whitetip reef sharks) accounted for 90% of the quantitative shark observations.

Nine species of jacks (Family Carangidae) larger than 50-cm TL were observed during towed-diver surveys (Table 1). The most common jacks were giant trevally (*Caranx ignobilis*), bluefin trevally (*C. melampygus*), and greater amberjack (*Seriola dumerili*). These three jack species accounted for 91% of the quantitative jack observations.

Comparisons Among Reefs

The mean density of sharks (all species combined) differed significantly among reefs in both numbers and biomass (Table 2). Shark densities ranged from 0 to 1.8 sharks per ha (57 kg/ha). Necker had significantly higher densities and Laysan had significantly lower densities of sharks than most other reefs (Table 3). Gardner, Midway, and Maro Reef also had relatively high shark densities compared to the other reefs (Fig. 2).

The mean density of jacks (all species combined) also differed significantly among reefs in both numbers and biomass (Table 2). Jack densities ranged from 0 to 4.4 jacks per ha (95 kg/ha). Pearl and Hermes Atoll and Lisianski-Neva Shoals had significantly higher densities of jacks than most other reefs (Table 3). Gardner, Necker, and Kure also had high jack densities, while Midway Atoll and Maro Reef had comparatively low densities (Fig. 3).

Comparisons Among Habitats

Within Atolls. The four atolls (French Frigate Shoals, Pearl and Hermes, Midway, and Kure Atoll) were pooled for habitat analysis for both sharks and jacks because densities did not differ significantly among atolls during *post-hoc* multiple comparison tests (Table 3).

Only one of the three major shark species showed a significant difference in densities among atoll habitats (Table 2). Galapagos sharks were the most abundant shark at NWHI atolls and were recorded in all four reef zones (forereef, backreef, channel, lagoon). Densities of Galapagos sharks were significantly higher in channel and forereef habitats (Table 4), with a peak mean of 0.35 sharks per ha (16.14 kg per ha) in the channels. Gray reef sharks were also recorded at all four atoll habitats, though they were rarely encountered in the channels. Gray reef sharks were most abundant in forereef habitats (Fig. 4), where the mean density was 0.10 gray reefs per ha (7.09 kg per ha). Whitetip reef sharks were recorded at all four atoll habitats without any significant difference among habitats, with an average density of 0.11 sharks per ha (2.36 kg per ha). Whitetip reef sharks were not recorded by towed divers at the two northernmost atolls, Midway and Kure, but were relatively common at all of the other banks, atolls, and pinnacles.

The three major jack species appeared to be distributed unevenly among atoll habitats (Fig. 4), but only amberjack demonstrated a statistically significant difference (Table 2), undoubtedly because variance was high and the power of tests low for the other two species. The mean density of giant trevally was 2.23 fish per ha (37.42 kg per ha) on forereefs, compared to 0.21 fish per ha (6.32 kg per ha) in channels. Bluefin trevally were observed more frequently on forereef habitats with a mean of 0.83 fish per ha (2.90 kg per ha), although they were scarce in backreef and lagoon habitats. Amberjack were significantly more abundant on the forereef than on the backreef or lagoon reefs (Table 4; Fig. 4), with an overall mean of 0.18 fish per ha (2.28 kg per ha).

Within Banks. The three NWHI banks (Maro Reef, Lisianski Island-Neva Shoals, and Laysan) were pooled for within-bank habitat comparisons for shark species because densities (for the family) did not differ significantly among banks ($p>0.025$). For jack species, Lisianski Island-Neva Shoals and Laysan were pooled but Maro Reef was excluded because its jack densities differed significantly from other banks ($p<0.025$, Table 3).

The density of one of the three shark species was significantly higher on outside-facing, exposed bank reefs than on more insular, protected reefs (Table 2; Fig. 5). Galapagos were the most abundant shark at NWHI banks. Galapagos sharks were recorded exclusively in exposed reef habitats, with a mean density of 0.49 sharks per ha (24.26 kg per ha). Gray reef sharks were also recorded in greater numbers on exposed reef habitats although the difference was not significant, with an overall mean of 0.08 gray reefs per ha (2.49 kg per ha). Whitetip reef sharks were spread more evenly across bank reef habitats and did not differ significantly in density between exposed and insular reefs, with an overall mean of 0.10 whitetips per ha (1.90 kg per ha).

The three major species of jacks showed no significant difference in densities between exposed and insular bank habitats (Table 2; Fig. 5). Overall, giant trevally were the most abundant jack by number and biomass, with a mean density of 0.93 fish per ha (26.14 kg per ha). Bluefin trevally were the second most common jack on bank reef habitats with a mean of 0.27 fish per ha (2.06 kg per ha). Amberjack were relatively scarce on NWHI banks, recorded at mean density levels of 0.02 fish per ha (0.10 kg per ha).

Maps of Spatial Distribution

Shark Species. The three major shark species were mapped at the atoll and bank where sharks were most abundant (Midway Atoll and Maro Reef). At Midway Atoll, Galapagos shark biomass was concentrated along the south and southeast forereef, as well as the western channels (Fig. 6). Gray reef shark biomass was scattered more evenly along the east and southeast forereef, with a single observation on the south backreef. No whitetip reef sharks were observed at Midway during towed-diver surveys. At Maro Reef, Galapagos shark biomass was high at all four corners of the bank, especially the northeast and southeast outer reefs (Fig. 6). Gray reef shark biomass was sparser, with a few sharks in the southeast, and one sighting along the lower northwest corner. Whitetip reef sharks were generally observed singly, and their biomass was distributed relatively evenly across Maro Reef.

