Fishes

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BIOGEOGRAPHY OF FISHES

The Hawaiian Archipelago is among the most isolated on earth and exhibits the highest level of marine fish endemism of any archipelago in the Pacific (Randall, 1995, 1998, 2007; Randall and Earle, 2000; Allen, 2002). Owing to limited human influence, the Northwestern Hawaiian Islands (NWHI) reefs are nearly pristine and represent one of the last remaining intact large-scale, predator-dominated coral reef ecosystems on earth (Friedlander and DeMartini, 2002). Because of its high level of endemism and the near pristine nature of its reefs, the NWHI represents an important global biodiversity hot spot and provides a view of what reefs in the may have MHI looked like before human contact.

Despite centuries of exploitation, the MHI today has even higher biodiversity of fishes than the NWHI. Randall et al. (1993) reported 258 species of reef and shore fishes from Midway Atoll compared with 612 species in the MHI (Randall, 2007). Mundy (2005) lists 21 species that are known from the NWHI, but not the MHI (Table 5.1). Of these, most are either deep-water or mesopelagic and therefore poorly sampled waifs, or species with poor taxonomic resolution. In contrast, 406 species are known from the Main Hawaiian Islands (MHI) but not the NWHI and overall richness and diversity are greater in the MHI compared with the NWHI (Mundy, 2005).

Table 5.1. Fish species known from the NWHI but not found in the MHI. Source: Mundy, 2005.

FAMILY	SPECIES	COMMON NAME	LOCATIONS	HABITAT
Scyliorhinidae	*Apristurus spongiceps*	Spongehead catshark	Nihoa	Deep-water
Muraenidae	*Gymnothorax atolli*	Atoll moray	Pearl and Hermes to Midway	Cryptic
Platytroctidae	*Mentodus mesalirus*	Tubeshoulders	Pearl and Hermes to Midway	Deep-water
Stomiidae	*Astronesthes nigroides*	Dragonfish	Pearl and Hermes to Midway	Mesopelagic
	Eustomias cancriensis	Scaleless black dragonfish	Pearl and Hermes to Midway	Mesopelagic
Ophidiidae	*Bassozetus zenkevitchi*	Cusk-eel	Midway to Kure	Deep-water
	Spectrunculus grandis	Cusk-eel	Maro	Deep-water
Macrouridae	*Cetonurus crassiceps*	Grenadier, Rattail	Pearl and Hermes	Deep-water
Holocentridae	*Myripristis murdjan*	Blotcheye soldierfish	Midway to Kure	Shallow reefs
Fistulariidae	*Fistularia petimba*	Serrate coronetfish	Nihoa to Kure	Mod-deep-water
Laysan	*Scorpaenopsis pluralis*	Laysan scorpionfish	Lasyan	Deep-water
Callanthiidae	*Grammatonotus macrophthalmus*	Splendid perch	French Frigate Shoals	Deep-water
Epigonidae	*Epigonus devaneyi*	Deepwater cardinalfish	Mokumanamana to Maro	Deep-water
Carangidae	*Caranx lugubris*	Black trevally	Mokumanamana to Midway	Shallow to deep
Carangidae	*Decapterus macrosoma*	Shortfin scad	Maro	Pelagic
Pomacanthidae	*Centropyge interruptra*	Japanese angelfish	Kure and Midway	Shallow reefs
Kyphosidae	*Girella leonina*	Blackedge nibbler	Midway	Waif
Labridae	*Epibulus insidiator*	Slingjaw wrasse	French Frigate Shoals north to Kure	Shallow reefs
Ammodytidae	*Lepidammodytes macrophthalmus*	Sand lance	Maro	Poorly known
Ephippidae	*Platax boersii*	Boer's spadefish	Midway	Waif
Luvaridae	*Luvarus imperialis*	Louvar	Laysan	Epipelagic

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The few demersal species found in the NWHI but not the MHI include the blotcheye soldierfish (*Myripristis murdjan*), an Indo-Pacific species but restricted to the NWHI in the Hawaiian archipelago, and the Japanese angelfish (*Centropyge interruptra*; Figure 5.1) which is known only from the NWHI and Japan (Mundy, 2005). Evidence of larval pelagic transport from Japan to the NWHI via the Kuroshio and North Pacific Currents is supported by the presence of a number of species that are common only off Japan and the northwestern end of the Hawaiian Archipelago (Randall, 2007). In addition to the Japanese angelfish, these include two lizardfishes (*Synodus lobelia* and *S. ulae*), the manyspine squirrelfish (*Sargocentron spinosissimum*), two species of knifejaws (*Oplegnathus fasciatus* and *O. punctatus*) and the blackedge nibbler (*Girella punctata , family Girellidae*), a close relative of the chubs of the family Kyphosidae (Randall, 2007).

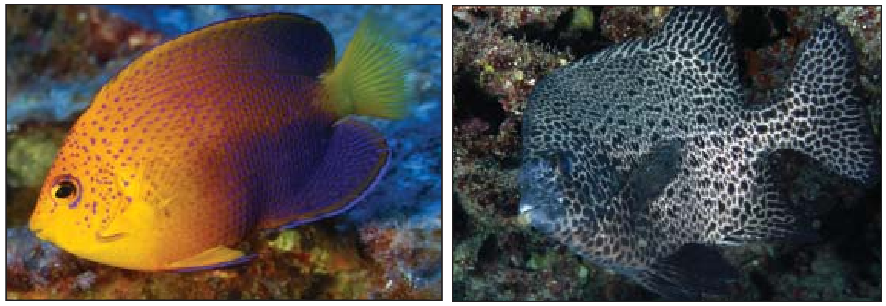

*Figure 5.1. The Japanese angelfish (*Centropyge interruptra*; left) and the spotted knifejaw (*Oplegnathus punctatus*; right) are known only from the NWHI and Japan, although the latter is occasionally observed in the MHI. Photo: J. Watt.*

Two species, the slingjaw wrasse (*Epibulus insidiator*) and the chevron butteryflyfish (*Chaetodon trifascialis*), are associated with *Acropora* corals that occur only in the central portion of the NWHI, and although these fish species are occasionally observed in the MHI and the far northern end of the chain, they are most abundance from French Frigate Shoals to Pearl and Hermes (Mundy, 2005). Despite the taxonomic similarity with the MHI fauna, the NWHI fish assemblage differs from that of the MHI at various ecological and demographic levels owing to oceanographic conditions (e.g., water temperature), habitat (e.g., coral and reef type) and anthropogenic influences (e.g., effects of fishing in the MHI).

There are a variety of environmental and other reasons for lower reef fish diversity in the NWHI versus MHI. Many shallow-water fish species that are adapted to warmer water cannot survive in the NWHI since winter water temperatures can be as much as 7ºC cooler than the MHI (Mundy, 2005). Some shallow-water species are adapted to cooler water and can be found in deeper waters at the southern end of the archipelago. This phenomenon known as tropical submergence is exemplified by species such as the yellowfin soldierfish (*Myripristis chryseres*), the endemic Hawaiian grouper (*Epinephelus quernus*), and the masked angelfish (*Genicanthus personatus*), all of which occur in shallow water at Midway but are restricted to much greater depths in the MHI (Figure 5.2; Randall et al., 1993; Mundy, 2005). Other reasons for the lower number of species in the NWHI include insufficient sampling effort and the lack of many high island habitats such as estuaries and rocky shorelines

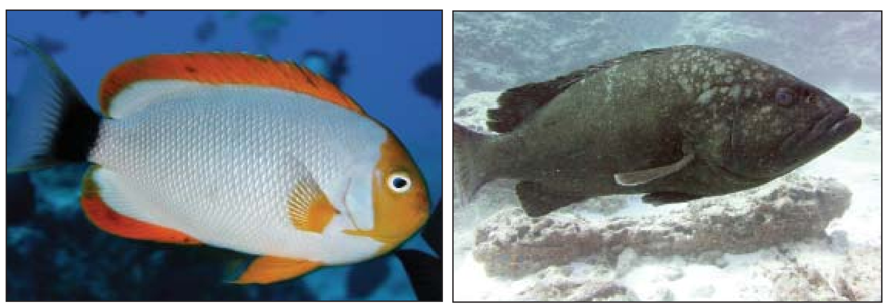

*Figure 5.2. The endemic masked angelfish (*Genicanthus personatus*, left) and Hawaiian grouper (*Epinephelus quernus*, right) are found in shallower water at Midway Atoll but are restricted to deeper depths in the MHI. Photos: J. Watt (left); J. Maragos (right).*

Some of the non-endemic species abundant at higher latitude reefs in the NWHI have antitropical distributions and are thought to have established themselves in the archipelago when surface waters were previously cooler (Randall, 1981). The Hawaiian morwong, (*Goniistius vittatus*) for example, may be a cryptic species that diverged during the late Miocene-early Pliocene from the lineage presently represented by nominal conspecifics in the southern hemisphere (Burridge and White, 2000). Interestingly, most Hawaiian endemic species do not appear to exhibit submergence (greater depth distributions) in the MHI, although rigorous comparisons are lacking (DeMartini and Friedlander, 2004).

Fish Species Richness

Despite lower species richness in the NWHI as compared with the MHI (Mundy 2005), the total number of species (210) observed on quantitative transects in the NWHI (DeMartini and Friedlander, 2004) was similar to the number of species (215) reported in a recent comprehensive quantitative study around the MHI (Friedlander et al., 2007). The lowest overall fish species richness in the NWHI occurs at the small basalt islands (Mokumanamana, Gardner and Nihoa; Figure 5.3) and highest at French Frigate Shoals and Pearl and Hermes. The former may be related to the higher coral richness and greater diversity of habitats (Maragos et al., 2004), while the latter is likely related to large size, habitat diversity and presence of subtropical and temperate species which occur at much greater depths southward in the chain of islands.

Total species richness observed on surveys (y) showed a positive, linear relationship ($y=8.05 * \ln(x+1) + 112.2$, $R^2=0.51$, $p=0.02$, Table 5.2, Figure 5.4) with a logarithmic function of total reef area less than 10 fathoms (x). This relationship is consistent with the general theory of island biogeography and likely reflects the greater diversity of habitats present in larger reef areas.

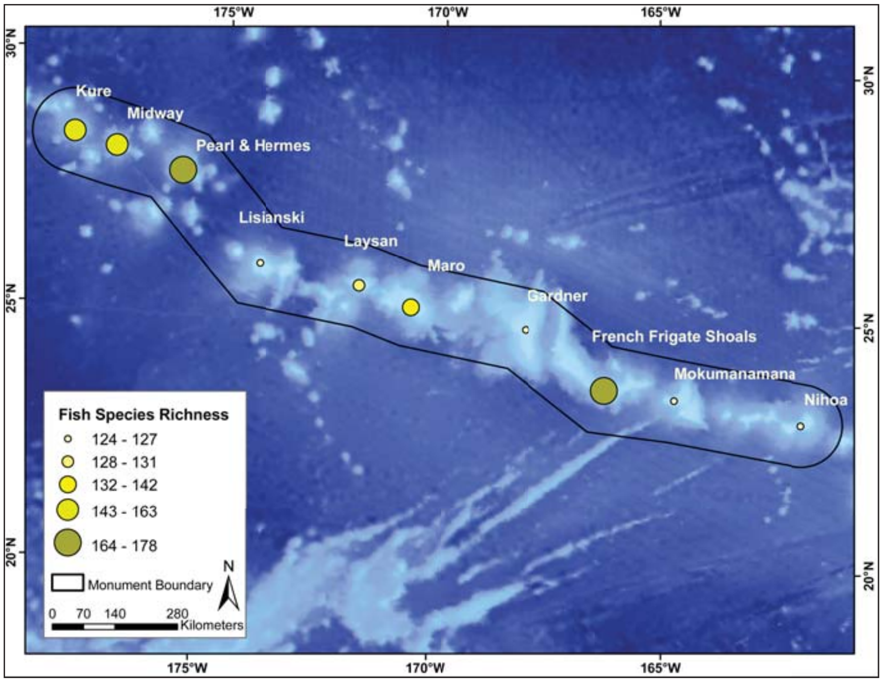

Figure 5.3. Total fish species richness at each of 10 emergent NWHI reefs. Source: NWHI RAMP, unpub. data; map: L. Wedding.

Table 5.2. Results of least squares linear regression model for total number of species by ln (total reef area within 10 fathoms +1). R^2 = 0.51, N = 10. Source: NWHI RAMP, unpub. data.

ANALYSIS OF VARIANCE				
Source	**DF**	**Mean Square**	**F Ratio**	**Prob > F**
Model	1	2105.32	8.20	0.0211
Error	8	256.85		
C. Total	9			
PARAMETER ESTIMATES				
Term	**Estimate**	**Standard Error**	**t Ratio**	**Prob>|t|**
Intercept	112.21	12.3	9.12	<0.001
Ln (area)	8.052	2.81	2.86	0.0211

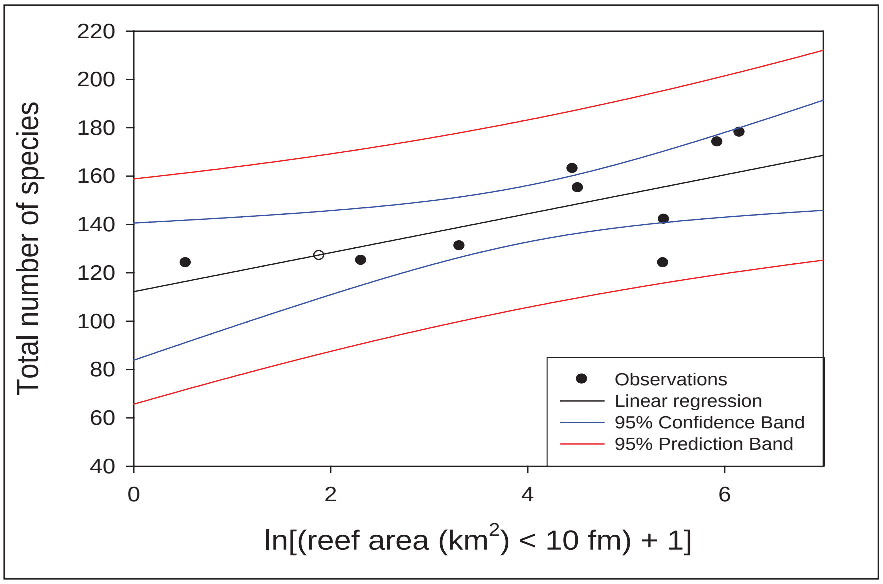

Figure 5.4. Relationship between cumulative number of fish species at each reef and total reef area (km^2) within 10 fathoms. Source: Friedlander et al., in prep.

Endemism

The Hawaiian Island chain is among the most isolated on earth and exhibits the highest level of marine fish endemism of any archipelago in the Pacific (Randall, 1995, 1998; Randall and Earle, 2000; Allen, 2002). Endemism is a key attribute of biotic communities that is generally a great concern of conservation ecology. One reason of general biogeographic interest is that speciation and the origin and maintenance of biodiversity are undoubtedly related to degrees of isolation and endemism (Gray, 1997). Because of the decline in global marine biodiversity, endemic "hot spots" like Hawaii are important areas for global biodiversity conservation. The endemic fishes of Hawaii are small bodied and have very restricted geographic ranges of less than 50,000 km^2 (Roberts et al., 2002). Small body size, per se, may be associated with higher extinction risk because small-bodied species tend to have narrower habitat requirements (Hawkins et al., 2000). Therefore both body size and endemic status argue for the conservation of these species.

Based on species-presence, endemism is equivalent for fishes in the NWHI (20.6% using all available data) and the MHI (MHI, 20.9%; DeMartini and Friedlander, 2004). On average, percentage endemism was much higher based on numerical densities (52%) and biomass (37%) which increased with latitude, and was especially pronounced at the four northernmost reefs that are the oldest emergent geological features of the archipelago (Figure 5.5). Greater endemism towards Midway and Kure appears related to consistently higher rates of replenishment by young-of-the-year (YOY) upchain following dispersal as pelagic larvae and/or juveniles. There were significant positive relationships between number and biomass of endemics with latitude (Tables 5.3, 5.4, 5.5; Figures 5.6). However endemism based on species presence was not significantly correlated with latitude (Figure 5.7).

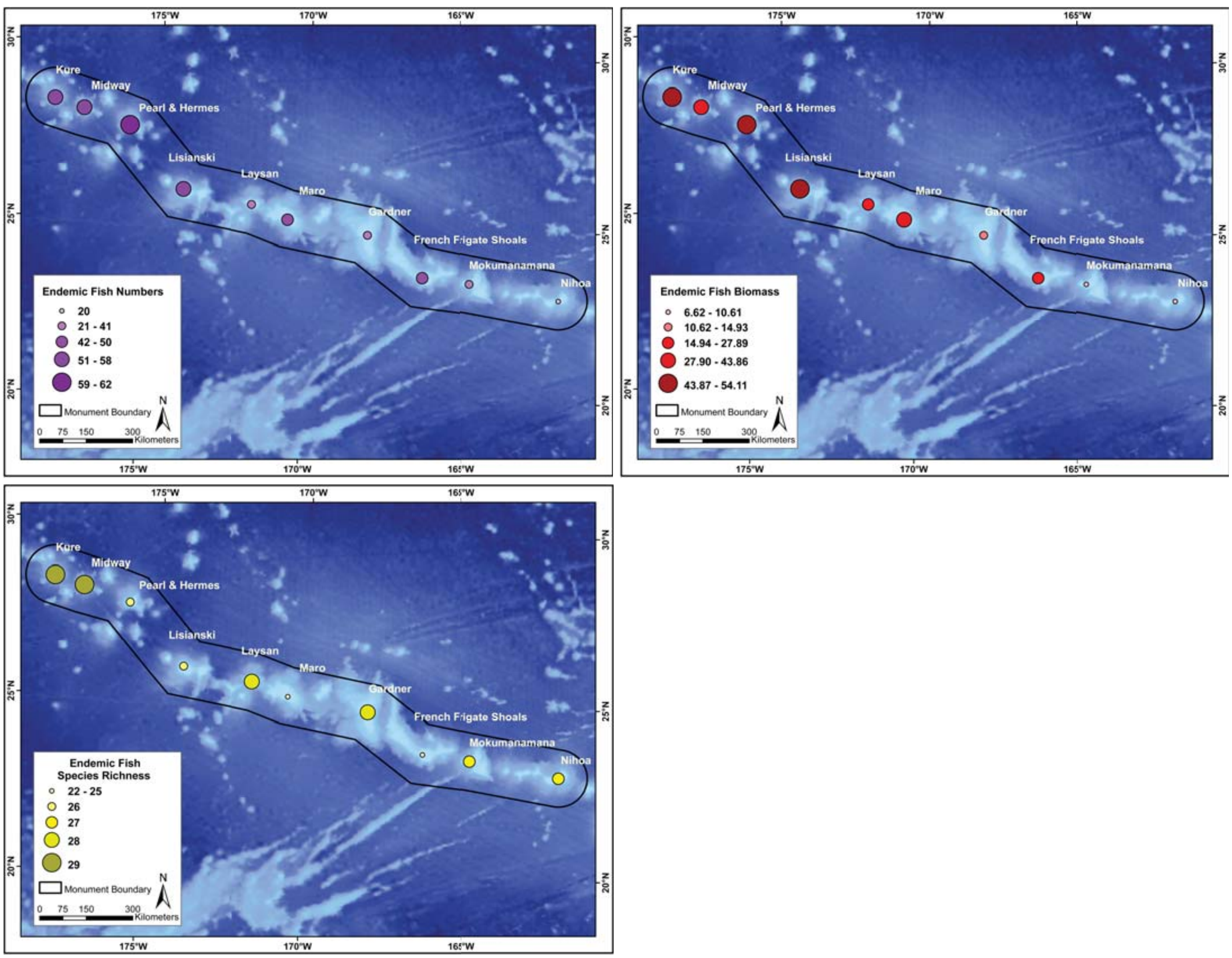

Figure 5.5. Percent endemism based on numerical densities (top left), biomass (top right) and species richness (bottom left) at each of 10 emergent NWHI reefs. Source: DeMartini and Friedlander, 2004; maps: L. Wedding.

Endemic reef fishes are appreciably smaller bodied than nonendemics within the NWHI (DeMartini and Friedlander, 2004). Median body size does not vary with latitude and longitude for either endemics or nonendemics, which obviates possibly confounding environmental effects. Reef fish populations at higher latitude reefs included larger proportions of YOY recruits. YOY length frequencies did not differ for most species between northern and southern reefs, suggesting that a seasonal lag in spawning and recruitment at higher latitudes cannot explain the greater YOY densities observed. Disproportionate recruitment at higher-latitude reefs may be related to better growth and survivorship after settlement onto reefs, higher levels of within-reef and regional reseeding at higher latitudes, or other factors.

Table 5.3. Results of least squares linear regression model for total number of species by ln (total reef area within 10 fathoms +1). R^2 = 0.51, N = 10. Source: DeMartini and Friedlander, 2004.

ANALYSIS OF VARIANCE				
Source	**DF**	**Mean Square**	**F Ratio**	**Prob > F**
Model	1	962.8	15.86	0.004
Error	8	60.72		
C. Total	9			
PARAMETER ESTIMATES				
Term	**Estimate**	**Standard Error**	**t Ratio**	**Prob>|t|**
Intercept	-89.86	34.15	-2.63	0.0301
Latitude	5.28	1.32	3.98	0.004

Table 5.4. Results of least squares linear regression model for total number of species by ln (total reef area within 10 fathoms +1). R^2 = 0.51, N = 10. Source: DeMartini and Friedlander, 2004.

ANALYSIS OF VARIANCE				
Source	**DF**	**Mean Square**	**F Ratio**	**Prob > F**
Model	1	1817.66	14.7374	0.005
Error	8	123.34		
C. Total	9			
PARAMETER ESTIMATES				
Term	**Estimate**	**Standard Error**	**t Ratio**	**Prob>|t|**
Intercept	-153.734	48.67219	-3.16	0.0134
Latitude	7.249942	1.888528	3.84	0.005

Table 5.5. Results of least squares linear regression model for total number of species by ln (total reef area within 10 fathoms +1). R^2 = 0.51, N = 10. Source: DeMartini and Friedlander, 2004.

ANALYSIS OF VARIANCE				
Source	**DF**	**Mean Square**	**F Ratio**	**Prob > F**
Model	1	8.18	3.53	0.0971
Error	8	2.32		
C. Total	9			
PARAMETER ESTIMATES				
Term	**Estimate**	**Standard Error**	**t Ratio**	**Prob>|t|**
Intercept	13.77	6.67	2.06	0.0729
Latitude	0.49	0.26	1.88	0.0971

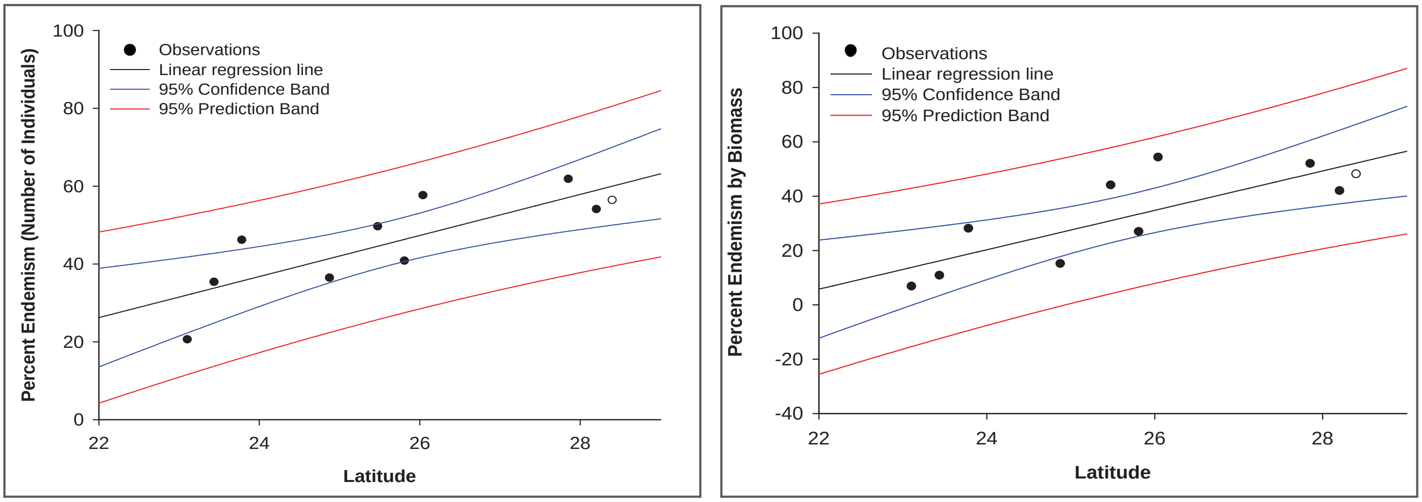

Figure 5.6. Least squares linear regression model for percent endemism by numerical abundance versus latitude (left). Least squares linear regression model for percent endemism by biomass versus latitude (right). Source: DeMartini and Friedlander, 2004.

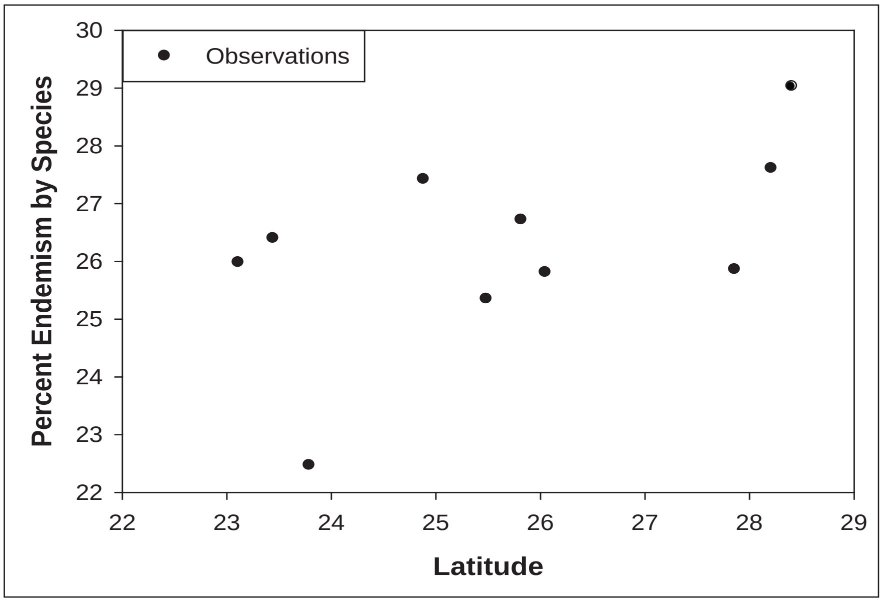

Figure 5.7. Least squares linear regression model for percent endemism by species versus latitude. Source: DeMartini and Friedlander, 2004

LATITUDINAL AFFINITIES AMONG FISHES

Biogeographic forces may promote disparate abundance patterns among some species at opposite ends of the archipelago owing to differences in temperature and other environmental factors. Some species might have a temperate or subtropical bias, whereas others might be better suited to more tropical conditions. To identify latitudinal gradients of abundance, numerical densities as a function of latitude was examined within the NWHI using Spearman rank correlation. Positive correlations indicated a temperate affinity, while negative correlations indicated a tropical affinity. The percentage of individuals with either temperate/ subtropical or temperate affinities is an indication of the total fish assemblage affinity at each reef (Table 5.6; Figure 5.8).

Thirty species showed a significant positive correlation (Spearman Rank Correlation, $p<0.05$) with latitude based on numerical density from quantitative fish surveys conducted between 2000 and 2002 (Table 5.7). Of these, 17 (57%) were endemics. Wrasses (Labridae) had the greatest number of species (eight) showing higher latitude affinity followed by damselfishes (Pomacentridae) with four species. Several other species such as knifejaws (*Oplegnathus* spp.) and boarfish (*Evistias acutirostris*) were more abundant at higher latitudes but their low numbers during surveys made the results inconclusive statistically.

Table 5.6. Percentage of numerical abundance at each reef that consisted of species that showed either a temperate/subtropical (northerly) affinity or tropical (southerly) affinity in abundance. Source: Friedlander et al., in prep.

REEF	TEMPERATE/SUBTROPICAL AFFINITY	TROPICAL AFFINITY
NIH	12.97%	16.35%
MMM	28.01%	28.44%
FFS	27.45%	8.57%
GAR	24.52%	14.15%
MAR	51.94%	4.27%
LAY	44.91%	10.24%
LIS	52.90%	3.22%
PHR	52.34%	1.99%
MID	56.08%	0.93%
KUR	63.43%	1.24%

Island/atoll abbreviations used throughout this chapter: NIH = Nihoa Island; MMM = Mokumanamana, FFS = French Frigate Shoals; GAR = Gardner Pinnacles; MAR = Maro Reef; LAY = Laysan Island; LIS = Lisianski Island; PHR = Pearl and Hermes; MID = Midway Atoll; KUR = Kure Atoll

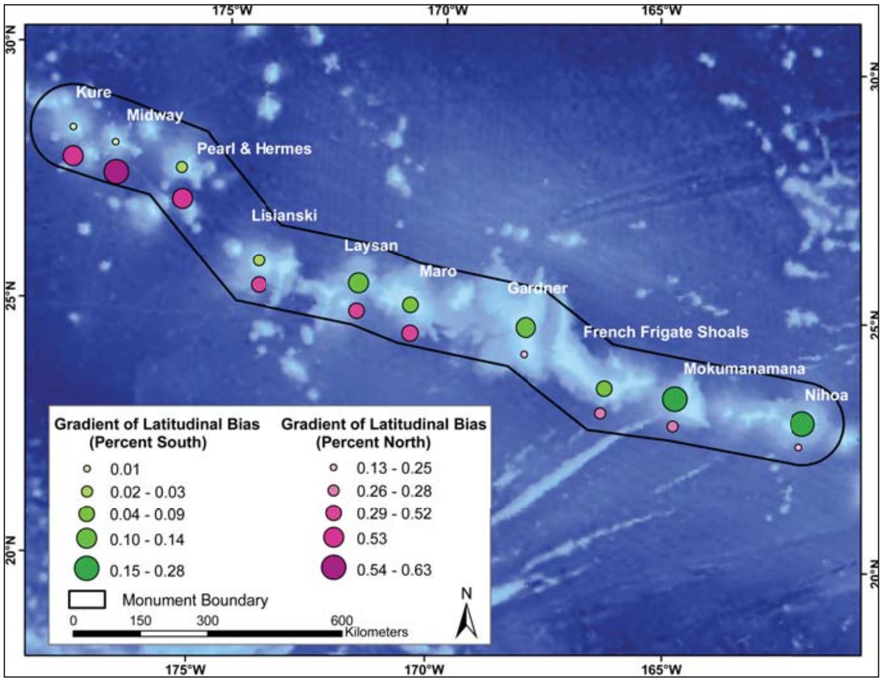

Figure 5.8. Percentage of total numerical abundance (numbers m^{-2}) for species showing a significant latitude gradient of distribution. Source: Friedlander et al., in prep.

Table 5.7. Species with temperate/subtropical affinity (positive correlation with latitude). Endemics in bold. Source: Friedlander et al., in prep.

FAMILY	TAXON NAME	COMMON NAME	HAWAIIAN NAME
Synodontidae	*Synodus ulae*	Ulae Lizardfish	ulae
Holocentridae	***Sargocentron xantherythrum***	**Hawaiian Squirrelfish**	**alaihi**
Scorpaenidae	***Pterois sphex***	**Hawaiian Turkeyfish**	
Serranidae	***Epinephelus quernus***	**Hawaiian Grouper**	**hapuu**
Priacanthidae	***Priacanthus meeki***	**Hawaiian Bigeye**	**aweoweo**
Chaetodontidae	*Chaetodon auriga*	Threadfin Butterflyfish	kikakapu
Pomacanthidae	***Genicanthus personatus***	**Masked Angelfish**	
Pomacentridae	***Abudefduf abdominalis***	**Sargent Major**	**mamo**
Pomacentridae	***Chromis hanui***	**Chocolate-dip Chromis**	

Table 5.7 (continued). Species with temperate/subtropical affinity (positive correlation with latitude). Endemics in bold. Source: Friedlander et al., in prep.

FAMILY	TAXON NAME	COMMON NAME	HAWAIIAN NAME
Pomacentridae	***Chromis ovalis***	**Oval Chromis**	
Pomacentridae	*Stegastes fasciolatus*	Pacific Gregory	
Cirrhitidae	*Paracirrhites forsteri*	Blackside Hawkfish	hilu pili koa
Labridae	***Anampses cuvier***	**Pearl Wrasse**	**opule**
Labridae	***Coris flavovittata***	**Yellowstrip coris**	**hilu**
Labridae	*Gomphosus varius*	Bird Wrasse	hinaleaiiwi, akilolo
Labridae	***Labroides phthirophagus***	**Hawaiian Cleaner Wrasse**	
Labridae	***Stethojulis balteata***	**Belted Wrasse**	**omaka**
Labridae	***Thalassoma ballieui***	**Blacktail Wrasse**	
Labridae	***Thalassoma duperrey***	**Saddle Wrasse**	**hinalea lauwili**
Labridae	*Thalassoma purpureum*	Surge Wrasse	hou
Scaridae	***Calotomus zonarchus***	**Yellowbar Parrotfish**	
Scaridae	***Chlorurus perspicillatus***	**Spectacled Parrotfish**	**uhu uliuli**
Scaridae	***Scarus dubius***	**Regal Parrotfish**	**lauia**
Cheilodactylidae	*Cheilodactylus vittatus*	Hawaiian Morwong	
Acanthuridae	*Acanthurus nigroris*	Bluelined Surgeonfish	maiko
Acanthuridae	*Zebrasoma veliferum*	Sailfin tang	maneoneo
Gobiidae	*Coryphopterus sp.*	Goby	oopu
Gobiidae	*Gnatholepis anjerensis*	Eyebar goby	
Balistidae	*Xanthichthys mento*	Crosshatch Triggerfish	
Diodontidae	*Diodon holocanthus*	Spiny Puffer	oopu okala

Over 63% of the total numerical abundance of fishes at Kure Atoll was composed of species with a high latitude correlation (Figure 5.8). The percentage of high latitude affinity individuals was also substantial at Midway Atoll (56%), Pearl and Hermes Atoll (52%) and Lisianski Island-Neva Shoals (53%). The major break occurs between Maro Reef and Gardner Pinnacle where the numerical abundance of high latitude affinity species dropping from 52% to 25% between these two locations. The lowest percentage of high latitude affinity individuals was observed at Nihoa Island (13%). There was a relatively large shift towards more high latitude affinity individuals between Nihoa and Mokumanamana (28%).

Twenty-one species were significantly and positively correlated ($p<0.05$) with low latitudes based on numerical density estimated on surveys conducted between 2000-2002 (Table 5.8). Only two of these species (9%) were endemics in contrast to the species with high latitude bias, where 54% were found to be endemic. Based on total numerical abundance, the highest percentage of low latitude species was observed at Mokumanamana

Table 5.8 Species with tropical affinity (negative correlation with latitude). Endemics in bold. Source: Friedlander et al., in prep.

FAMILY	TAXON NAME	COMMON NAME	HAWAIIAN NAME
Carcharhinidae	*Carcharhinus amblyrhynchos*	Gray Reef Shark	mano
Carcharhinidae	*Triaenodon obesus*	Whitetip Reef Shark	mano lalakea
Lutjanidae	*Aphareus furca*	Smalltooth Jobfish	wahanui
Lethrinidae	*Monotaxis grandoculis*	Bigeye Emperor	mu
Mullidae	*Parupeneus bifasciatus*	Doublebar Goatfish	munu
Mullidae	*Parupeneus multifasciatus*	Manybar Goatfish	moano
Chaetodontidae	***Chaetodon multicinctus***	**Multiband Butterflyfish**	**kikakapu**
Chaetodontidae	*Chaetodon quadrimaculatus*	Fourspot Butterflyfish	lau hau
Pomacentridae	*Plectroglyphidodon imparipennis*	Brighteye Damselfish	
Cirrhitidae	*Paracirrhites arcatus*	Arc-eye Hawkfish	pili koa
Scaridae	*Calotomus carolinus*	Stareye Parrotfish	
Acanthuridae	*Acanthurus blochii*	Ringtail Surgeonfish	pualu

Table 5.8 (continued). Species with tropical affinity (negative correlation with latitude). Endemics in bold. Source: Friedlander et al., in prep.

FAMILY	TAXON NAME	COMMON NAME	HAWAIIAN NAME
Acanthuridae	*Acanthurus nigrofuscus*	Brown Surgeonfish	maiii
Acanthuridae	*Acanthurus olivaceus*	Orangeband Surgeonfish	naenae
Acanthuridae	*Naso lituratus*	Orangespine Unicornfish	umaumalei
Monacanthidae	***Cantherhines sandwichiensis***	**Squaretail Filefish**	**oili lepa**
Balistidae	*Melichthys niger*	Black Durgon	humuhumuelele
Monacanthidae	*Pervagor aspricaudus*	Lacefin Filefish	
Balistidae	*Rhinecanthus rectangulus*	Reef Triggerfish	humuhumunukunukuapuaa
Balistidae	*Sufflamen bursa*	Lei Triggerfish	humuhumulei
Tetraodontidae	*Canthigaster amboinensis*	Ambon Toby	

(28%) and Nihoa (14%; Figure 5.8). Less than 1% of the number density of fishes counted at Midway consisted of species with a low latitude preference. Similarly, Kure Atoll (1.2%) Pearl and Hermes Atoll (2.0%) and Lisianski Island-Neva Shoals (3.2%) had low numbers of more tropical affinity individuals.

There is a strong positive linear relationship between the percentage of individuals with temperate/subtropical affinities and latitude (Table 5.9, Figure 5.9), while there is a strong negative linear relationship with the percentage of individuals with tropical affinities and latitude (Table 5.10, Figure 5.9). A major faunal break occurred around Maro and Laysan, where the numerical abundance of northern and southern affinity species were more similar. Although species with northern affinities were still more abundant than species with southern affinities south of Maro, the overall numerical abundance of these northern species averaged 23% south of Maro, but 54% to the north. Species with tropical affinities account for 17% of fish numbers south of Maro, but only 4% to the north.

Table 5.9. Least squares linear regression model for species exhibiting temperate/subtropical affinity and latitude. Source: Friedlander et al., in prep.