Jack Species. The three major jacks were likewise mapped by species at the atoll and bank where jacks were most abundant (Pearl and Hermes Atoll and Lisianski Island-Neva Shoals). At Pearl and Hermes Atoll, giant trevally biomass was extremely high and was scattered throughout forereef and backreef habitats all around the atoll (Fig. 7). Giant trevally biomass was especially high in the northeast corner on the outside of the barrier, as well as along the east forereef, and the south central forereef. Bluefin trevally biomass was distributed differently, with the majority of biomass concentrated in the southeast corner, where the barrier reef is breached by numerous channels. Amberjack biomass was more evenly distributed with individuals recorded along the south, southwest, and northwest reefs outside the barrier. At Lisianski Island-Neva Shoals, jack biomass was scattered throughout the bank's outer reefs. The highest concentrations of giant trevally were in the northwest adjacent to the island, and of bluefin trevally in the southeast corner of Neva Shoals (Fig. 7). No amberjacks were observed during towed-diver fish surveys at Lisianski.

DISCUSSION

Based on 2000-03 towed-diver surveys, apex predator densities were highest at Gardner Pinnacles and Necker. These two pinnacles show the intense concentrations of biomass that can occur around an abrupt topographical feature such as a seamount or pinnacle (Boehlert and Genin, 1987). Our towed-diver surveys documented the high biomass of predators occupying the area immediately surrounding the pinnacle, but we did not survey the bank surrounding the pinnacles due to diving depth constraints. This bias should be taken into account when comparing predator densities at these pinnacles to those obtained for the other reefs, where we surveyed a variety of habitats.

Three of the four atolls surveyed had similar patterns of shark and jack distribution. Kure, French Frigate Shoals, and Pearl and Hermes Atoll all had moderate to high levels of jacks, and moderate levels of sharks, with jack biomass outweighing shark biomass. This is consistent with results of previous studies using standard belt transect methods, based on which jacks were the dominant apex predator by biomass at NWHI atolls (Friedlander and DeMartini, 2002). Pearl and Hermes Atoll was the most extreme case with the greatest numerical and biomass densities of jacks in the NWHI. The latter is consistent with previous estimates (Friedlander and DeMartini, 2002; DeMartini et al., 2005), although the mean densities of apex predators estimated using towed-diver surveys in the present paper are lower than those estimated previously using belt transects and stationary point counts (Friedlander and DeMartini, 2002; Parrish and Boland, 2004; DeMartini et al., 2005). In part this reflects the differing data parameters (i.e., which size classes and families were included) and time periods used for the characterizations, but it also reflects the different biases inherent in the various methods. Densities estimated using towed-diver surveys are not directly comparable to results from survey methods such as belt transects (Brock, 1954; Brock, 1982) or stationary point counts (Bohnsack and Bannerot, 1986). Temporal and spatial comparisons using a given survey method are still valid, however, and it may be informative to compare the direction and magnitude of future trends in abundance and biomass using different survey methods.

Relatively few jacks were encountered at Midway, and this represented the lone exception to the general pattern of jacks being dominant over sharks by biomass at atolls. The scarcity of jacks may be related to the recreational fishing that has occurred at Midway during the past 50 years (Green, 1997). The atoll served as a military base for over four decades, and Midway-Phoenix Corporation operated eco-tourism ventures there from 1996 to 2000, including recreational scuba diving and a catch-and-release trophy fishery for giant trevally. Fishing activities may have affected the jack populations at Midway by removing individuals directly, by indirectly making them more susceptible to shark predation or physiological death after release in an exhausted state, or both. Alternatively, or additionally, the catch-and-release fishery and diving operation may have affected the behavior of jacks by promoting emigration to greater depths or by causing them to develop a conditioned aversion to boats and divers (e.g., Kulbicki, 1998). Each of the latter two factors might result in jacks being underrepresented on diver surveys. A combination of chronic, prior extraction and recent indirect mortality, plus conditioned aversion, is most likely (DeMartini et al., 2002).

Midway had the highest densities of sharks in the NWHI, in contrast to other atolls in the chain which generally had moderate densities. One possibility is that Midway's shark populations have responded functionally to competitive release with increased reproductive output. Another, non-mutually exclusive possibility is that adult sharks have immigrated to Midway in response to the depressed abundance of jacks. Now that sportfishing and persistent daily diving have been discontinued, it will be interesting to see if the jack populations increase at Midway and, if so, whether shark densities decrease. Understanding the movements of sharks and jacks to and from Midway will probably require the use of acoustic tags or sonic transmitters (e.g., Holland et al., 1999) to track individual animals, research that has already been initiated by the Hawaii

Institute of Marine Biology (HIMB) shark research group (Lowe et al., 2006).

The three banks surveyed each had unique patterns of apex predator density. The largest bank in the chain, Maro Reef, had higher densities of sharks than jacks, which matched the general pattern observed in a previous study of NWHI banks (Parrish and Boland, 2004). Neva Shoals, an extensive bank associated with Lisianski Island, had the opposite pattern, with high densities of jacks and very few sharks. The smaller reef associated with Laysan Island had low densities of both types of apex predator. Differences in habitat may explain some of the variation in densities and relative proportions of apex predators at these three banks. The reef around Laysan Island is relatively featureless, with low relief, and much of it is covered in turf algae. Lisianski Island-Neva Shoals and Maro Reef have much greater topographical complexity, with reticulated reefs and submerged pinnacles (NOAA, 2003). However, in surveys of deeper bank summits in the NWHI, Parrish and Boland (2004) found that the number of apex predators did not differ with scales of relief, although density of most other fishes did, perhaps in response to predators. Future analysis, which will include mapping predator densities in relation to oceanographic parameters, may give us greater insight into the variation in jack and shark distribution among banks.

Habitat preferences were well defined in the midwater reef-associated sharks. Galapagos and gray reef sharks at atolls were found mainly in forereef habitats and sometimes in the channels (Galapagos only), and on banks they were concentrated on the exposed reefs. Other investigations have found fish abundance in general to be higher on the forereef than other habitats (e.g., Sedberry and McGovern, 1995). Gray reef shark distribution at Maro and Midway was dispersed, with solitary individuals rather than aggregations as reported for other atolls (McKibben and Nelson, 1986; Economakis and Lobel, 1998) and in the NWHI by previous researchers (Taylor, 1993). These aggregations were predominantly female and linked to breeding-related behaviors. Our surveys were conducted during late summer and early fall rather than spring when the majority of aggregations were observed.

Whitetip reef sharks (a benthic species) were scattered throughout atoll and bank habitats. Maps of their distribution on Maro Reef showed mostly solitary individuals spaced at regular intervals across the reef. There are reports that whitetip reef sharks may be somewhat site attached, returning to a home cave between foraging excursions (Randall, 1977). Whitetips were recorded at all reefs south of and including Pearl and Hermes. While there were rare sightings of whitetip reef sharks at Midway and Kure during previous studies (Schroeder and Parrish, 2005), these atolls appear to lie just north of an undetermined distributional limit, perhaps related to winter water temperatures.

The habitat use of jack species was more difficult to specify. On banks, the three major species of jacks showed no preference for insular or exposed reefs. At atolls, the three major species of jacks were observed most often in forereef habitats, although the difference was significant only for amberjack. Amberjack were generally recorded as solitary individuals and were spaced relatively evenly throughout the habitats they occupied.

Giant trevally were often recorded in large, roving groups, although also observed singly. The two different modes of travel are probably related to prey spacing- e.g., grouped and single trevally have greater success foraging on schooled and isolated prey, respectively (Major, 1978). Plots of jack distributions at Lisianski Island-Neva Shoals indicated possible hotspots of giant trevally biomass on the leeward (western) reef near the island, and at the southernmost point of the shoals. Giant trevally biomass was greater along most of the forereef and much of the backreef of Pearl and Hermes, with highest concentrations along the windward side (east and northeast). The spatial distribution of giant trevally is likely to be dynamic as this species demonstrates long-term and long-distance movements at the scale of whole island reefs (Wetherbee et al., 2004), and at perhaps larger spatial scales.

Bluefin trevally biomass was most concentrated at the southwest corner of Pearl and Hermes Atoll, a distribution pattern that may be relatively persistent because site fidelity is strong in this species (Holland et al., 1996). Studies of bluefin trevally at Johnston Atoll showed that they prey heavily on spawning fishes using midwater and ambush hunting techniques (Sancho, 2000; Sancho et al., 2000). Bluefin trevally may be using similar strategies to feed on midwater planktivores, which are abundant along the southwest forereef of PHR. The forereef in the southwest corner of PHR is pockmarked with narrow channels and reef passes, and bluefin trevally may elect to hunt in these channels, a behavior that was well documented at an atoll in the Indian Ocean (Potts, 1980).

In summary, these baseline abundances provide the necessary starting point for understanding the population fluctuations of jacks and sharks that abound on the reefs of the NWHI and that, as apex predators, are important determinants of fish assemblage structure in these reef ecosystems (DeMartini and Friedlander, 2006). As monitoring surveys begin, it will be interesting to see if shark and jack hotspots within each reef are predictable from year to year. In general, it would be useful to evaluate whether relative abundances of the different predator species fluctuate temporally to appreciable extents. Towed-diver surveys potentially provide an effective method to assess the abundances of patchily distributed shark and jack predators at the remote, expansive atolls and banks of the NWHI. Continued towed-diver surveys will enable us to monitor the status of these important apex predators in an ecosystem relatively undisturbed by humans.