ANALYSIS OF VARIANCE				
Source	**DF**	**Mean Square**	**F Ratio**	**Prob > F**
Model	1	0.20	33.57	0.0004
Error	8	0.01		
C. Total	9			
PARAMETER ESTIMATES				
Term	**Estimate**	**Standard Error**	**t Ratio**	**Prob>|t|**
Intercept	-1.57	0.34	-4.57	0.0018
Latitude	0.08	0.01	5.79	0.0004

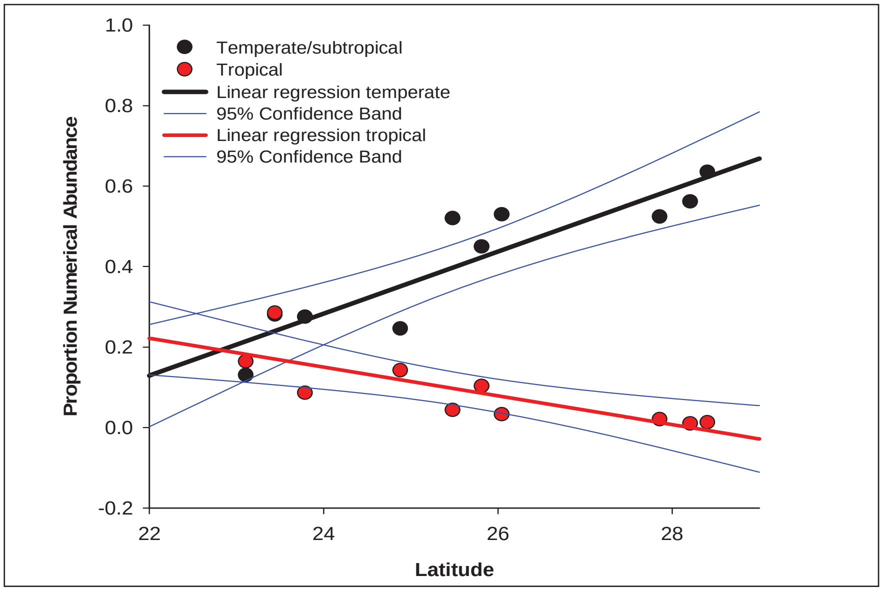

*Figure 5.9. Relationship between latitude and numerical abundance of species with temperate/subtropical and tropical affinities. Results of least squares linear regression. Temperate/subtropical = -1.56 + 0.07*Latitude, Tropical = 1.00 - 0.03*Latitude. Source: Friedlander et al., in prep.*

Fish Recruitment

The planktonic dispersal of reef fishes is an important process linked to the persistence of benthic reef populations. Recruitment of reef fishes increased with latitude, and was especially pronounced at the four northernmost reefs that had a larger proportion of YOY recruits (DeMartini and Friedlander, 2004). During 2000-2002, 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 (Figure 5.10; DeMartini and Friedlander, 2004). YOY recruit length frequencies did not differ for most species between northern and southern reefs, suggesting that a seasonal lag in spawning and recruitment at higher latitudes cannot explain the greater YOY densities observed there. Disproportionate recruitment at higher-latitude reefs may be related to higher levels of within-reef and regional reseeding at higher latitudes. This was first indicated by survey data collected during the 1990s at French Frigate Shoals and Midway (DeMartini et al., 2002; DeMartini, 2004). During this period, there was consistently higher recruitment of YOY life stages of fishes at Midway Atoll versus French Frigate Shoals despite the generally greater densities of older-stage fishes at French Frigate Shoals (Figure 5.11).

Table 5.10. Least squares linear regression model for species with tropical affinity and latitude. Source: NWHI RAMP, unpub. data.

ANALYSIS OF VARIANCE				
Source	**DF**	**Mean Square**	**F Ratio**	**Prob > F**
Model	1	0.04	14.17	0.0055
Error	8	0.01		
C. Total	9			
PARAMETER ESTIMATES				
Term	**Estimate**	**Standard Error**	**t Ratio**	**Prob>|t|**
Intercept	1.01	0.24	4.12	0.0033
Latitude	-0.04	0.01	-3.76	0.0055

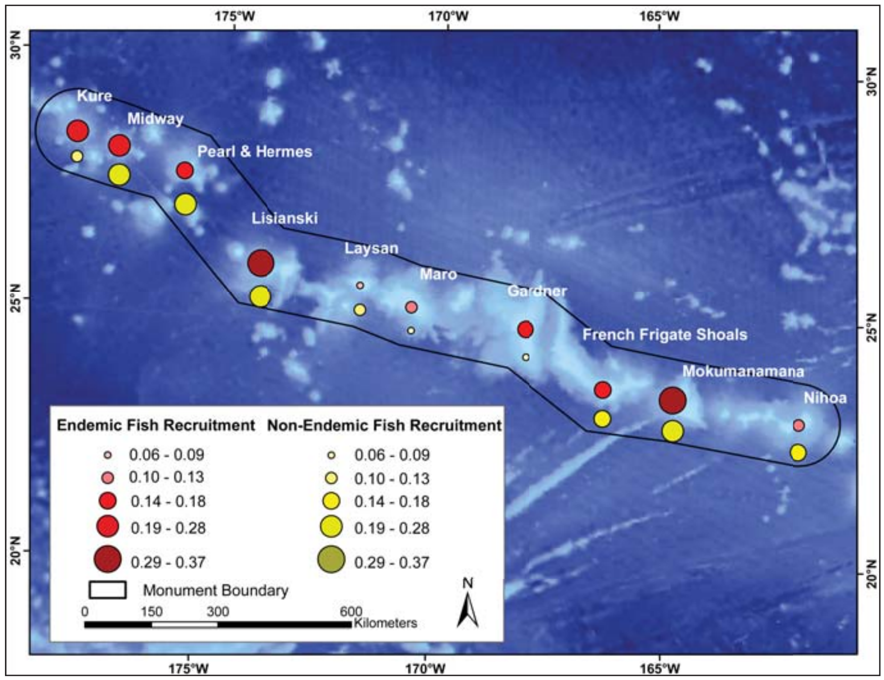

Figure 5.10. Geographic patterns of the Recruit Index (ratio of YOY sized to larger individuals) for all pooled major species of endemic and non-endemic reef fishes. Source: DeMartini and Friedlander, 2004; map: L. Wedding.

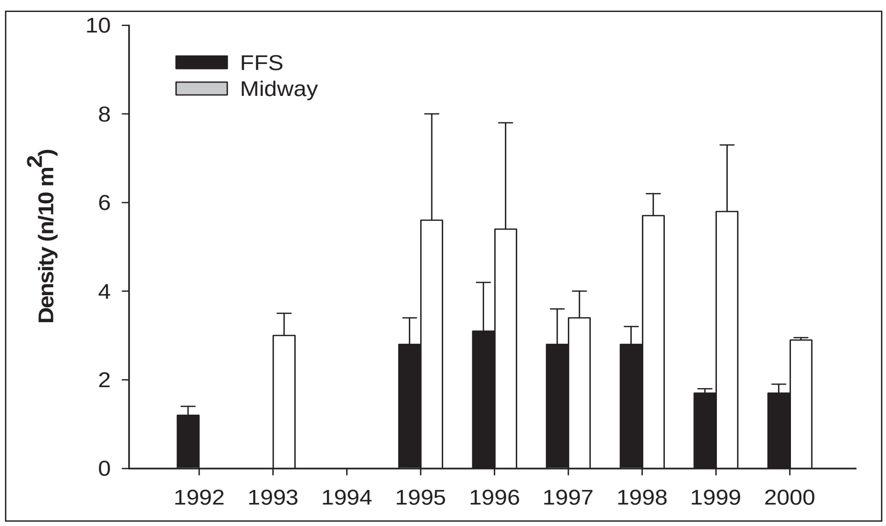

Figure 5.11. Time series of the estimated mean numerical density of YOY of all taxa at French Frigate Shoals and Midway during each survey year. Each vertical bar represents one southeast of the estimated survey year grand mean for both major habitats. Source: DeMartini, 2004.

GENERAL FISH ASSEMBLAGE STRUCTURE

Dominance by species was revealed by plotting relative percent contribution by each species to total biomass at each reef. A limited number of species accounted for the majority of the biomass for most locations. Giant trevally (ulua, *Caranx ignobilis*) was the dominant species by weight at Lisianski (50% of total biomass), Pearl and Hermes (43%), Laysan (32%) and Maro (30%; Figure 5.12). Chub (nenue, *Kyphosus* spp.) is the most dominant taxa by weight at Nihoa and accounts for 35% of the biomass.

The similarity of fish assemblages among reefs in the NWHI was compared based on biomass density for each species at each reef (Figures 5.13, 5.14). Two atolls (Kure and Midway) had high concordance and formed a distinct cluster relative to all other islands. The two basalt islands (Nihoa and Mokumanamana) were also distinct in their fish assemblages while Gardner Pinnacles, the other basalt rock, was unique in its fish assemblage based on biomass. Pearl and Hermes and Lisianski were the most similar based on fish assemblage biomass but also cluster at lower levels with Maro, Laysan, and to a lesser extent, French Frigate Shoals.

Similarity based on numerical abundance showed two distinct clusters with Nihoa being an extreme outlier (Figures 5.15, 5.16). Midway and Pearl and Hermes exhibited similar assemblage structure, as did French Frigate Shoals with Maro, and Kure with Lisianski. Mokumanamana, Gardner, and to a lesser extent, Laysan, exhibited similar assemblage structure but were less correlated than those in the other cluster. Nihoa was unique in its assemblage structure based on numerical abundance.

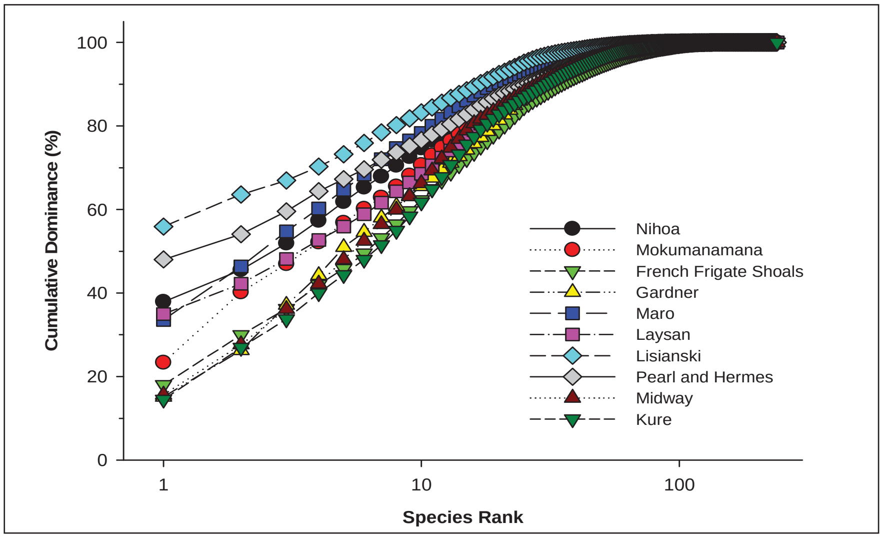

Figure 5.12. Ordinary dominance curve for each reef based on biomass. Source: NWHI RAMP, unpub. data.

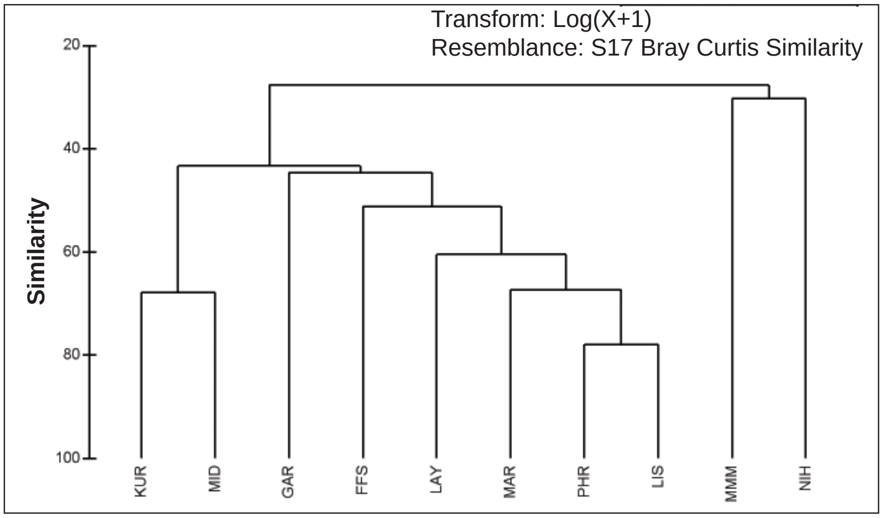

Figure 5.13. Bray Curtis similarity dendrogram showing similarities among reef based on biomass. Source: NWHI RAMP, unpub. data.

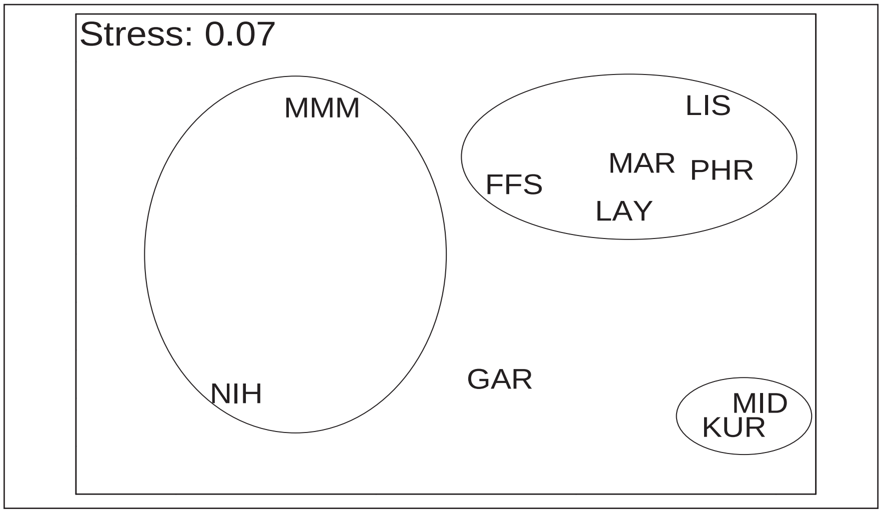

Figure 5.14. Nonmetric multi-dimensional scaling plot of reef similarities derived from biomass abundance of species. Similarities based on Bray-Curtis Similarity Index. Biomass abundance ln(x+1) transformed. Source: NWHI RAMP, unpub. data.

Trophic Structure

Overall, apex predators accounted for 47% of total fish biomass, followed by herbivores (31%) and secondary consumers (22%). Pearl and Hermes had the highest percentage of apex predators (67%), with French Frigate Shoals (61%) and Lisianski-Neva Shoal (58%) also having substantial apex predator biomass (Figure 5.17). More than 65% of the apex predator biomass observed within the NWHI consisted of giant trevally.

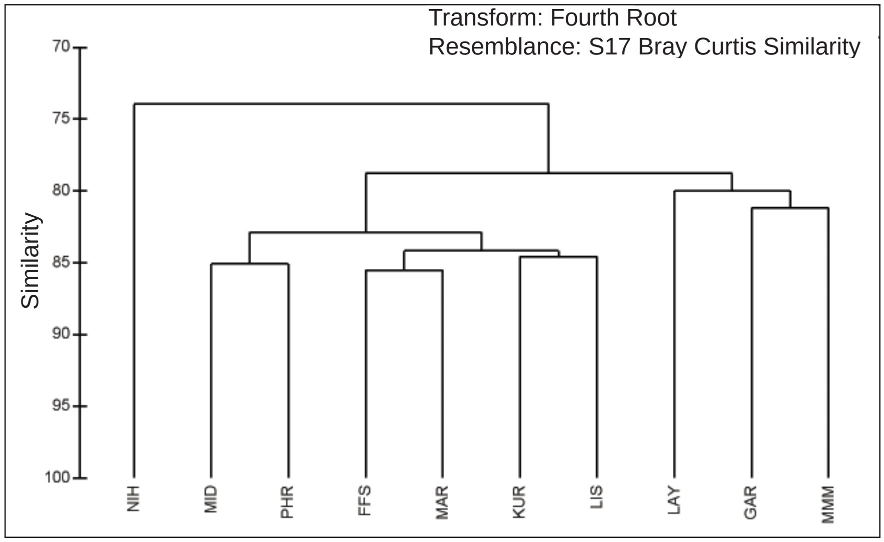

Figure 5.15. Bray Curtis similarity dendrogram showing similarities among reef based on numerical abundance. Source: NWHI RAMP, unpub. data.

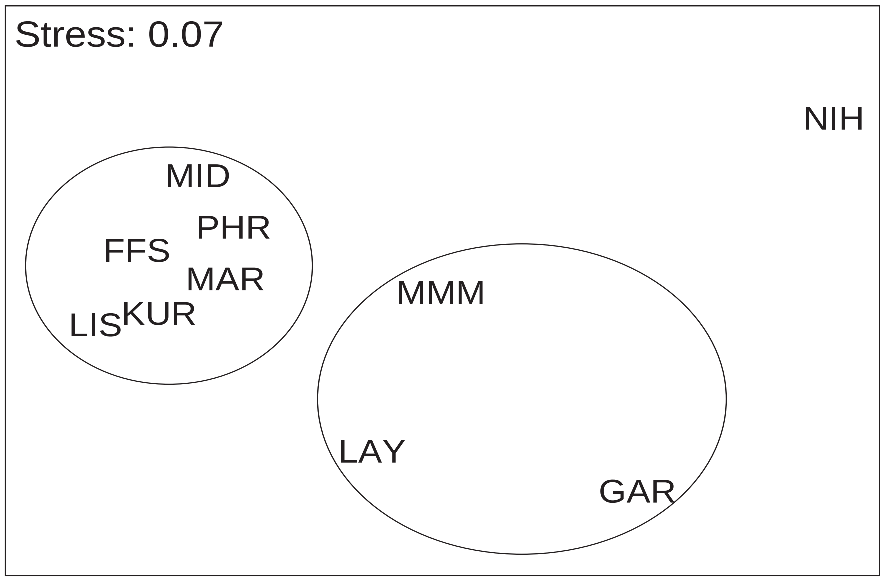

Figure 5.16. Nonmetric multi-dimensional scaling plot of reef similarities derived from numerical abundance of species. Similarities based on Bray-Curtis Similarity Index. Numerical abundance fourth root transformed. Source: NWHI RAMP, unpub. data.

Apex predator biomass increases up the chain reaching a maximum at Pearl and Hermes Atoll before declining dramatically at Midway and Kure atolls (Figure 5.17; DeMartini and Friedlander, 2004). The extremely low biomass of apex predators at Midway and Kure has been attributed to previous extractive fishing activities at both locations as well as a tag-and-release recreational sport fishery at Midway (DeMartini et al., 2002; DeMartini et al., 2005).

Herbivores were dominant in terms of biomass at Nihoa (56%) and Midway (56%). Chubs accounted for most of the herbivore biomass at Nihoa while the endemic spectacled parrotfish (*Chlorurus perspicillatus*) was most predominant at Midway and Kure. The lowest total biomass was recorded at Mokumanamana (0.45 t ha^{-1}) while Pearl and Hermes had the lowest percentage of herbivores (11%). Secondary consumer biomass ranged from a high at Midway (0.91 t ha^{-1}) and Pearl and Hermes (0.89 t ha^{-1}) to a low at Mokumanamana (0.26 t ha^{-1}). The saddle wrasse was the dominant species among secondary consumers at both Midway and Pearl and Hermes.