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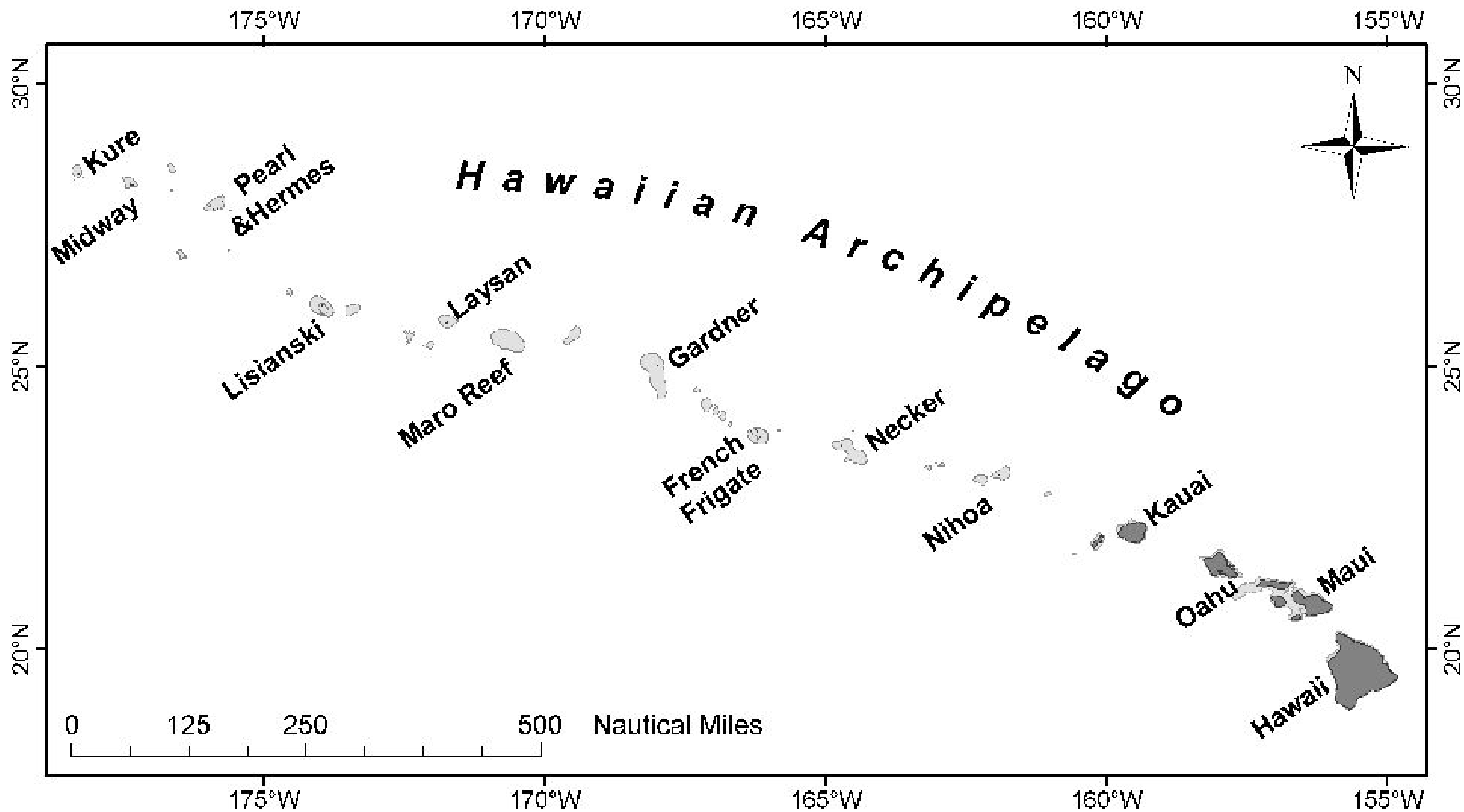


Figure 1. Map of the Hawaiian Archipelago, showing the Northwestern Hawaiian Islands study sites in relation to the main Hawaiian Islands.

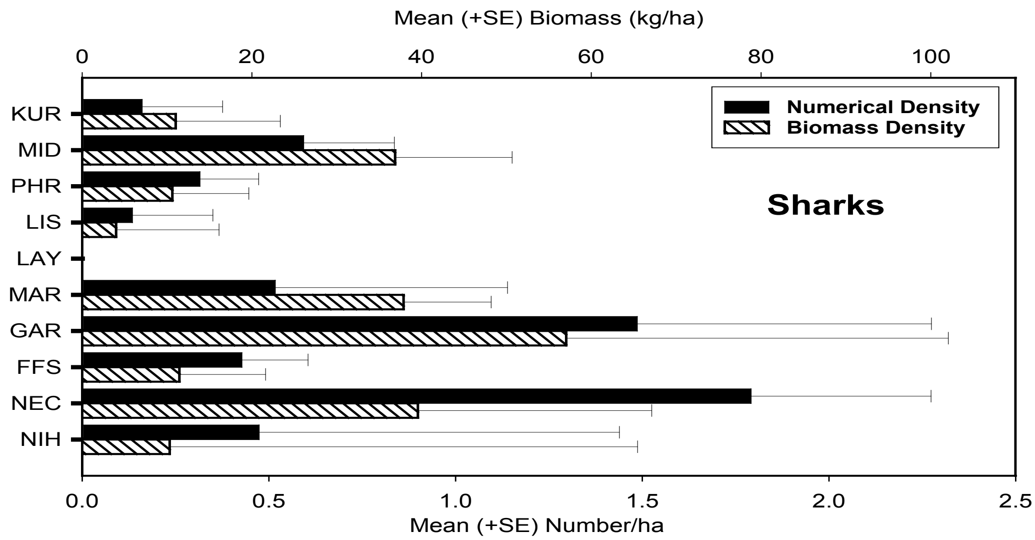


Figure 2. Mean numerical and biomass densities of sharks (Family Carcharhinidae) on NWHI reefs, listed from north to south.

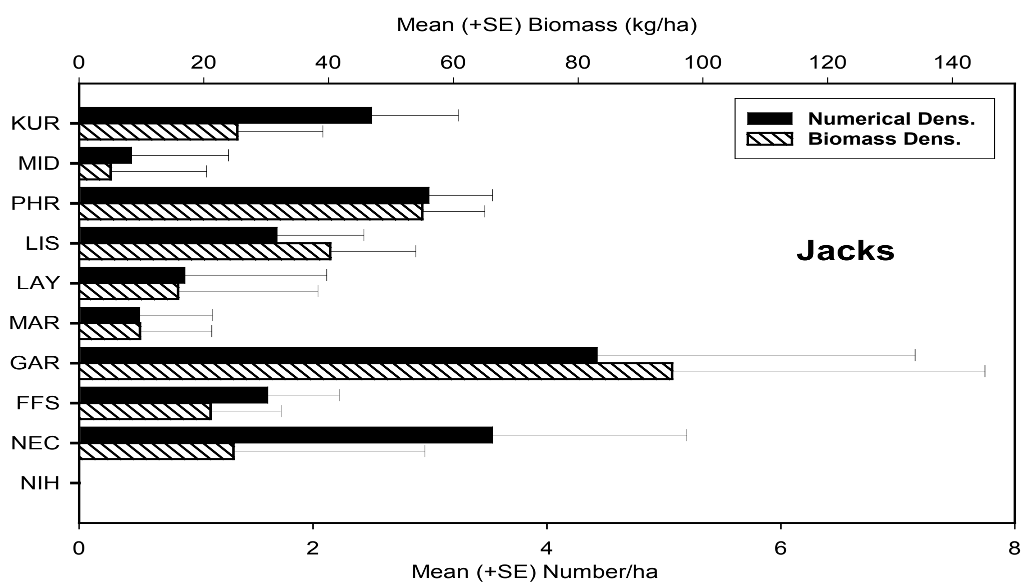


Figure 3. Mean numerical and biomass densities of jacks (Family Carangidae) on NWHI reefs, listed from north to south.

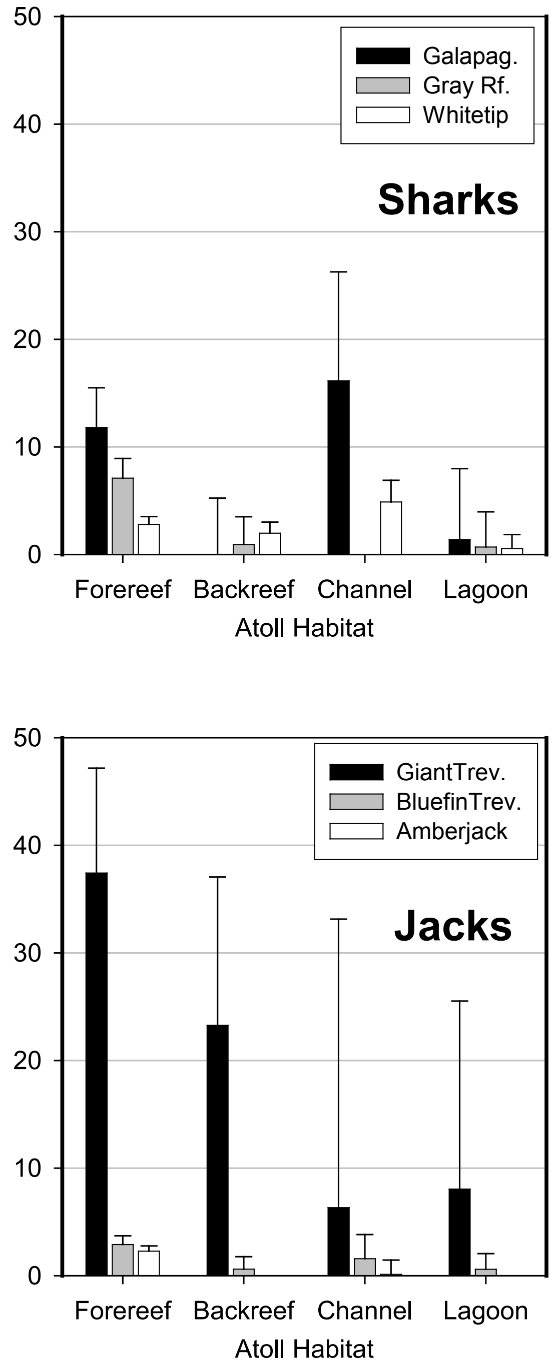


Figure 4. Mean biomass densities of top three shark and jack species on reef zone habitats within atolls (forereef, backreef, lagoon, and channel).