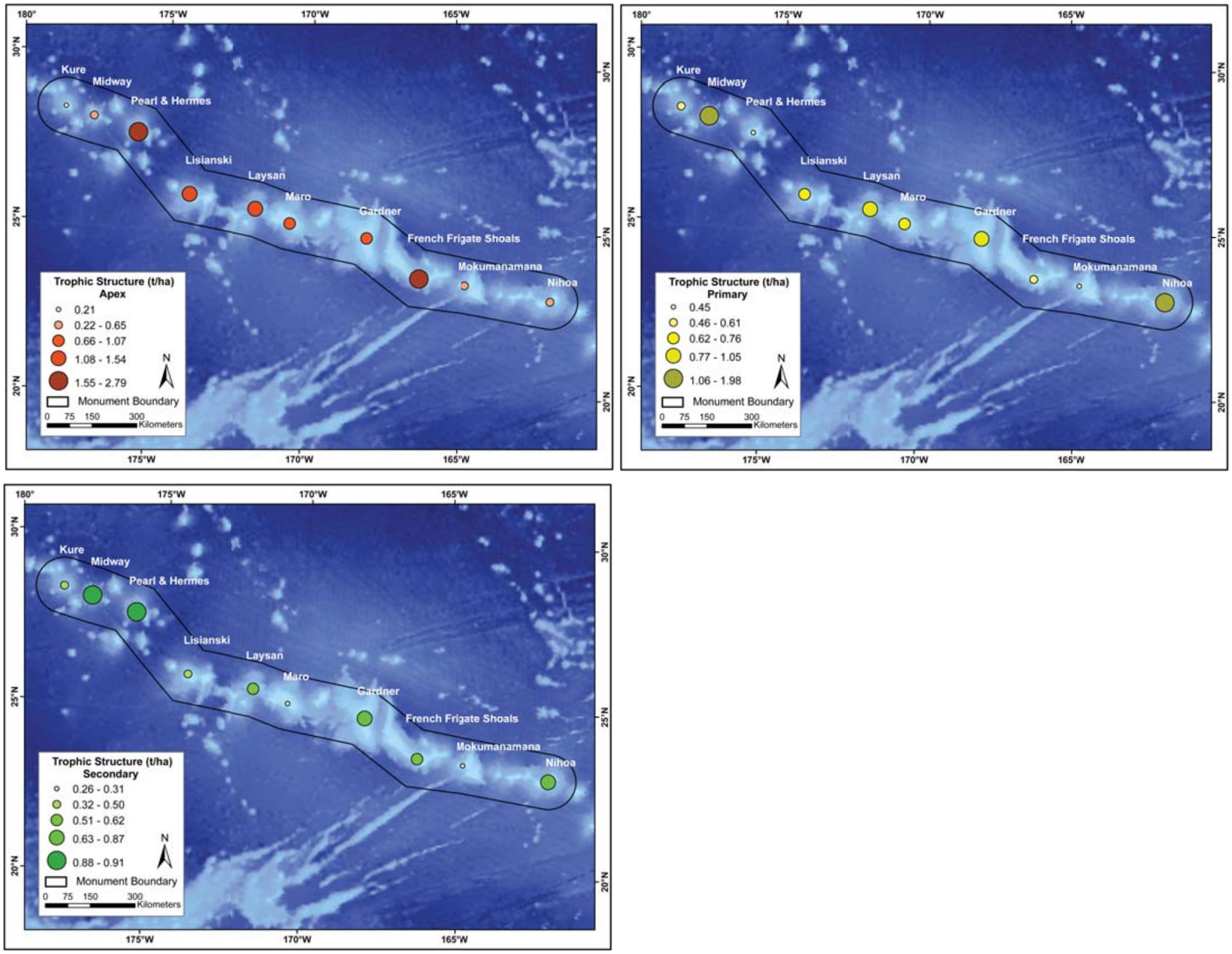

Figure 5.17. Percent biomass by consumer groups at each reef. Bubbles are proportional to total biomass (t ha^{-1}). Source: NWHI RAMP, unpub. data.

Biomass Size Spectra

Biomass densities of pooled taxa were evaluated as size spectra relative to standardized length classes; our analysis revealed that there were relatively more and greater numbers of large individual fish at Pearl and Hermes and French Frigate Shoals than elsewhere in the NWHI (Figure 5.18). Overall, biomass based on the intercept of the biomass-to-body size relation (i.e. abundance at the midpoint of the length distribution) was lowest at Kure, Mokumanamana and Nihoa (Figure 5.19).

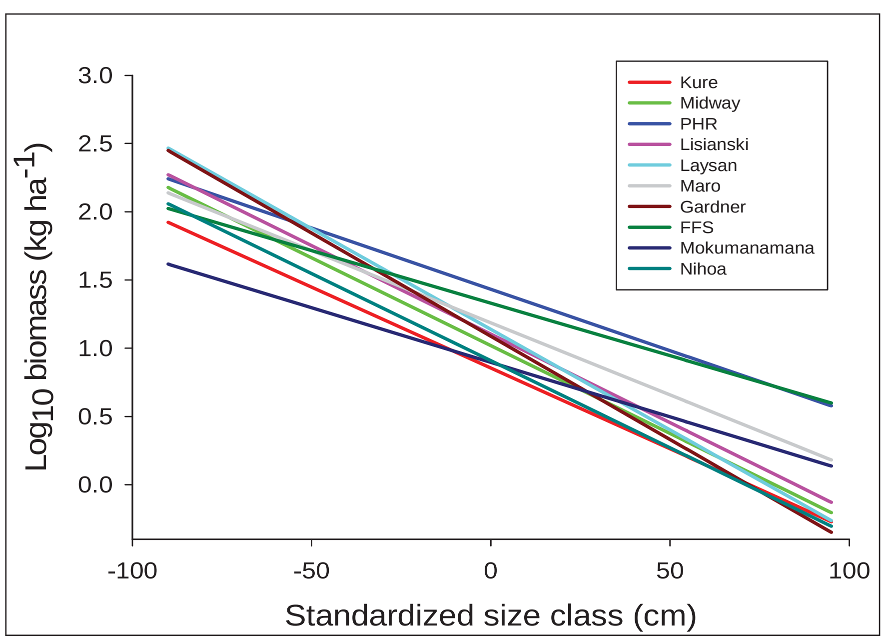

Figure 5.18. Biomass size spectra for all fishes greater than 15 cm at each of the major reefs in the NWHI. Source: NWHI RAMP, unpub. data.

Shark Distribution Patterns

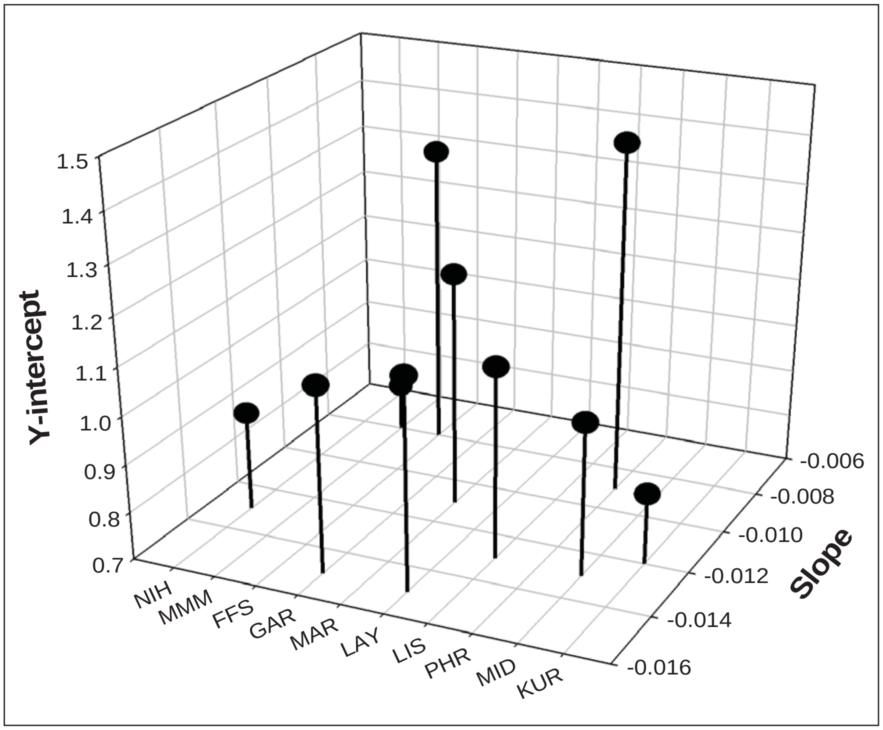

Figure 5.19. Plot of slope and y-intercept from size spectra regressions. Source: NWHI RAMP, unpub. data.

Sharks are an important component of the reef fish assemblage in the NWHI accounting for 28% of apex predator biomass and 13% of total reef fish biomass on the fore reef. Grey reef (*Carcharhinus amblyrhynchos*, 8.4%), Galapagos (*Carcharhinus galapagensis*, 10.2%; Figure 5.20) and whitetip reef sharks (*Triaenodon obesus*, 8.6%; Figure 5.20) comprised similar percentages of total apex predator biomass while blacktip reef sharks (*Carcharhinus melanopterus*) were much less abundant than the other three species and comprised only 0.3% of total biomass and 0.6% of apex predator biomass in the fore reef habitats. The biogeographic distribution patterns of gray reefs and Galapagos sharks were markedly different within the NWHI (Figure 5.21). Gray reef sharks were replaced by Galapagos sharks moving northward along the NWHI chain. Galapagos sharks are less abundant at Nihoa, Mokumanamana, and French Frigate Shoals but are very abundant northwest of Gardner Pinnacles. Gray reefs become less abundant northward. Papastamatiou et al. (2006) examined data from the Hawaii Shark Control Program between 1967 and 1980 and found Galapagos and tiger sharks (*Galeocerdo cuvier*) to be more abundant in the NWHI compared to the MHI, while sandbar sharks (*Carcharhinus plumbeus*) were more common in the MHI compared with the NWHI. These data showed gray reef sharks were more numerous in the NWHI compared with the MHI. Within the NWHI, this species was more abundant at Mokumanamana and French Frigate Shoals at the lower end of the NWHI and less abundant at the northern reefs of Maro and Midway. Interspecific competition, owing to dietary overlap, perhaps influences the distribution of these sharks throughout the Hawaiian Islands (Papastamatiou et al., 2006).


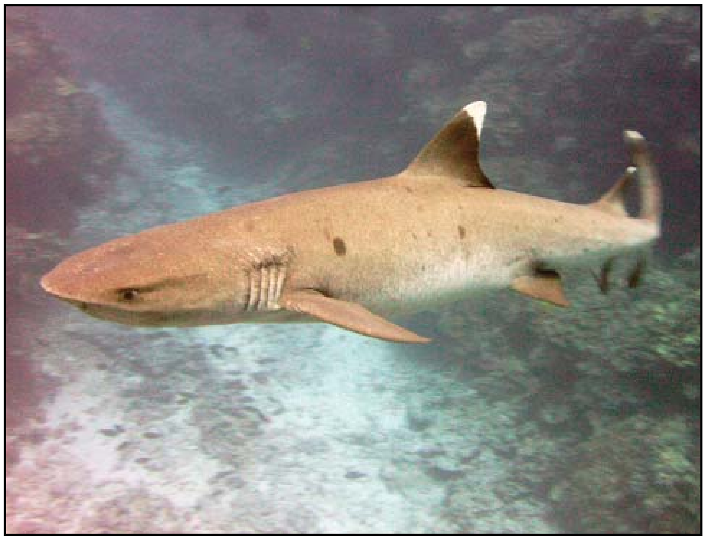

Figure 5.20. Galapagos sharks (left) and a whitetip shark (right). Photos: J. Maragos and A. Friedlander.

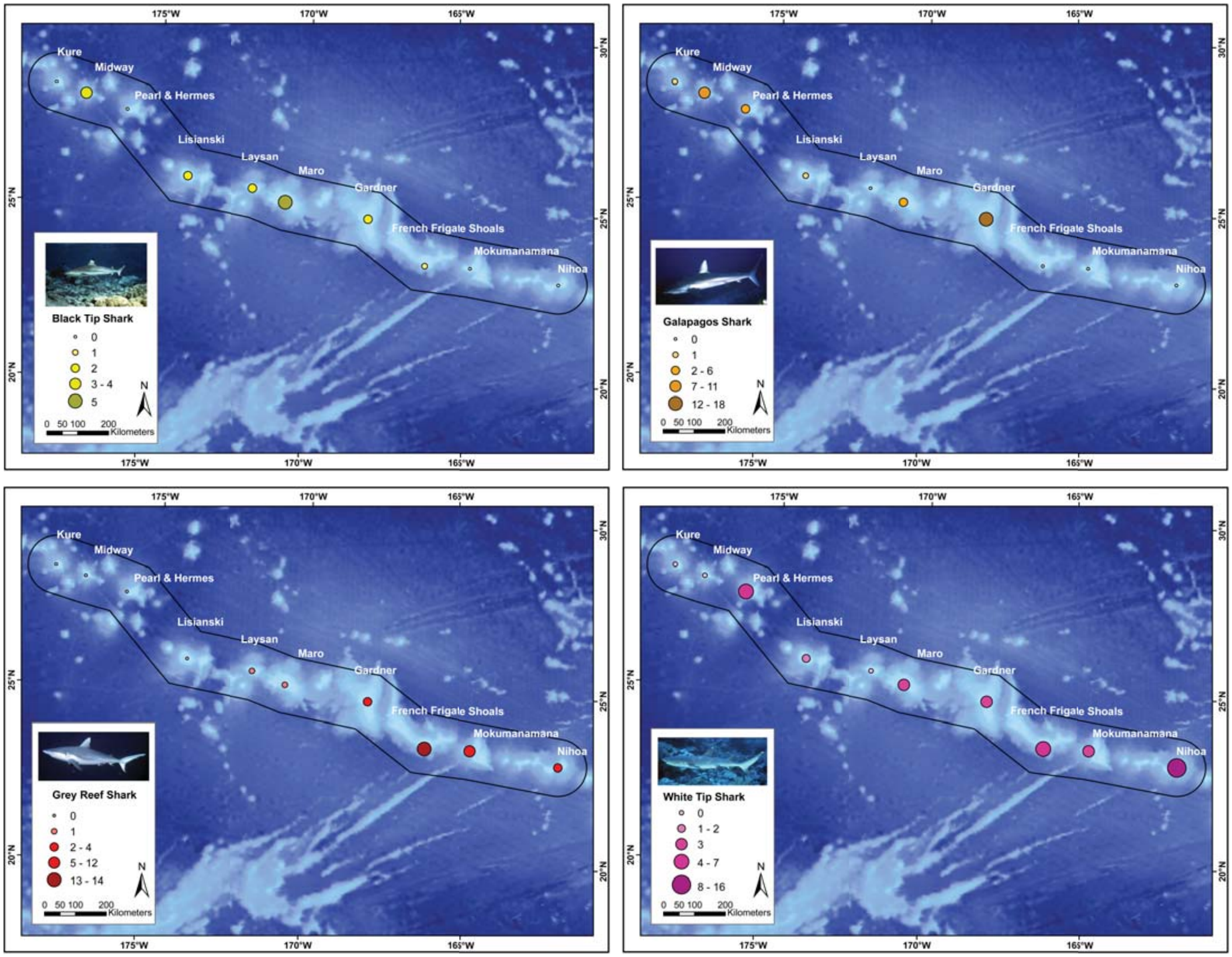

Figure 5.21. Biogeographic distribution of sharks in the NWHI based on number of individuals ha^{-1}. Values are numbers ha^{-1} and are for fore reef habitats only. Source: NWHI RAMP, unpub. data.

Influence of Influence of Predators on Prey Fishes

The effects of apex predation, primarily by giant trevally, are pervasive. Apex predators structure prey population sizes and age distributions and strongly influence the reproductive and growth dynamics of other harvested species (such as parrotfish) as well as smaller-bodied, lower-trophic-level fishes on shallow NWHI reefs (DeMartini and Friedlander, 2006). 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 (Figure 5.22; DeMartini et al., 2005).

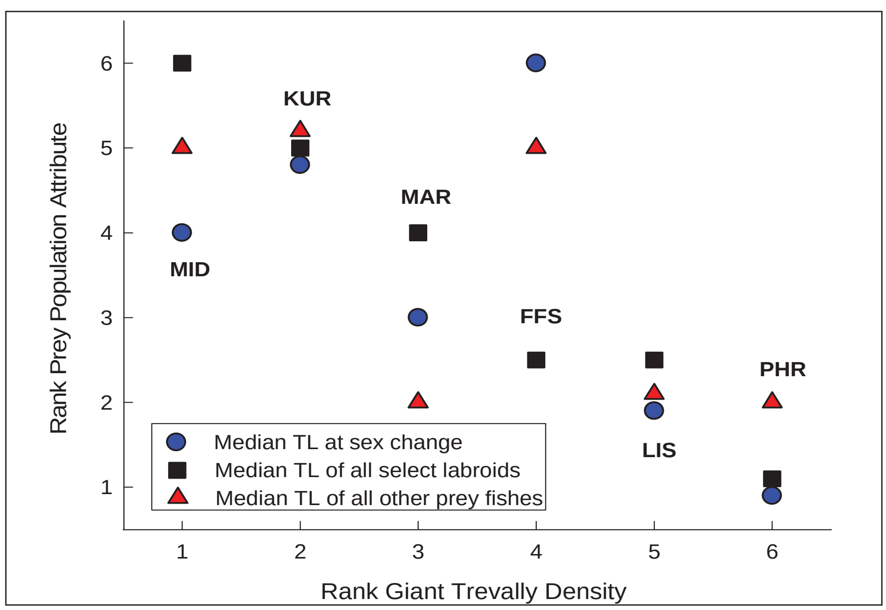

Figure 5.22. Scatterplot of the ranks of prey population attributes (median body length at sex change in the four major labroid species, median body lengths of all eight select species of labroids, and median body length of all other prey fishes) versus the ranks of giant trevally densities. Source: Demartini et al., 2005.

DeMartini (2004) documented the habitat-specific spatial distributions of juvenile and other small-bodied fishes particularly susceptible to predation and recognized the importance of back reef, lagoon patch reef and other sheltered (wave-protected) habitats as nursery areas for juvenile reef fishes (Figure 5.23). This study, based on re-analyses of data collected at French Frigate Shoals and Midway Atoll during the 1990s, has contributed substantially to development of both “essential fish habitat” and “habitat areas of particular concern” concepts in recognizing the greater per-unit-area value of atolls due to their larger proportion of sheltered juvenile nursery habitats (DeMartini, 2004).

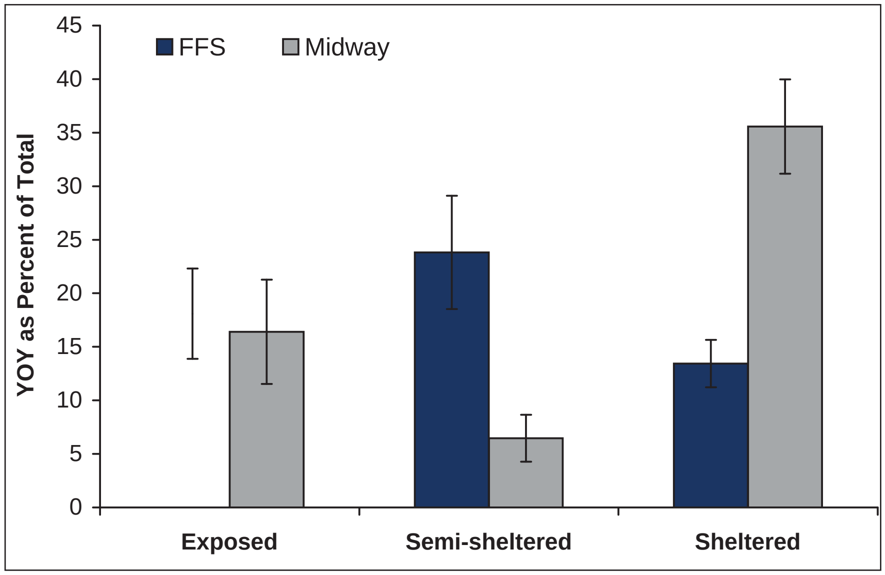

Figure 5.23. Percentage contribution of YOY to overall YOY plus older-stage densities. Source: adapted from DeMartini, 2004.

Updated Comparison of Fish Assemblage Metrics Among NWHI Reefs

Based on data collected from initial surveys in 2000, 2001, 2002 and new sites surveyed in 2007, fish assemblage characteristics were compared among all reefs. Fish species richness appeared highest at Nihoa, Gardner and Laysan and lowest at Mokumanamana, Maro and Kure but these differences were not significant (Table 5.11, Figure 5.24). The number of individual fishes observed on transects differed significantly different among reefs (Table 5.12, Figure 5.25,). Midway, followed by Pearl and Hermes had the highest number of individuals while Mokumanamana and Maro had the lowest. Biomass also differed significantly different among reefs (Table 5.13, Figure 5.26; $F_{9,409} = 3.64$, $p < 0.001$) with the highest biomass at Gardner, Nihoa and Pearl and Hermes. The lowest fish biomass was recorded at Kure and Mokumanamana.

Table 5.11. Fish species richness Analysis of Variance among reefs. Source: NWHI RAMP, unpub. data.