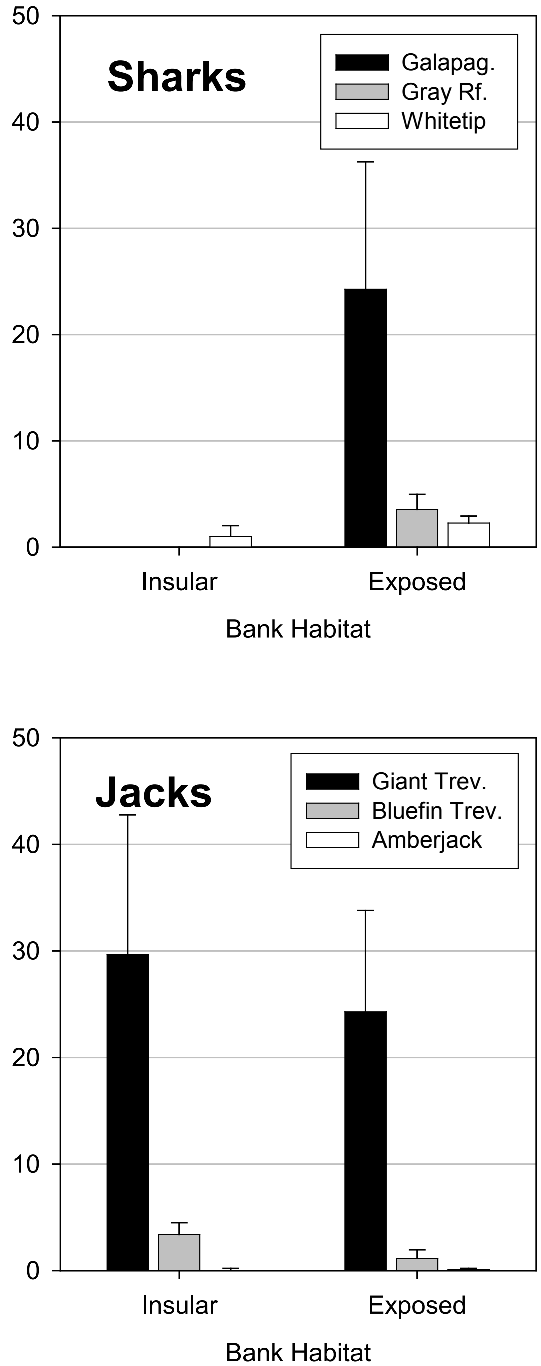
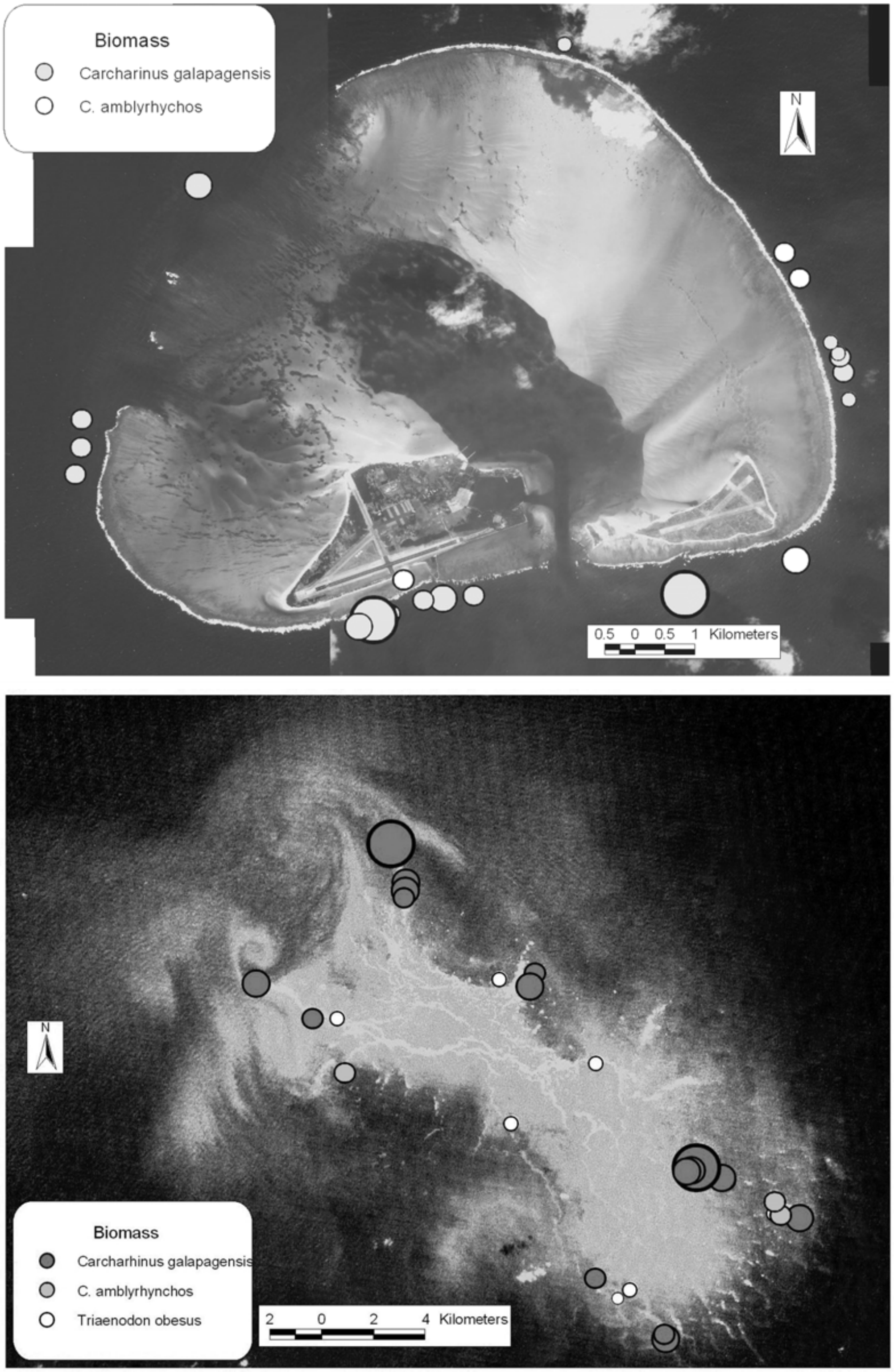


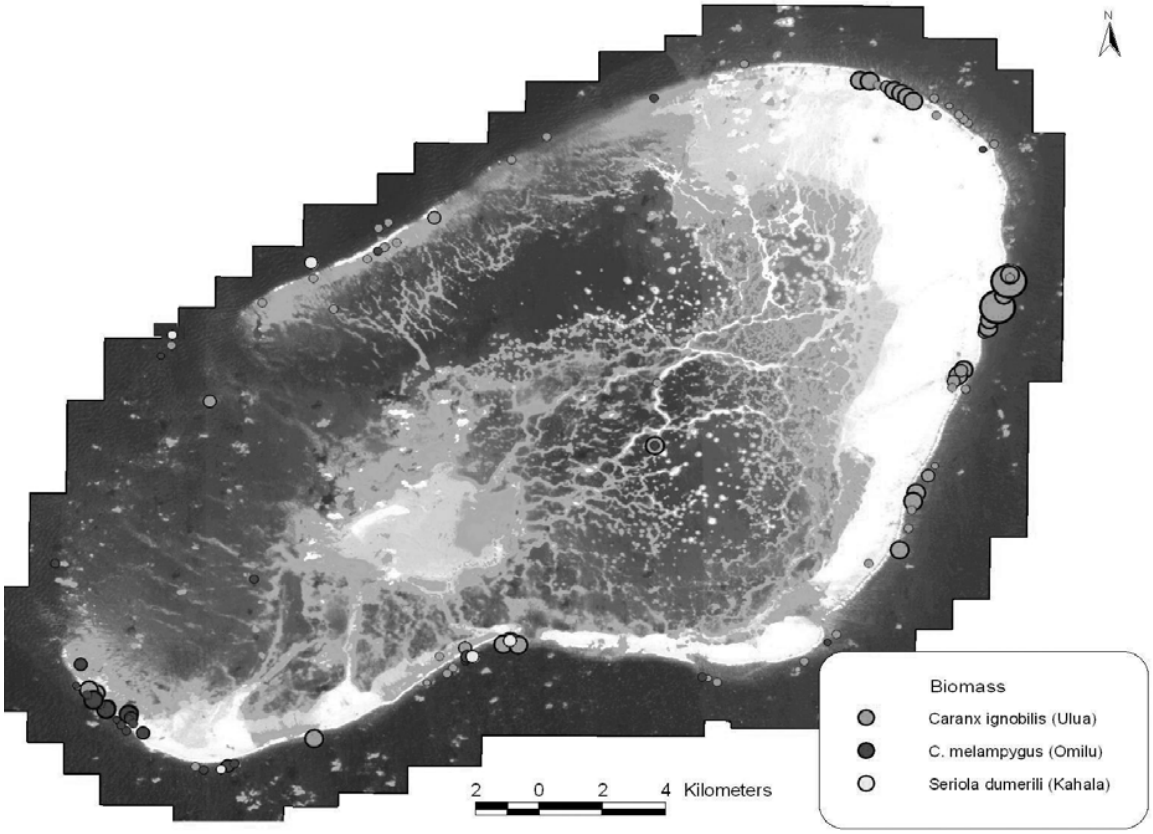
Figure 5. Mean biomass densities of top three shark and jack species in habitats within banks (insular and exposed reefs).



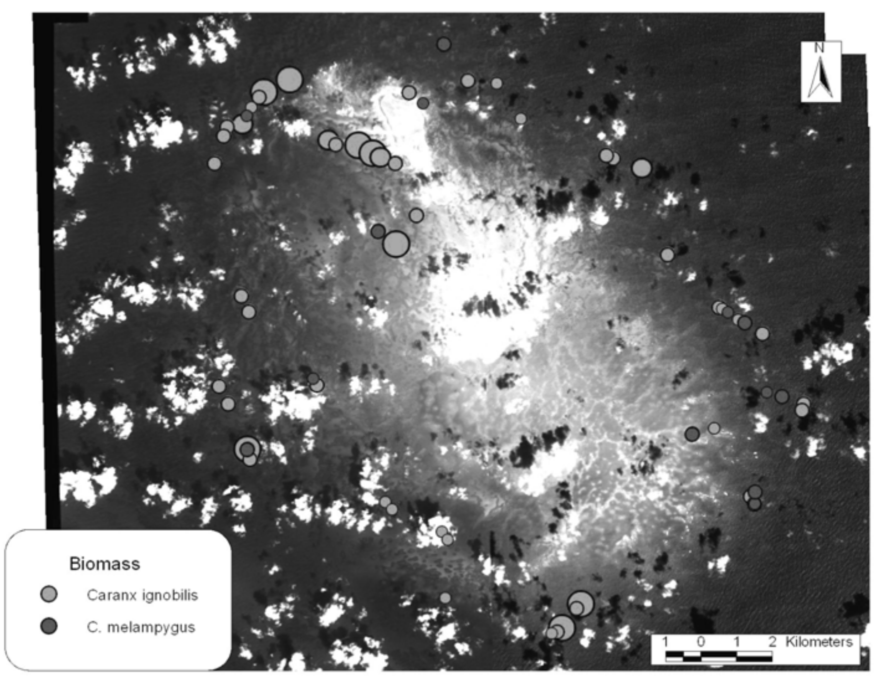
A

B

Figure 6. Spatial distribution of shark biomass by species at Midway Atoll (A) and Maro Reef (B) from towed-diver surveys (2000 to 2003). No whitetips were observed at Midway.