SOURCE	DF	SUM OF SQUARES	MEAN SQUARE	F RATIO	PROB > F
Reef	9	686.699	76.3	1.64	0.1005
Error	400	18548.44	46.37		
C. Total	409	19235.14			

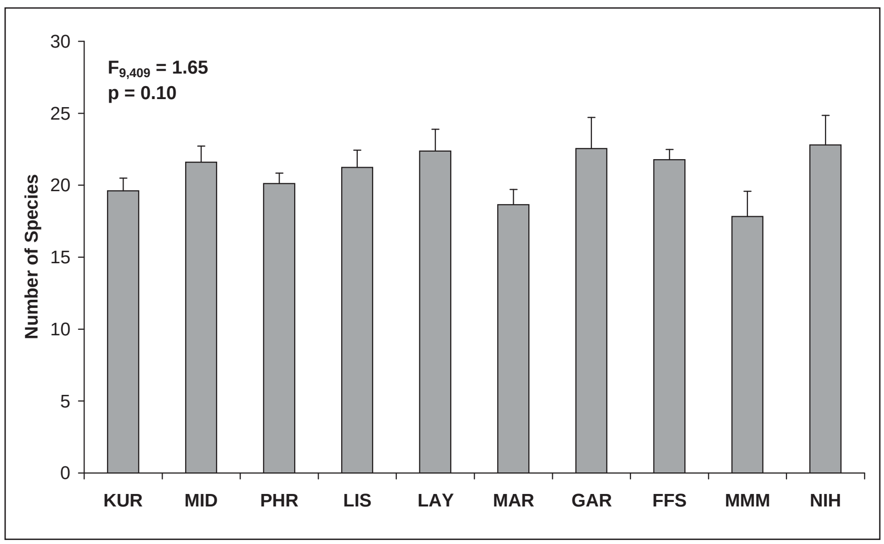

Figure 5.24. Mean species richness per transect from REA data from 2000-2002 and 2007. Error bars are standard error of the mean. Source: NWHI RAMP, unpub. data.

Table 5.12. Fish biomass in t ha-1 (ln[x+1]) Analysis of Variance among reefs. Comparisons for all pairs using Tukey-Kramer HSD. Levels not connected by same letter are significantly different. Source: NWHI RAMP.

ANALYSIS OF VARIANCE					
Source	**DF**	**Sum of Squares**	**Mean Square**	**F Ratio**	**Prob > F**
Reef	9	6.78	0.75	6.18	<.0001
Error	400	48.80	0.12		
C. Total	409	55.58			
Level	**Multiple Comparisons**	**Mean**			
Midway	A	1.20			
PHR	AB	0.99			
Lisianski	BC	0.87			
FFS	BC	0.86			
Gardner	ABC	0.83			
Kure	BC	0.83			
Laysan	BC	0.83			
Nihoa	BC	0.81			
Maro	BC	0.79			
MMM	C	0.58			

Table 5.13. Fish biomass in t ha-1 (ln[x+1]) Analysis of Variance among reefs. Comparisons for all pairs using Tukey-Kramer HSD. Levels not connected by same letter are significantly different. Source: NWHI RAMP.

ANALYSIS OF VARIANCE					
Source	**DF**	**Sum of Squares**	**Mean Square**	**F Ratio**	**Prob > F**
Reef	9	9.30	1.03	3.64	0.0002
Error	400	113.64	0.28		
C. Total	409	122.93			
Level	**Multiple Com-parisons**	**Mean**			
Gardner	AB	1.26			
Lisianski	A	1.14			
Laysan	AB	1.13			
Midway	A	1.12			
Nihoa	AB	1.11			
PHR	A	1.09			
FFSs	A	1.01			
Maro	AB	0.97			
MMM	AB	0.74			
Kure	B	0.70			

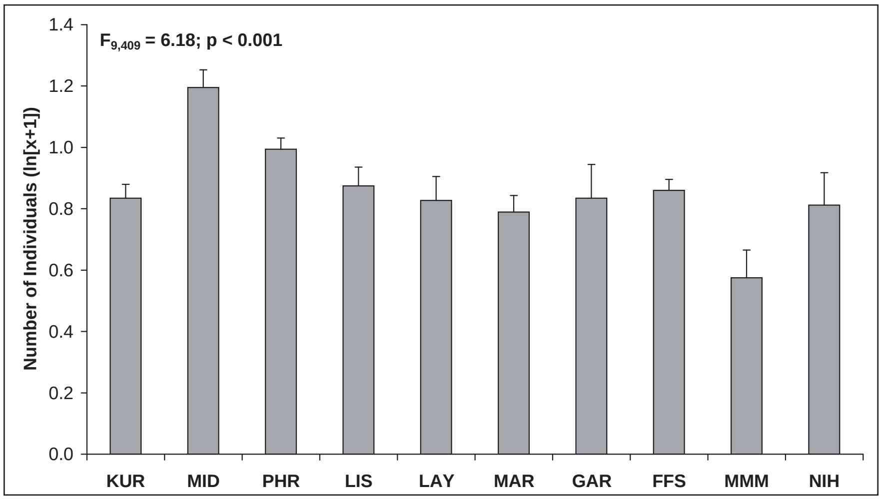

Figure 5.25. Mean number of individuals per transect from REA data from 2000-2002 and 2007. Error bars are standard error of the mean. Source: NWHI RAMP, unpub. data.

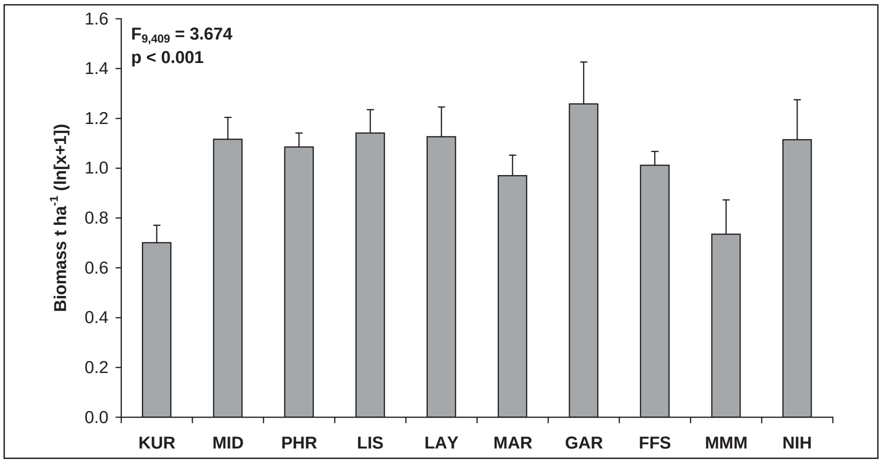

Figure 5.26. Mean biomass in t ha-1 (ln[x+1]) per transect from REA data from 2000-2002 and 2007. Error bars are standard error of the mean. Source: NWHI RAMP, unpub. data.

Comparisons of fish assemblage characteristics among reefs in the NWHI revealed Pearl and Hermes Atoll to have the highest average rank among the seven metrics examined (Table 5.14, Figure 5.27). Pearl and Hermes yielded the highest endemism, highest total biomass, and highest apex predator biomass among all reefs. Midway and French Frigate Shoals was second and third highest rank with Midway having the greatest number of individuals and French Frigate Shoals having the highest richness. Lisianski-Neva Shoals had the highest recruit index (ratio of YOY to older sized individuals).

Mokumanamana had the lowest rank integrated over all fish assemblage metrics and had the lowest number of species per transect and the lowest number of individuals per transect. Maro Reef and Kure Atoll also had low values for most fish assemblage metrics. Since all sampling was conducted within the boundaries of each Special Preservation Area (SPA), these rankings by reef should also serve as a ranking by SPA.

Table 5.14. Rank values for fish assemblage metrics among the 10 emergent reefs of the NWHI. Source: NWHI RAMP, unpub. data.

Reef	Endemism	Total Species	# Species	Number Individuals	Total Biomass*	Apex Predator Biomass	Mean Recruitment	Average Rank
Pearl and Hermes	10	9	4	9	10	10	6	8.29
Midway	7	8	6	10	9	3	8	7.29
French Frigate Shoals	5	10	7	7	8	8	5	7.14
Lisianski	9	2	5	8	4	9	10	6.71
Gardner	3	1	9	6	7	6	3	5
Laysan	4	5	8	4	5	7	1	4.86
Kure	8	7	3	5	2	1	7	4.71
Nihoa	1	4	10	3	6	2	4	4.29
Maro	6	6	2	2	3	5	2	3.71
Mokumanamana	2	3	1	1	1	4	9	3

**Total biomass excludes back reef and lagoon habitats to reduce bias and compares habitat types.*

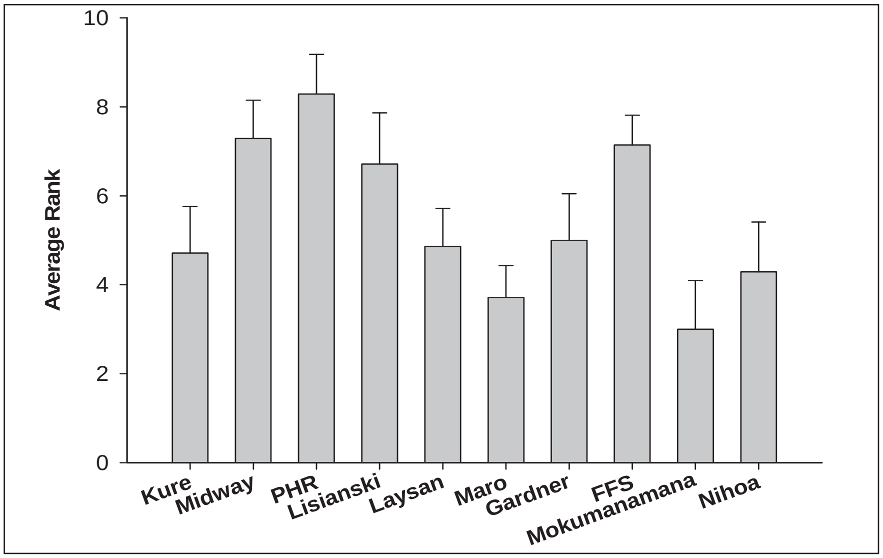

Figure 5.27. Mean rank values for fish assemblage metrics among the 10 emergent reefs of the NWHI. Source: NWHI RAMP, unpub. data.

Comparisons with the MHI

The most conspicuous biological patterns observed in the NWHI was 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 (Figure 5.28). Also notable is the overall reduced numbers and biomass density of lower trophic level fishes in the MHI, including lower-level carnivores. Differences in fish biomass density between the MHI and NWHI represent both the severe depletion of apex predators from fishing and the heavy exploitation of other species, primarily lower trophic-level carnivores on shallow reefs of the MHI (Friedlander and DeMartini, 2002). Fish densities at less exploited sites (such as uninhabited Kahoolawe and no-take areas) within the MHI further reinforce the conclusions that these differences are caused by fishing. Recent comparisons of fish biomass and size structure among accessible sites and inaccessible sites near versus distant from population centers in the MHI further indicate that depressed MHI stocks are primarily the result of fishing rather than other anthropogenic stressors such as poorer habitat quality (Williams et al., 2008). 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 densities of reef fishes in the MHI (Friedlander and DeMartini, 2002; Friedlander and Brown, 2004). The differences in fish assemblage structure provide evidence of the high level of exploitation in the MHI. Further, the sharp contrast between the two areas in terms of fish density and composition provides a valuable perspective for developing ecosystem-level management of reef systems in the MHI and the NWHI (Friedlander and DeMartini, 2002).

Catalogue of the NWHI Fish Assemblages

We conclude this chapter with a characterization of the fish assemblages at each of the 10 NWHI reefs, ordered from from Nihoa Island to Kure Atoll. The assemblages at each reef are described in terms of three basic metrics (species richness and numerical and biomass densities), with the latter two metrics examined for dominant species.

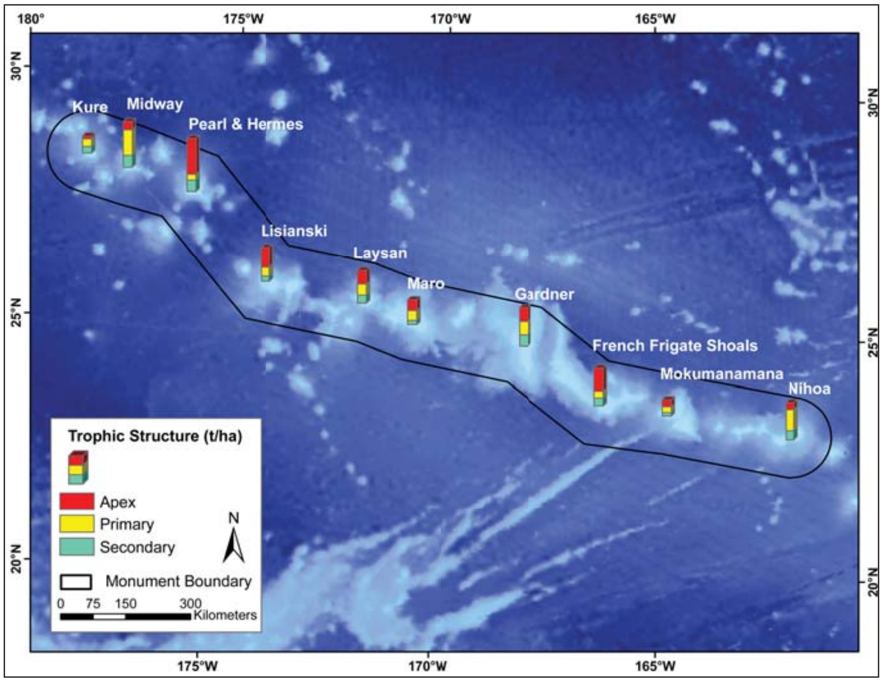

Figure 5.28. Comparisons of total biomass and biomass among consumer groups between the NWHI and MHI. Source: Friedlander and DeMartini, 2002.

Nihoa Island

Despite its small size (Figure 5.29), Nihoa Island ranked first overall in fish species richness per transect among all reefs surveyed in the NWHI. This is in contrast to the total species richness, which ranked amongst the lowest in the NWHI. High species richness is related to the proximity to MHI and our observation of the highest percentage of species with a tropical-biased distribution. Species richness ranged from to 36.6 to 8.6 ($\bar{x}$ =22.8, SD ± 11.02; Table 5.15, Figure 5.30).

Figure 5.29. Aerial image of Nihoa Island. Photo: J. Maragos.

Numerical abundance of fishes ranked eighth overall and ranged from 5.32 to 0.14 individuals m^{-2} ($\bar{x}$ =1.61, SD ± 1.57; Table 5.15, Figure 5.30). The blackfin chromis (*Chromis vanderbilti*), a planktivorous damselfish, comprised 35% of the total numerical density, followed by chubs (16%), and the brown surgeonfish (*Acanthurus nigrofuscus*, 6%). The highest species richness, biomass, and numerical abundance were observed off the leeward side of the island where high complexity basalt benches provided good quality habitat for a diversity of species of various sizes.

Table 5.15. Fish assemblage characteristics for Nihoa Island. Source: NWHI RAMP, unpub. data

LEVEL	NUMBER	MEAN	STD DEV	STD ERR MEAN	LOWER 95%	UPPER 95%
Species	11	22.8	11.02	3.32	15.4	30.21
Number of Individuals (m^2)	11	1.61	1.57	0.47	0.55	2.66
Biomass (t ha^{-1})	11	2.88	3.37	1.01	0.62	5.14

Biomass ranked fifth overall. Mean biomass per station was 2.88 t ha^{-1} (SD ± 3.37) and ranged from a high of 12.03 to a low of 0.39. Chubs accounted for 43% of the total biomass at Nihoa Island, followed by whitetip reef sharks (7%), the introduced blueline snapper (*Lutjanus kasmira*, 7%) and black durgons (*Melichthys niger*, 5.5%).

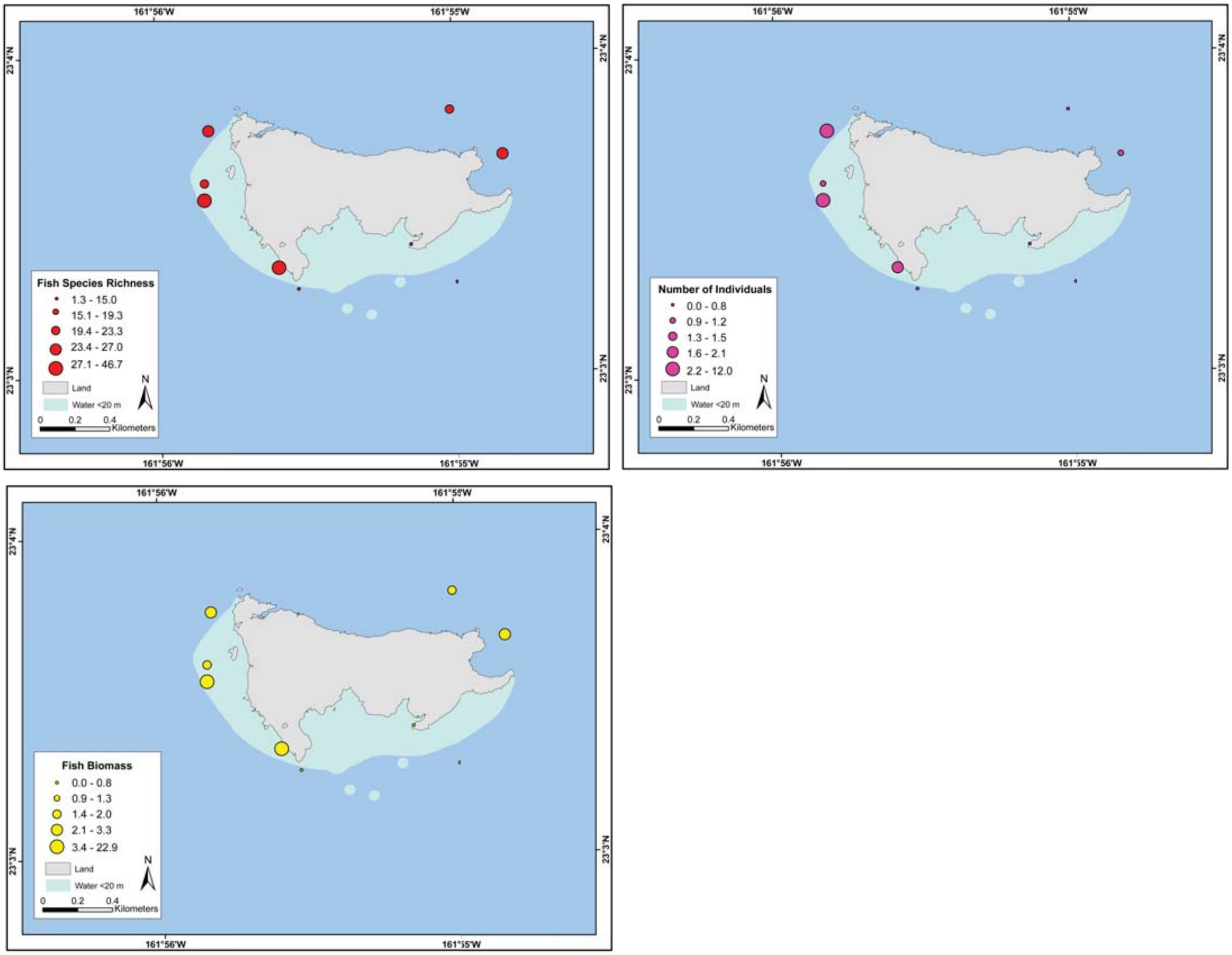

Figure 5.30. Fish assemblage characteristics for Nihoa Island. Species richness (top left), number of individuals (top right), and biomass (t ha^{-1}; bottom left). Source: NWHI RAMP, unpub. data; maps: L. Wedding.

Mokumanamana

Mokumanamana yielded the lowest species richness per transect ($\bar{x}$ =17.8, SD ± 4.45) among all reefs (Table 5.16, Figure 5.31, SD ± 4.45). Higher species richness was observed on the north-western portion of the island.

Table 5.16. Fish assemblage characteristics for Mokumanamana Island. Source: NWHI RAMP, unpub. data.