A



B

Figure 7. Spatial distribution of jack biomass by species at Pearl and Hermes Atoll (A) and Lisianski-Neva Shoals (B) from towed-diver surveys (2000 to 2003). No amberjack were observed at Lisianski-Neva

Table 1. Species of sharks and jacks recorded on NWHI towed-diver surveys. Species are listed within each family in decreasing order of total number of individuals (≥50-cm TL) observed during quantitative portions of towed-diver surveys. (* species seen only during non-quantitative portions of towed-diver surveys)

Family/Species	**Common name**	**Hawaiian/local name**	**Total *n***
Carcharhinidae			
Carcharhinus galapagensis	Galapagos shark	mano	171
Triaenodon obesus	whitetip reef shark	mano lalakea	99
C. amblyrhynchos	gray reef shark	mano	51
Galeocerdo cuvier	tiger shark	niuhi	1
C. limbatus	blackfin shark	mano	*
Carangidae			
Caranx ignobilis	giant trevally	‘ulua aukea	1004
C. melampygus	bluefin trevally	‘ōmilu	269
Psuedocaranx dentex	thicklipped jack	butaguchi	80
Seriola dumerili	greater amberjack	kāhala	60
Carangoides ferdau	barred jack	ulua	54
Elagatis bipinnulata	rainbow runner	kamanu	34
Caranx lugubris	black trevally	ulua la’uli	2
Carangoides orthogrammus	island jack	ulua	*
Caranx sexfasciatus	bigeye trevally	pake ulua	*

Table 2. Statistical results of comparisons among reefs and among habitats. Results are given from one-way Kruskal-Wallis ANOVA on ranks for numerical (n/ha) and biomass (kg/ha) densities of sharks and jacks. For the among reefs comparison only data from habitats common to all reefs was used. An adjusted p-value of p<0.025 was used for tests on higher-order taxa and p<0.016 for tests on species-level taxa (*significant).

Comparison	**K-W ANOVA χ^2**	**df**	**P-value**
Among Reefs			
Carcharhinidae			
Abundance	34.32	9	<0.001*
Biomass	25.33	9	<0.003*
Carangidae			
Abundance	46.49	9	<0.001*
Biomass	49.59	9	<0.001*
Within Atolls: Forereef vs Backreef vs Lagoon vs Channel			
Carcharhinidae			
gray reef shark			
Abundance	10.10	3	0.018
Biomass	9.16	3	0.027

Table 2. Continued.

Galapagos shark			
Abundance	13.64	3	0.003*
Biomass	13.83	3	0.003*
whitetip reef shark			
Abundance	5.65	3	0.130
Biomass	5.07	3	0.167
Carangidae			
giant trevally			
Abundance	6.55	3	0.088
Biomass	4.56	3	0.207
bluefin trevally			
Abundance	5.33	3	0.149
Biomass	7.11	3	0.068
amberjack			
Abundance	16.37	3	<0.001*
Biomass	15.39	3	0.001*
Within Banks: Insular vs Exposed Reefs			
Carcharhinidae			
gray reef shark			
Abundance	4.03	1	0.045
Biomass	4.03	1	0.045
Galapagos shark			
Abundance	6.53	1	0.011*
Biomass	6.53	1	0.011*
whitetip reef shark			
Abundance	1.10	1	0.294
Biomass	0.64	1	0.423
Carangidae			
giant trevally			
Abundance	0.20	1	0.653
Biomass	0.71	1	0.426
bluefin trevally			
Abundance	0.35	1	0.552
Biomass	0.38	1	0.538
amberjack			
Abundance	0.19	1	0.662
Biomass	0.19	1	0.662

Table 3. Statistical results of *post-hoc* multiple comparisons (Kruskal-Wallis z-value test) of reefs (listed by number on left), by family. Numerical density (N) and biomass density (Bio) were compared among reefs. Reefs that differed significantly are listed (adjusted p=0.025). A dash (--) indicates no difference between listed reef and any other reef.

	Reef differences			
	Shark N	Shark Bio	Jack N	Jack Bio
1-NIH	--	--	2,3	--
2-NEC	3,5,6,7,8,9,10	3,5,6,7,8,10	1,3,5,6,9,10	5,9
3-FFS	2,6	2,6	2,7,8	2,7,8
4-GAR	6	6	1,5,9	5
5-MAR	2	2	2,4,7,8	7,8
6-LAY	2,3,4,8,9	2,3,4,5,8,9	2	7,8
7-LIS	2	2	3,5,9,10	3,5,6,9,10
8-PHR	2,6	2,6	2,3,5,10	2,3,5,6,10
9-MID	2,6	6	2,4,7,8	2,7,8
10-KUR	2	2	2,7,8	7,8

Table 4. Statistical results of *post-hoc* multiple comparisons (Kruskal-Wallis z-value test) of habitats (listed by number on left), by species. Densities of the top three jack and shark species were compared among habitats. Abundance and biomass results were identical. Habitats that differed significantly are listed (adjusted p=0.016). A dash (--) indicates no difference between listed habitat and any other habitat.

	Habitat differences					
	Sharks			Jacks		
	GreyReef	Galapagos	Whitetip	GiantTrev	BluefinTrev	Amberjack
1-Forereef	2	2	--	--	--	2,3
2-Backreef	1	1,4	--	--	--	1
3-Lagoon	--	--	--	--	--	2
4-Channel	--	2	--	--	--	--

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