LEVEL	NUMBER	MEAN	STD DEV	STD ERR MEAN	LOWER 95%	UPPER 95%
Species	15	17.82	4.45	1.15	15.36	20.29
Number of Individuals (m^2)	15	0.81	0.35	0.09	0.61	1
Biomass (t ha^{-1})	15	1.25	1.06	0.27	0.67	1.84

Mokumanamana also had the lowest numerical density of fishes observed among reefs in the NWHI (0.81 individuals/m^2, SD±0.35) and ranged from 1.49 to 0.43. The planktivorous blackfin chromis accounted for 19% of total numerical density, followed by the saddle wrasse (*Thalassoma duperrey*,18%) and the orangeband surgeonfish (*Acanthurus olivaceus*, 10%). The low overall values for fish assemblage characteristics at Mokumanamana are likely the result of low habitat complexity where the majority of stations having extremely low relief. For example, Shark Bay, located on the northern portion of the island, exhibited substrate of flat planed surfaces as a result of scouring by surge and sediment suspension.

Fish biomass also ranked lowest at Mokumanamana. The distribution of biomass was extremely variable (CV = 0.85) but was highest off the points on the north and eastern parts of the island. Biomass ranged from 4.11 to 0.36 t ha^{-1} with a grand mean of 1.25 (SD ± 1.06). Apex predators accounted for 43% of the total biomass

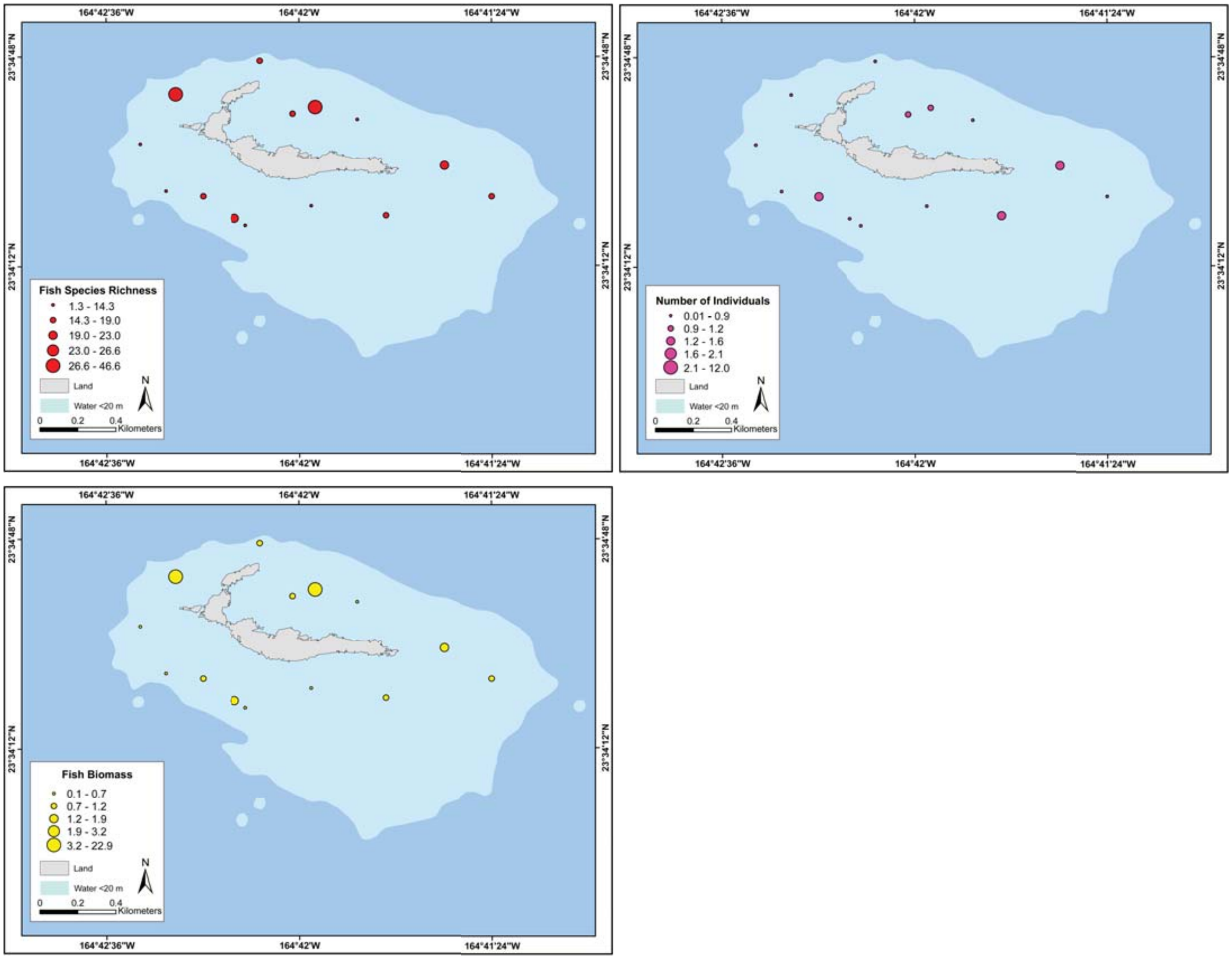

Figure 5.31. Fish assemblage characteristics for Mokumanamana. Species richness (top left), number of individuals (top right), and biomass (t ha^{-1}; bottom left). Source: NWHI RAMP, unpub. data; maps: L. Wedding.

and were dominated by grey reef sharks with 25% of total fish biomass. Other important contributors to fish biomass included orangeband surgeonfish (17%), black durgons (17%), giant trevally (6%) and whitetip reef sharks (5%).

French Frigate Shoals Fish

Species richness at French Frigate Shoals averaged 21.8 (SD ± 7.7) and was the forth highest among all reefs surveyed (Table 5.17, Figure 5.32). Fore reef habitats had the highest species richness ($\bar{x}$ = 26.1), followed by back reef ($\bar{x}$ = 20.7), and lagoon habitats ($\bar{x}$ = 19.3). Species richness tended to be higher on the windward fore reef (Table 5.18).

Table 5.17. Fish assemblage characteristics for French Frigate Shoals across all habitat types. Source: NWHI RAMP, unpub. data.

LEVEL	NUMBER	MEAN	STD DEV	STD ERR MEAN	LOWER 95%	UPPER 95%
Species	93	21.78	7.73	0.8	20.19	23.37
Number of Individuals (m^2)	93	1.69	1.83	0.19	1.31	2.07
Biomass (t ha^{-1})	93	2.28	2.22	0.23	1.83	2.74

Fish density ranged from 12.0 to 0.26 individuals/m^2 and averaged 1.69 (SD ± 1.8). Numerical abundance was highest in lagoon habitat (1.77 individuals/m^2) and was dominated by the domino damselfish (*Dascyllus albisella*, 9%), saddle wrasse (8%) and goldring surgeonfish (*Ctenochaetus strigosus*, 7%). Density was low-

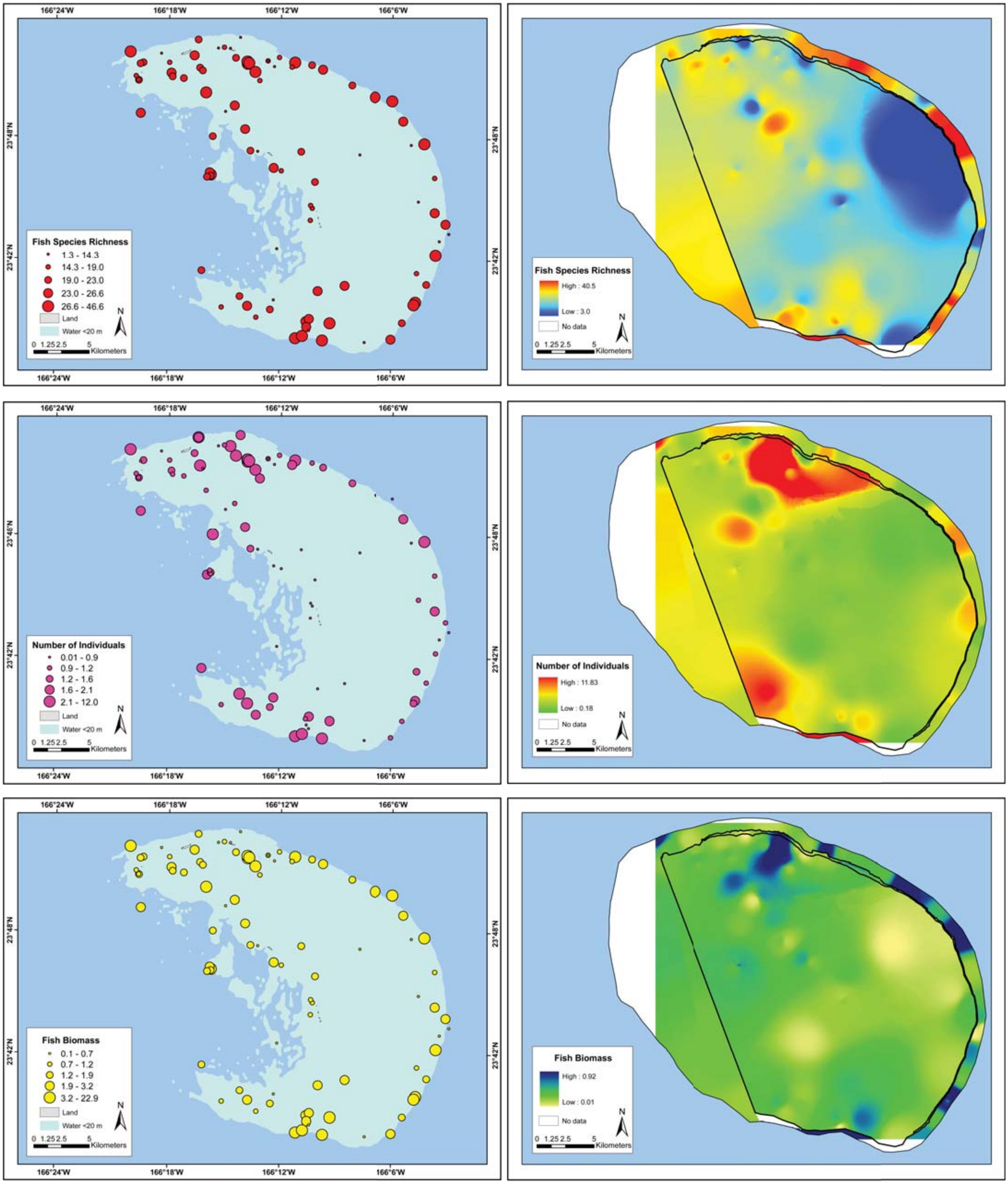

Figure 5.32. Fish assemblage characteristics for French Frigate Shoals: species richness (top row), number of individuals (middle row), and biomass (t ha^{-1}, bottom row). Source: NWHI RAMP, unpub. data; maps: L. Wedding.

est on the fore reef ($\bar{x}$ = 1.55 m^2), where the blackfin chromis and saddle wrasse each accounted for 10% of the total number of individuals. Numerical abundance on the back reef habitat ($\bar{x}$ = 1.55) was composed of the saddle wrasse (12%), the introduced blueline snapper (9%) and blackfin chromis (8%). The greatest number of individuals was observed at stations near Tern Island at the northern portion of the atoll and at the southern pass near Disappearing Island.

Table 5.18. Fish assemblage characteristics for French Frigate Shoals for each major habitat type. Source: NWHI RAMP, unpub. data.

BACK REEF	NUMBER	MEAN	STD DEV	STD ERR MEAN	LOWER 95%	UPPER 95%
Species	2	20.67	0.47	0.33	16.43	24.9
Number of Individuals (m^2)	2	1.55	0.68	0.48	-4.52	7.61
Biomass (t ha^{-1})	2	0.97	0.1	0.07	0.06	1.87
LAGOON						
Species	58	19.34	6.83	0.9	17.54	21.14
Number of Individuals (m^2)	58	1.77	2.16	0.28	1.2	2.34
Biomass (t ha^{-1})	58	1.87	1.72	0.23	1.42	2.33
FORE REEF						
Species	33	26.13	7.63	1.33	23.43	28.84
Number of Individuals (m^2)	33	1.56	1.12	0.19	1.16	1.96
Biomass (t ha^{-1})	33	3.08	2.8	0.49	2.09	4.08

Fish biomass density (t ha^{-1}) was highest on the fore reef ($\bar{x}$ = 3.08 t ha^{-1}) and was dominated by giant trevally (26%) and grey reef sharks (21%). French Frigate Shoals ranked third in total fore reef biomass among all locations. Species composition by weight in the lagoon ($\bar{x}$ = 1.87) primarily consisted of giant trevally (13%), followed by grey reef sharks (6%), the endemic spectacled parrotfish (6%) and bluespine unicornfish (*Naso unicornis*, 6%). The back reef habitat yielded the lowest biomass ($\bar{x}$ = 0.97) where giant trevally (25%), bluelined snappers (14%) and grey reef sharks (10%) comprised nearly half of the total biomass. Biomass was highest near Tern Island at the northern portion of the atoll and at the southern pass near Disappearing Island.

Gardner Pinnacles

A total of 10 stations were sampled for fishes at Gardner Pinnacles with the sampling effort representing a large portion of the hard bottom habitat less than 18.2 m in depth including windward and leeward exposures. Mean species richness was 22.5 (SD ± 6.5) with a range from 36 to 13.3 species per transect. Gardner ranked second in mean species richness even though total species richness was low (Table 5.19 and Figure 5.33).

Table 5.19. Fish assemblage characteristics for Gardner Pinnacles across all habitat types. Source: NWHI RAMP, unpub. data.

	NUMBER	MEAN	STD DEV	STD ERR MEAN	LOWER 95%	UPPER 95%
	10	22.55	6.48	2.05	17.91	27.19
	10	1.39	0.72	0.23	0.88	1.91
	10	2.99	2.11	0.67	1.48	4.5

Despite its small size, the biomass density of fishes at Gardner Pinnacles ranked fourth overall. Fish biomass ranged from 7.68 to 0. 29 t ha-1 ($\bar{x}$ = 2.99, SD ± 2.11; Table 5.19, Figure 5.33). Chubs dominated by weight, comprising 17% of the total fish biomass. This species was followed by bluefin trevally (*Caranx melampygus*, 11%) and grey reef sharks (10%). Highest biomass was observed off the northwest basalt pinnacle where large boulders formed a highly complex habitat with a vertical wall down to the reef pavement at 18.2 m. This station was dominated by bluefin (25%) and giant trevally (13%).

Fish density ranged from 2.88 to 0.62 individuals/m^2 ($\bar{x}$ = 1.39, SD ± 0.73). Chubs accounted for 16% of total numerical abundance, followed by saddle wrasse (9%), and oval chromis (*Chromis ovalis*, 7%). The drop-off at the northwest sea stack harbored a large number of planktivores including oval chromis and milletseed butterflyfish (*Chaetodon miliaris*). These two species comprised 32% of the numerical density of fishes at this station.

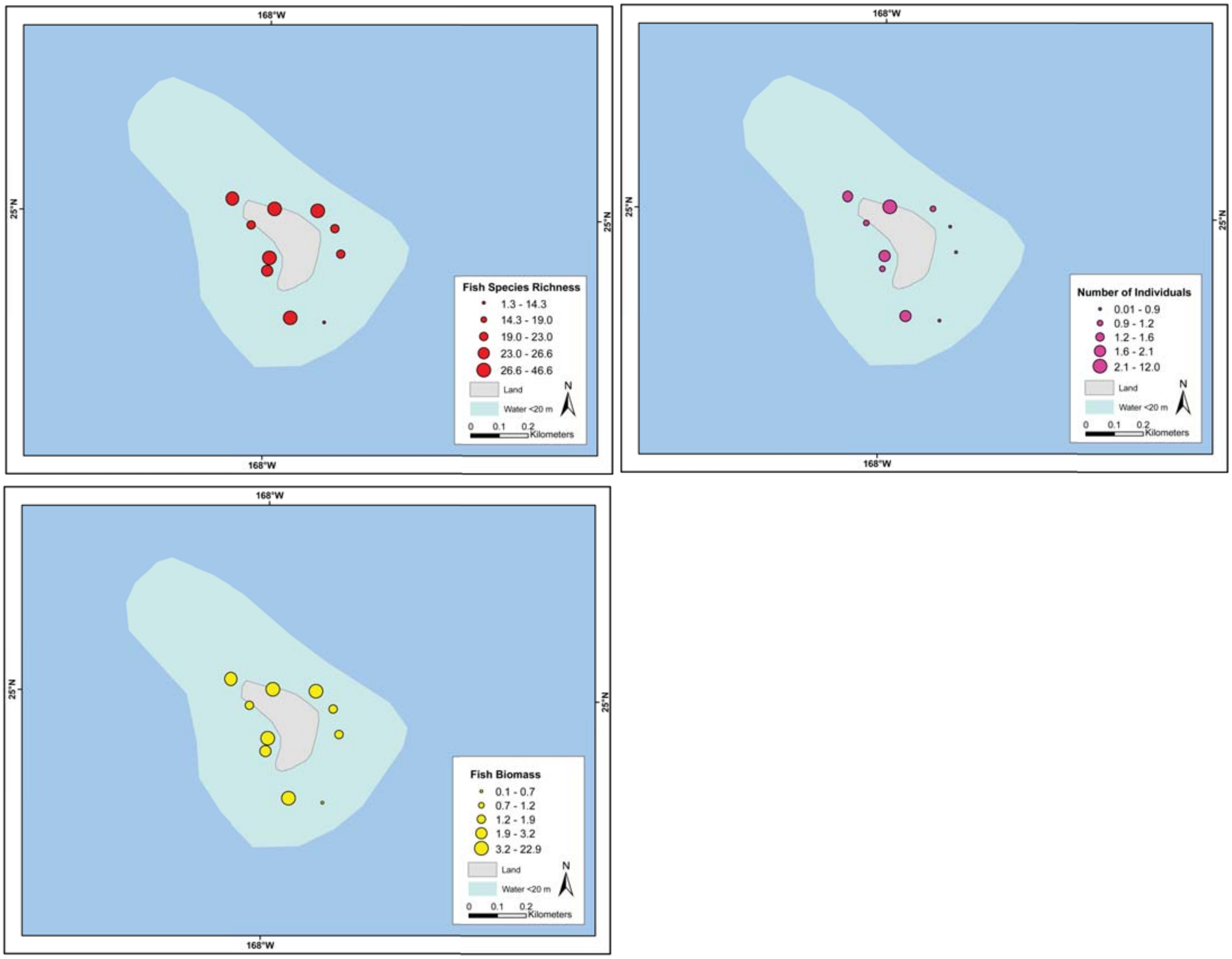

Figure 5.33. Fish assemblage characteristics for Gardner Pinnacles. Species richness (top left), number of individuals (top right), and biomass (t ha^{-1}; bottom left). Source: NWHI RAMP, unpub. data; maps: L. Wedding.

Maro Reef

Maro Reef was second only to Mokumanamana Island in having the lowest mean species richness observed on quantitative surveys (Table 5.20, Figure 5.34). Mean species richness was 18.6 (SD ± 4.6) and ranged from 27.67 to 12.56 per station. Relatively high species numbers were recorded at stations along the westernmost, leeward reef sections.

Table 5.20. Fish assemblage characteristics for Maro Reef across all habitat types. Source: NWHI RAMP, unpub. data.

LEVEL	NUMBER	MEAN	STD DEV	STD ERR MEAN	LOWER 95%	UPPER 95%
Species	42	18.65	4.58	0.71	17.22	20.08
Number of Individuals (m^2)	42	1.26	0.51	0.08	1.1	1.42
Biomass (t ha^{-1})	42	1.92	1.7	0.26	1.39	2.46

The number of individual fish observed on transects at Maro was also low compared with other reefs in the NWHI ($\bar{x}$ = 1.3, SD ± 0.5). Small resident species such as saddle wrasse (16%), Pacific Gregory (*Stegastes fasciolatus*,13%) and juvenile parrotfishes (11%) comprised much of the numerical density observed at Maro. Several stations on the windward, northeast side of the reef possessed higher numbers of individuals compared to other stations and were dominated by small juvenile parrotfishes.

Biomass also was low compared to most other locations and ranked second lowest after Mokumanamana Island. Biomass density ranged from 6.12 to 0.41 t m^{-2} ($\bar{x}$ = 1.9, SD ± 1.7); and similar to the observed richness

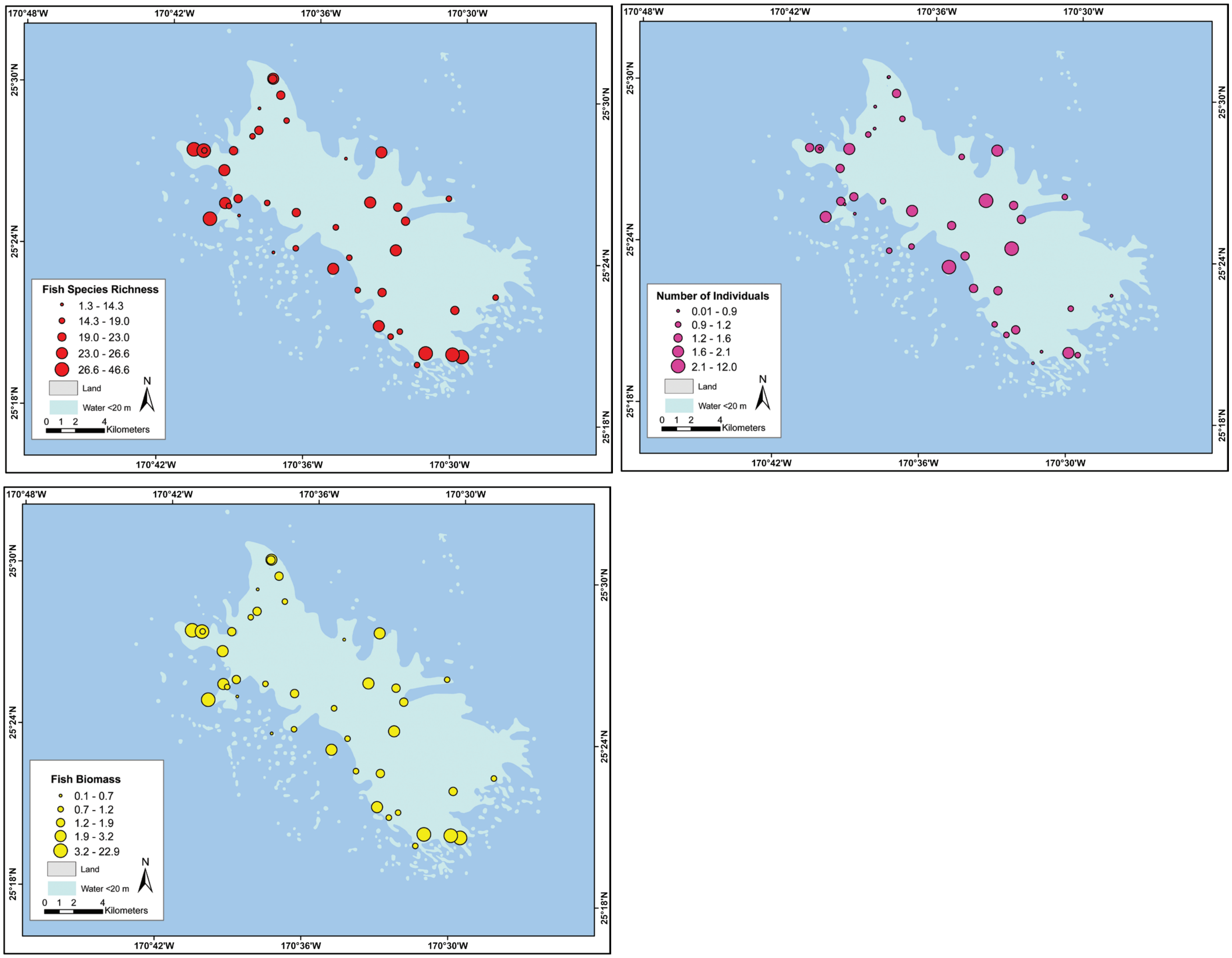

Figure 5.34. Fish assemblage characteristics for Maro Reef. Species richness (top left), number of individuals (top right), and biomass (t ha^{-1}; bottom left). Source: NWHI RAMP, unpub. data; maps: L. Wedding.

patterns, relatively high biomass was observed along the westernmost, leeward reef sections. More than 25% of the biomass at Maro Reef consisted of giant trevally, followed by spectacled parrotfish (11%), Galapagos sharks (7%), bullethead parrotfish (*Chlorurus sordidus*, 6%) and whitetip reef sharks (6%).

Laysan Island Fish

Laysan Island ranked third in mean species richness ($\bar{x}$ = 22.4, SD ± 5.2; Table 5.21, Figure 5.35), ranging from 32.7 to 13.3. The highest species richness occurred on the windward fore reef, off the northeast corner of the island.

Table 5.21. Fish assemblage characteristics for Laysan Island across all habitat types. Source: NWHI RAMP, unpub. data.

LEVEL	NUMBER	MEAN	STD DEV	STD ERR MEAN	LOWER 95%	UPPER 95%
Species	20	22.37	5.19	1.16	19.94	24.79
Number of Individuals (m^2)	20	1.34	0.53	0.12	1.1	1.59
Biomass (t ha^{-1})	20	2.55	2.09	0.47	1.58	3.53

Numerical abundance ranged from 2.46 to 0.42 individuals m^{-2} ($\bar{x}$ = 1.3, SD ± 0.5) and was dominated by saddle wrasses (18%), followed by convict tangs (*Acanthurus triostegus*, 11%), and Pacific Gregory (7%), respectively. No strong spatial patterns to numerical abundance were observed among the sampling stations at Laysan.

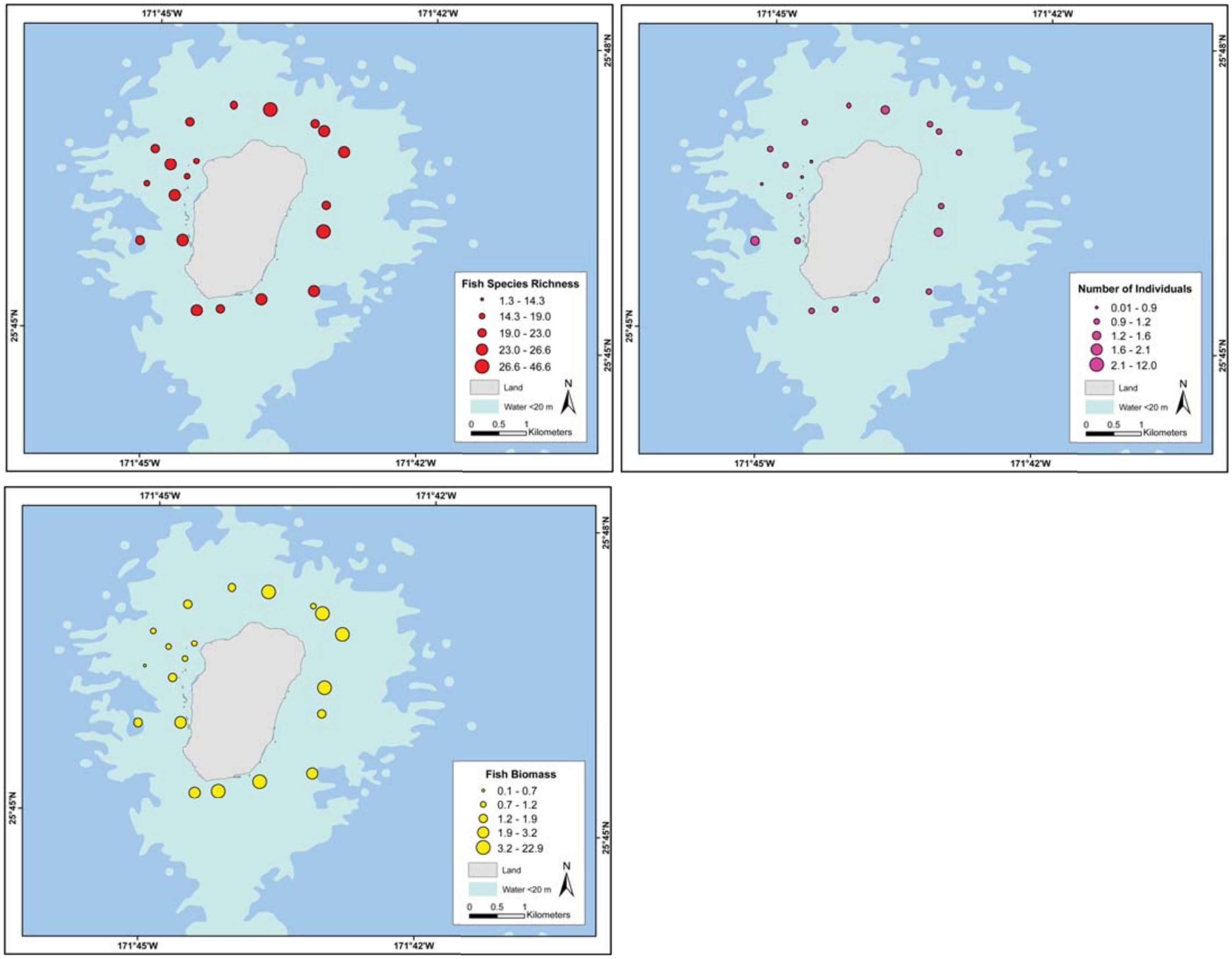

Figure 5.35. Fish assemblage characteristics for Laysan Island. Species richness (top left), number of individuals (top right), and biomass (t ha^{-1}; bottom left). Source: NWHI RAMP, unpub. data; maps: L. Wedding.

Laysan Island ranked sixth in mean biomass ($\bar{x}$ = 2.5, SD ± 2.1), ranging from 5.15 to 0.85 t ha^{-1}. The windward, northeast fore reef harbored the highest biomass. Giant trevally comprised 37% of total biomass, followed by whitebar surgeonfish (*Acanthurus leucopareius*, 6%) and the endemic spectacled parrotfish (6%).

Lisianski Island-Neva Shoals

Lisianski Island-Neva Shoals ranked sixth in mean species richness per station ($\bar{x}$ = 21.2, SD ± 4.13) and ranged from 24.7 to 20.7 (Table 5.22, Figure 5.36). The greatest number of species per station was observed on the leeward side (northwest and west) of Lisianski.

Table 5.22. Fish assemblage characteristics for Lisianski Island-Neva Shoals across all habitat types. Source: NWHI RAMP, unpub. data.

LEVEL	NUMBER	MEAN	STD DEV	STD ERR MEAN	LOWER 95%	UPPER 95%
Species	32	21.23	4.13	0.73	19.75	22.72
Number of Individuals (m^2)	32	1.45	0.53	0.09	1.26	1.64
Biomass (t ha^{-1})	32	2.47	1.71	0.3	1.85	3.08

Numerical abundance at Lisianski Island-Neva Shoals ranked third overall. Mean fish density was 1.45 individuals/m^2 (SD ± 0.5) and ranged from 1.66 to 0.99 individuals/m^2. Dominant species include saddle wrasse (12%), goldring surgeonfish (11%), Pacific Gregory (11%) and juvenile parrotfish (8%). No spatial patterns were observed for fish density across the reef system.

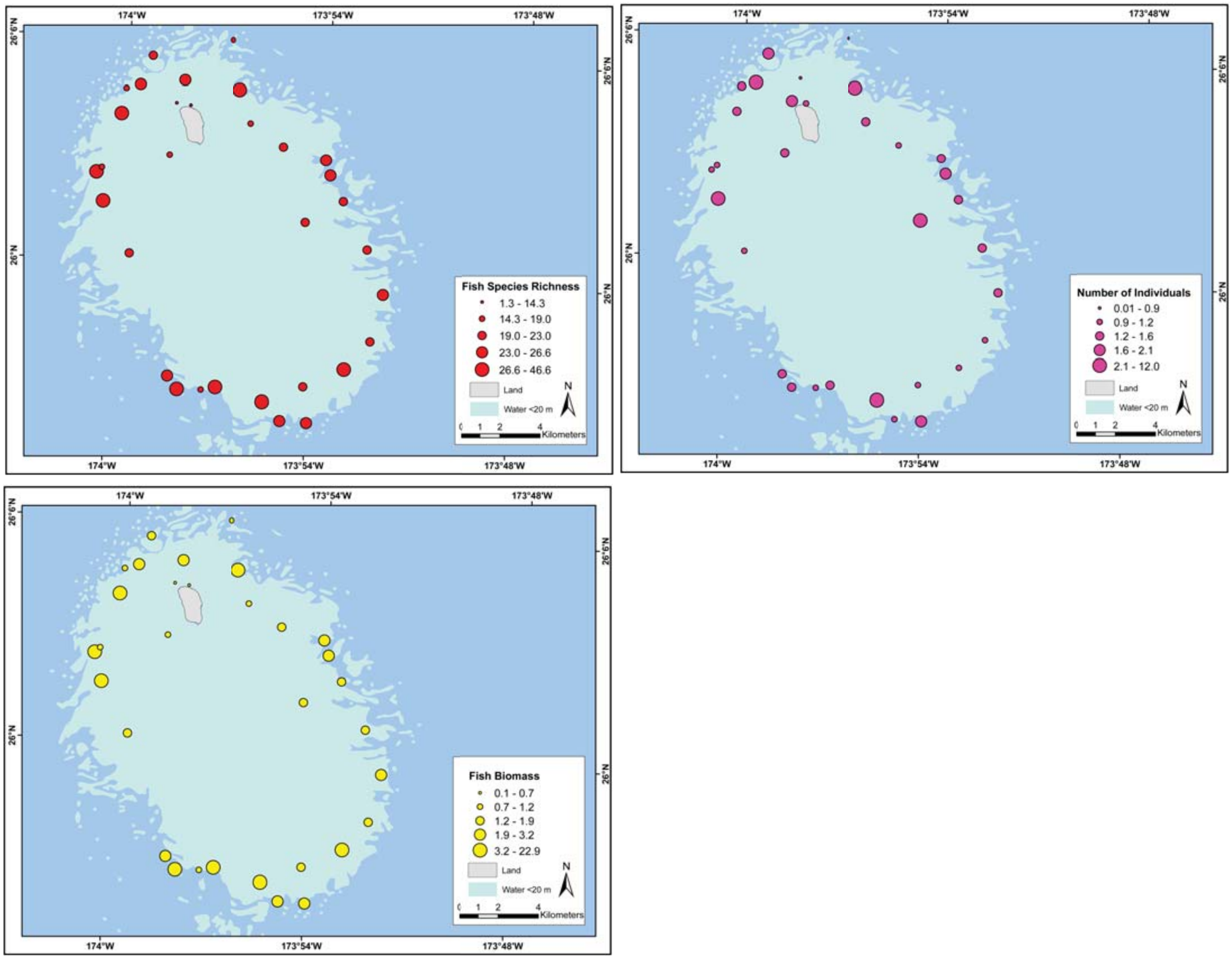

Figure 5.36. Fish assemblage characteristics for Lisianski Island-Neva Shoals. Species richness (top left), number of individuals (top right), and biomass (t ha^{-1}; bottom left). Source: NWHI RAMP, unpub. data; maps: L. Wedding.

Lisianski Island-Neva Shoals ranked seventh in mean biomass compared to all other reefs. Mean fish biomass was 2.5 t ha^{-1} (SD ±1.7) and ranged from 5.15 to 0.8. Biomass was highest along the southeast portion of Neva Shoals, in an area of high coral cover and high habitat complexity. Giant trevally accounted for the majority (51%) of the total biomass. This was followed in importance by three species of parrotfishes: the endemic spectacled parrotfish (8%), bullethead parrotfish (4%) and the endemic regal parrotfish (*Scarus dubius*, 4%).

Pearl and Hermes Atoll

Mean species richness at Pearl and Hermes Atoll was 20.1 (SD ± 7.2) and ranked seventh overall (Table 5.23, Figure 5.37). Species richness was significantly higher (F_{291} = 24.49, p<0.001) on the fore reef ($\bar{x}$ = 24.0, SD ± 6.9) compared with the lagoon ($\bar{x}$ = 16.9, SD ± 6.0) and back reef ($\bar{x}$ = 17.0, SD ± 4.6) habitats (Table 5.24).

Table 5.23 Fish assemblage characteristics for Pearl and Hermes Atoll across all habitat types. Source: NWHI RAMP, unpub. data.

LEVEL	NUMBER	MEAN	STD DEV	STD ERR MEAN	LOWER 95%	UPPER 95%
Species	91	20.12	7.21	0.76	18.62	21.62
Number of Individuals (m^2)	91	1.82	0.83	0.09	1.65	1.99
Biomass (t ha^{-1})	91	2.78	3.75	0.39	2	3.56

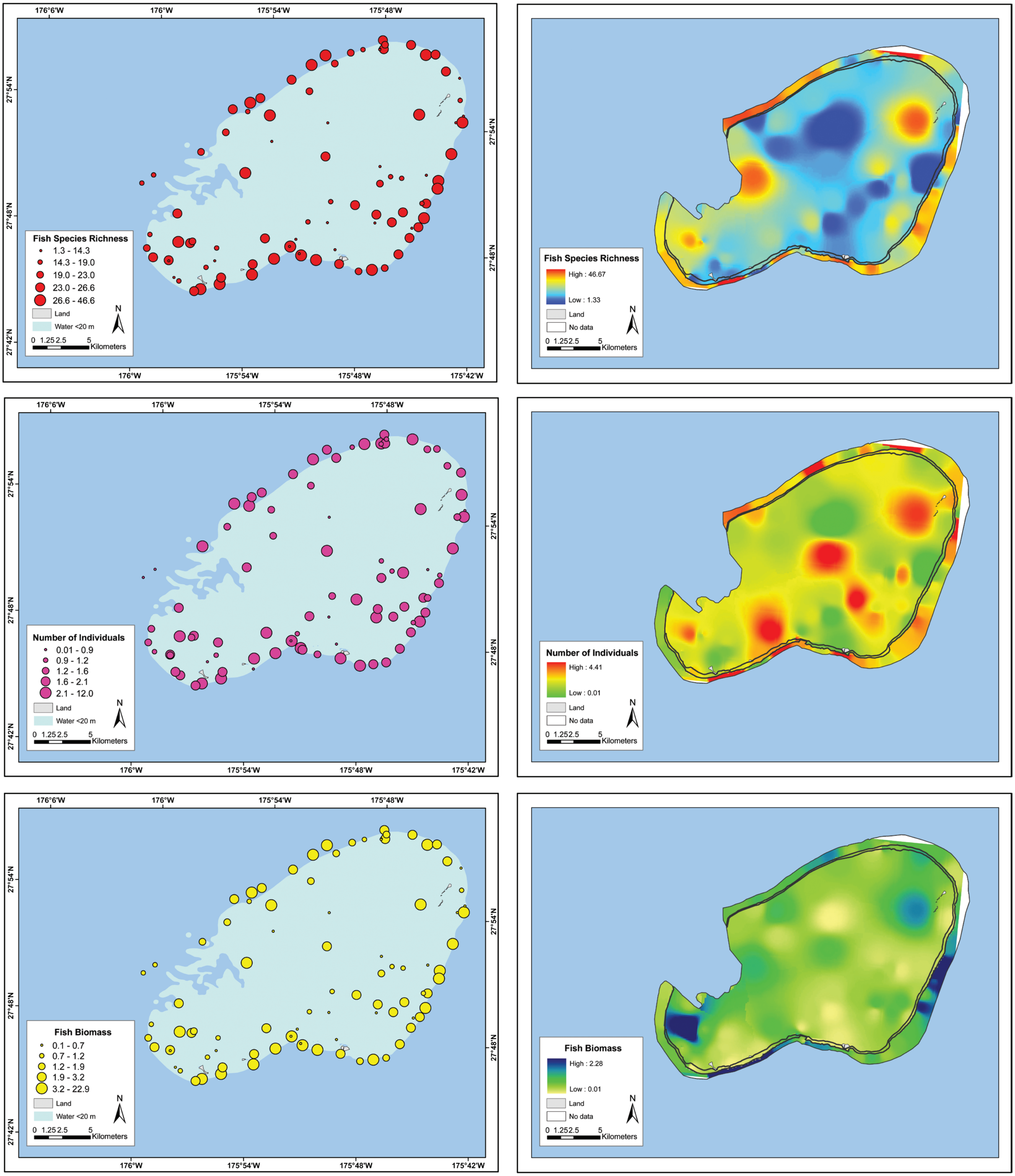

Figure 5.37. Fish assemblage characteristics for Pearl and Hermes Atoll. Species richness (top row), number of individuals (middle row) and biomass (t ha^{-1}, bottom row). Source: NWHI RAMP, unpub. data; maps: L. Wedding.

The numerical density of fishes at Pearl and Hermes ranked second overall ($\bar{x}$ = 1.8, SD ± 0.8). Overall, planktivores comprised a third (37%) of total density, which included oval chromis (11%) blackfin chromis (7%) and chocolate dip chromis (*Chromis hanui*, 5%). The number of individuals observed on the fore reef ($\bar{x}$ = 2.1, SD ± 0.9) was significantly higher ($p<0.05$) than the back reef ($\bar{x}$ = 1.9, SD ± 0.6) and lagoon ($\bar{x}$ = 1.6, SD ± 0.8) habitats.

Table 5.24. Fish assemblage characteristics for Pearl and Hermes Atoll for each major habitat type. Source: NWHI RAMP, unpub. data.

BACK REEF	NUMBER	MEAN	STD DEV	STD ERR MEAN	LOWER 95%	UPPER 95%
Species	7	17	4.59	1.74	12.75	21.25
Number of Individuals (m^2)	7	1.88	0.55	0.21	1.37	2.39
Biomass (t ha^{-1})	7	1.05	0.85	0.32	0.26	1.83
LAGOON						
Species	43	16.91	5.99	0.91	15.07	18.76
Number of Individuals (m^2)	43	1.63	0.78	0.12	1.39	1.87
Biomass (t ha^{-1})	43	2.02	3.02	0.46	1.09	2.95
FORE REEF						
Species	41	24.02	6.91	1.08	21.84	26.2
Number of Individuals (m^2)	41	2.01	0.88	0.14	1.73	2.29
Biomass (t ha^{-1})	41	3.88	4.42	0.69	2.49	5.28

Pearl and Hermes ranked first in fish biomass on the fore reefs ($\bar{x}$ = 3.9, SD± 4.4) among all locations. Biomass was significantly higher on the fore reef ($p < 0.05$) than the lagoon ($\bar{x}$ = 2.0, SD ± 3.0), which, in tern, was significantly higher ($p < 0.05$) than at back reef ($\bar{x}$ = 1.0, SD± 0.9). Apex predators dominated the fish biomass, with giant trevally accounting for 48%, followed by whitetip reef sharks (6%), and Galapagos sharks (5%). Stations with the highest biomass were located along the leeward, southwest fore reef.

Midway Atoll

Midway ranked fifth in species richness among all reef locations (Table 5.25, Figure 5.38). The mean number of species per transect differed significantly ($p<0.05$) among all three habitats. Fore reef habitats harbored 27.0 (SD ± 6.0) species, followed by back reefs ($\bar{x}$ = 19.1, SD ± 4.8), and lagoon habitats ($\bar{x}$ = 15.8, SD ± 6.1). Richness was highest along the southern fore reef (Table 5.26).

Table.5.25. Fish assemblage characteristics for Midway Atoll across all habitat types. Source: NWHI RAMP, unpub. data.

LEVEL	NUMBER	MEAN	STD DEV	STD ERR MEAN	LOWER 95%	UPPER 95%
Species	37	21.59	7.97	1.31	18.94	24.25
Number of Individuals (m^2)	37	2.69	2.04	0.34	2.01	3.37
Biomass (t ha^{-1})	37	2.5	2.14	0.35	1.78	3.21

Midway ranked first in numerical density ($\bar{x}$ = 2.7 individuals/m^2, SD ± 2.0). The lagoon harbored the greatest number of individuals ($\bar{x}$ = 2.9 individuals/m^2, SD ± 2.7) consisting of damselfishes (oval chromis – 11%, Pacific Gregory – 10%, domino damselfish – 5%, blackfin chromis – 5% and chocolate dip chromis – 5%). All except the Pacific Gregory are planktivores. Saddle wrasse (13%) and schools of convict tangs (6%) also contributed to the large number of individuals observed at Midway. Numerical abundance was highest on the northwestern leeward fore reef and in Welles Harbor.

Table 5.26. Fish assemblage characteristics for Midway Atoll for each major habitat type. Source: NWHI RAMP, unpub. data.

BACK REEF	NUMBER	MEAN	STD DEV	STD ERR MEAN	LOWER 95%	UPPER 95%
Species	4	19.08	4.79	2.4	11.45	26.71
Number of Individuals (m^2)	4	1.59	0.46	0.23	0.85	2.32
Biomass (t ha^{-1})	4	1.46	0.65	0.33	0.42	2.49
LAGOON						
Species	15	15.76	6.14	1.59	12.35	19.16
Number of Individuals (m^2)	15	2.9	2.69	0.69	1.41	4.39
Biomass (t ha^{-1})	15	1.58	1.22	0.31	0.91	2.26
FORE REEF						
Species	18	27.02	6.05	1.43	24.01	30.03
Number of Individuals (m^2)	18	2.76	1.58	0.37	1.97	3.54
Biomass (t ha^{-1})	18	3.49	2.52	0.59	2.24	4.74

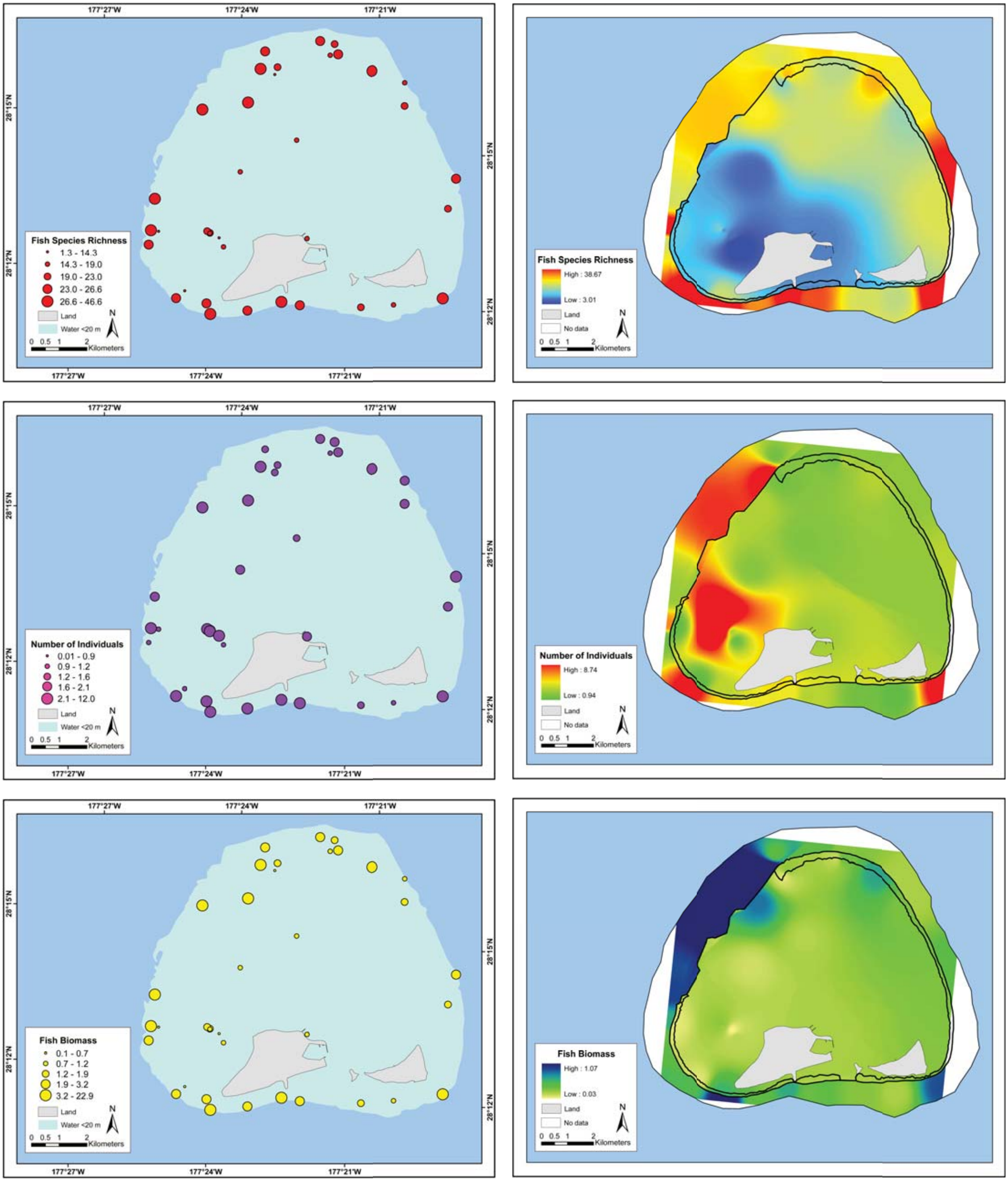

Figure 5.38. Fish assemblage characteristics for Midway Atoll. Species richness (top row), number of individuals (middle row) and biomass (t ha^{-1}; bottom row). Source: NWHI RAMP, unpub. data; maps: L. Wedding.

Biomass at Midway averaged 2.5 t ha^{-1} (SD ±2.1) and ranked second overall among locations. There were large differences in biomass among habitat types with biomass on the fore reef ($\bar{x}$ = 3.5, SD ± 2.5) more than two times higher than the back reef ($\bar{x}$ = 1.5, SD ± 0.7), and the lagoon ($\bar{x}$ = 1.6, SD ± 1.2). Herbivores accounted for the majority of the biomass (57%) with considerable contributions from the spectacled parrotfish (13%), whitebar surgeonfish (8%), convict tang (7%), and bluespine unicornfish (6%). Galapagos sharks (8%) and giant trevally (5%) were the major predators by weight. The highest biomass was observed along the northwest fore reef where the reef crest becomes submerged and along the southern fore reef off Sand Island.

Kure Atoll

Species richness at Kure was low ($\bar{x}$ = 19.6, SD ± 6.3) ranking eighth overall (Table 5.27, Figure 5.39). Significantly higher ($p<0.05$) numbers of species were observed on the fore reef ($\bar{x}$ = 21.5, SD ± 6.3) compared to the lagoon ($\bar{x}$ = 17.4, SD ± 6.0) and back reef ($\bar{x}$ = 15.3, SD ± 2.0). Richness was high around the entire fore reef (Table 5.28).

Table 5.27. Fish assemblage characteristics for Kure Atoll across all habitat types. Source: NWHI RAMP, unpub. data.

LEVEL	NUMBER	MEAN	STD DEV	STD ERR MEAN	LOWER 95%	UPPER 95%
Species	59	19.6	6.32	0.82	17.96	21.25
Number of Individuals (m^2)	59	1.41	0.81	0.1	1.2	1.62
Biomass (t ha^{-1})	59	1.22	1.13	0.15	0.93	1.51

Table 5.28. Fish assemblage characteristics for Kure Atoll for each major habitat type. Source: NWHI RAMP, unpub. data.

BACK REEF	NUMBER	MEAN	STD DEV	STD ERR MEAN	LOWER 95%	UPPER 95%
Species	5	15.27	2.05	0.92	12.73	17.81
Number of Individuals (m^2)	5	1.11	0.21	0.09	0.85	1.37
Biomass (t ha^{-1})	5	0.61	0.19	0.09	0.38	0.85
LAGOON						
Species	20	17.42	5.96	1.33	14.63	20.21
Number of Individuals (m^2)	20	1.31	1.09	0.24	0.8	1.82
Biomass (t ha^{-1})	20	1.22	1.53	0.34	0.5	1.94
FORE REEF						
Species	34	21.53	6.3	1.08	19.33	23.73
Number of Individuals (m^2)	34	1.52	0.65	0.11	1.29	1.75
Biomass (t ha^{-1})	34	1.31	0.91	0.16	0.99	1.63

An average of 1.4 individuals/m^{-2} were observed at Kure (sixth overall). Saddle wrasse (20%), oval chromis (12%), Pacific Gregory (9%) and chubs (6%) were most important numerically. No strong patterns in the distribution of individuals was observed and no significant difference among habitat types ($p>0.05$) were detected. The fore reef averaged 1.6 individuals/m^{-2}, followed by lagoon ($\bar{x}$ = 1.3, SD ± 1.1) and back reef ($\bar{x}$ = 1.1, SD ± 0.2). Fish density was highest on the leeward fore reef and central western patch reefs.

Kure had the second lowest biomass of any location ($\bar{x}$ = 1.2, SD ± 1.1) and the lowest proportion of apex predators (16%). Spectacled parrotfish (17%), chubs (10%) and giant trevally (5%) were most important by weight. There were no strong patterns in the spatial distribution of biomass. Unlike other locations, the lagoon ($\bar{x}$ = 1.2, SD ± 1.5) and fore reef ($\bar{x}$ = 1.3, SD ± 0.9) biomass estimates were very similar.

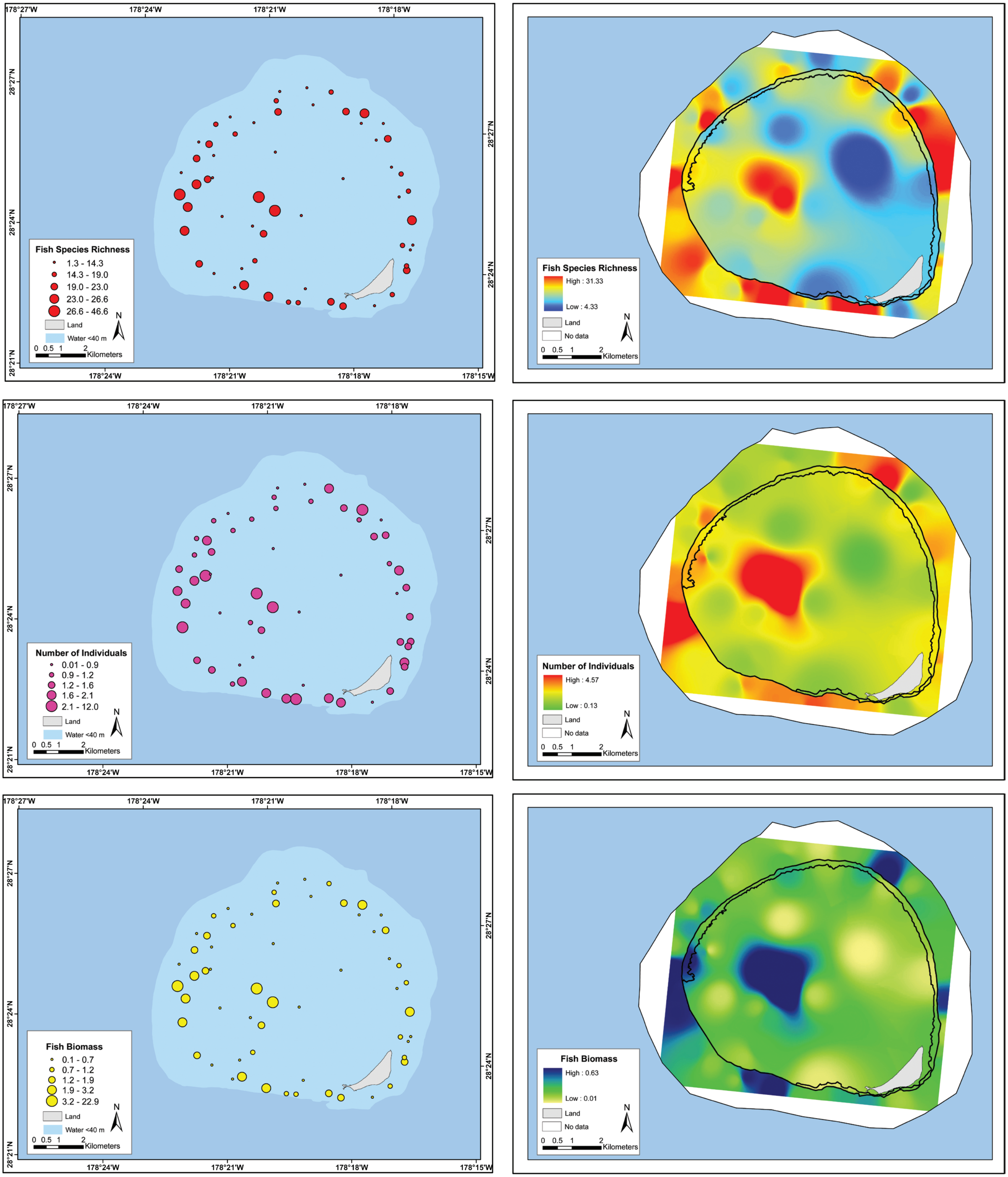

Figure 5.39. Fish assemblage characteristics for Kure Atoll. Species richness (top row), number of individuals (middle row) and biomass (t ha^{-1}; bottom row). Source: NWHI RAMP, unpub. data; maps: L. Wedding.

EXISTING DATA GAPS

Two major issues dominate the management and conservation of reef resources in the NWHI and throughout the Hawaiian Archipelago. The dispersal, connectivity, and genetic exchange between reef populations of NWHI and MHI organisms is undoubtedly the issue of greatest consequence for future management and conservation of reef fish and other resources in the NWHI as well as the MHI. Much recent progress has been made obtaining the empirical data needed to begin unraveling patterns of planktonic dispersal and more directed adult movements of fishes in the NWHI (see the Connectivity and Integrated Ecosystem Studies chapter of this document). The habitat relations of fishes are arguably the second most important issue to consider for fishes in the NWHI. Habitat alterations (sea level rise, warming, acidification) resulting from global climate change are expected to be the most significant impacts and likely to occur in the NWHI (Selkoe et al., 2008). Although the effects of global warming and coral bleaching on coral reef fishes are of concern worldwide (Pratchett et al., 2008a), they are relatively more important in the NWHI where resources are now protected from other human impacts by establishment of the Monument.

The prevalence and dynamics of coral and related substrata (e.g., algal secondary cover) represent the most obvious habitat issues for shallow-water reef fishes in the NWHI. Although corals are important as a food source only for relatively few, specialized fishes in tropical reef ecosystems including Hawaii (Cole et al. 2008), corals provide exceedingly important shelter resources (Caley and St. John, 1996). These shelter resources are especially important for the relatively small-bodied and predator-vulnerable juvenile life stages of reef fishes, particularly early YOY near the time when they settle from the plankton as “recruits” to benthic populations (Jones et al., 2004; DeMartini and Anderson, 2007). Coral shelter is nonetheless also important for larger, older juveniles and adults (Beukers and Jones, 1997).

A comprehensive and systematic characterization of the habitat relations of Hawaiian reef fishes is lacking and needed. The only published work to date is limited to finger coral habitat on shallow (10 m) fringing reefs of the leeward Big Island and further restricted to the recruits of a suite of summer-recruiting species, primarily tangs of the family Acanthuridae (DeMartini and Anderson, 2007). Work is in progress to expand this catalogue both taxonomically and across additional habitats, with initial emphasis on the diverse labroids (parrotfishes, wrasses) that recruit in spring-summer to very shallow (1-3 m deep) and wave-protected coral rubble habitats. Several recent case studies exemplify the need for distinguishing habitat relations between juvenile and adult conspecifics (Pratchett et al., 2008b; Wellenreuther and Clements, 2008). For this reason, the habitat relations of adult as well as juvenile Hawaiian reef fishes are being described.

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