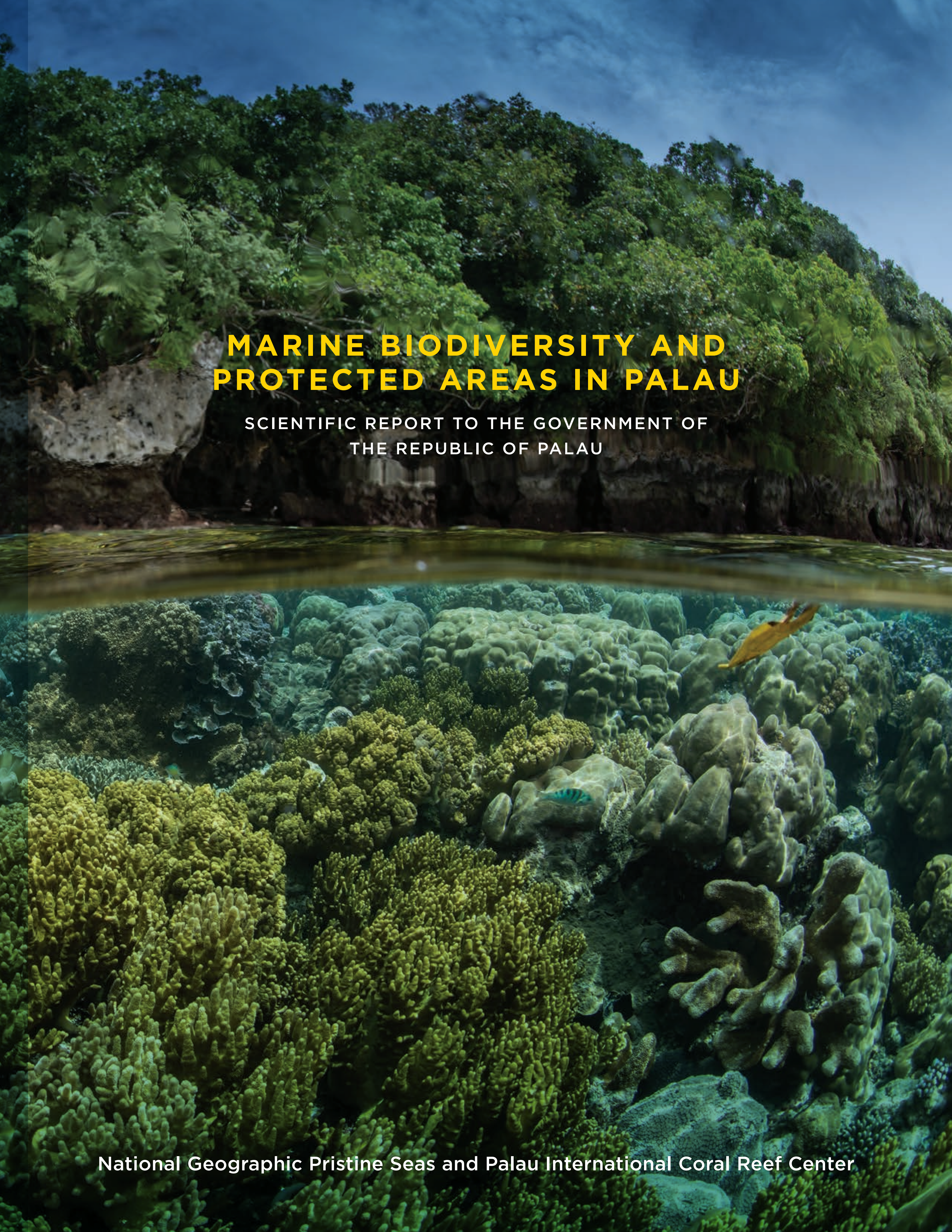

MARINE BIODIVERSITY AND PROTECTED AREAS IN PALAU

SCIENTIFIC REPORT TO THE GOVERNMENT OF THE REPUBLIC OF PALAU

National Geographic Pristine Seas and Palau International Coral Reef Center

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SUMMARY

The Republic of Palau has committed to the creation of a new National Marine Sanctuary, which would include a very large no-take marine reserve and a strictly regulated local fishery. National Geographic's Pristine Seas partnered with the Palau International Coral Reef Center to provide scientific data to the Palau government in order to inform the establishment of the sanctuary. In September 2014, we conducted an expedition to Palau to assess the efficacy of current marine protected areas (MPAs) and explore the deep sea and open ocean realms, with the ultimate goal of evaluating the health of Palau's marine ecosystems under different levels of protection.

Most of the reefs we surveyed were healthy with live coral averaging greater than 50% and abundant fish life (Figure 1). Our surveys showed that most MPAs had larger biomass of 'resource fish' (commercially important species) than nearby unprotected areas. Total resource fish biomass was, on average, twice as large in MPAs as at nearby control areas. The most striking difference between MPAs and unprotected areas was the fivefold greater biomass of top predators in the MPAs, which shows that no-take marine reserves in Palau are effective at conserving top predators (Figure 2). A recent economic study showed that divers would be willing to pay more for diving in no-take marine reserves because of the greater number and size of fishes (Figure 3). This suggests that greater levels of protection may bring greater economic revenue to Palau.

We conducted the first fisheries-independent description of pelagic (open ocean) fishes around Palau, and the first survey of the deep sea down to 3,500 m. Our pelagic cameras revealed a diverse fish fauna including numerous sharks and schools of tunas. The number of species and individuals observed were comparable to the 640,000 km^2 Chagos Marine Reserve in the Indian Ocean.

The creation of a sanctuary around Palau would provide protection for these valuable pelagic resources, allowing them to grow larger, become more abundant, and generate higher reproductive output. This would benefit the fishing within and around Palau, and protect biodiversity by reducing by-catch of a wide range species critical to ecosystem function.

Our deep-sea video cameras showed a diverse and rich fauna that included at least 26 different taxa of deep-water fishes from 19 families. Cutthroat eels were the most numerous fishes (occurring in 65% of the samples), followed by rattails (46%) and lantern sharks (27%). One interesting observation was the presence of a tiger shark *(Galeocerdo cuvier)* at 515 m. In addition, we observed a wide range of mobile and sessile invertebrates from five different phyla, with crustaceans (e.g. shrimps and crabs) being the most diverse and numerous.

We conducted water samples for microplastics to better understand their impact in the ocean food web, and found that every one of our samples (n = 22) contained pieces of plastic. These results have implications for human health and the health of the entire food web, and indicates the need to reduce the input of plastics into the ocean.

With a strong tradition of fisheries management and stewardship of national waters, Palau is a world leader in marine conservation. Our results indicate that the creation of a large sanctuary around Palau will increase diving tourism revenues, improve of local fisheries, and allow for the long-term sustainability of marine resources.

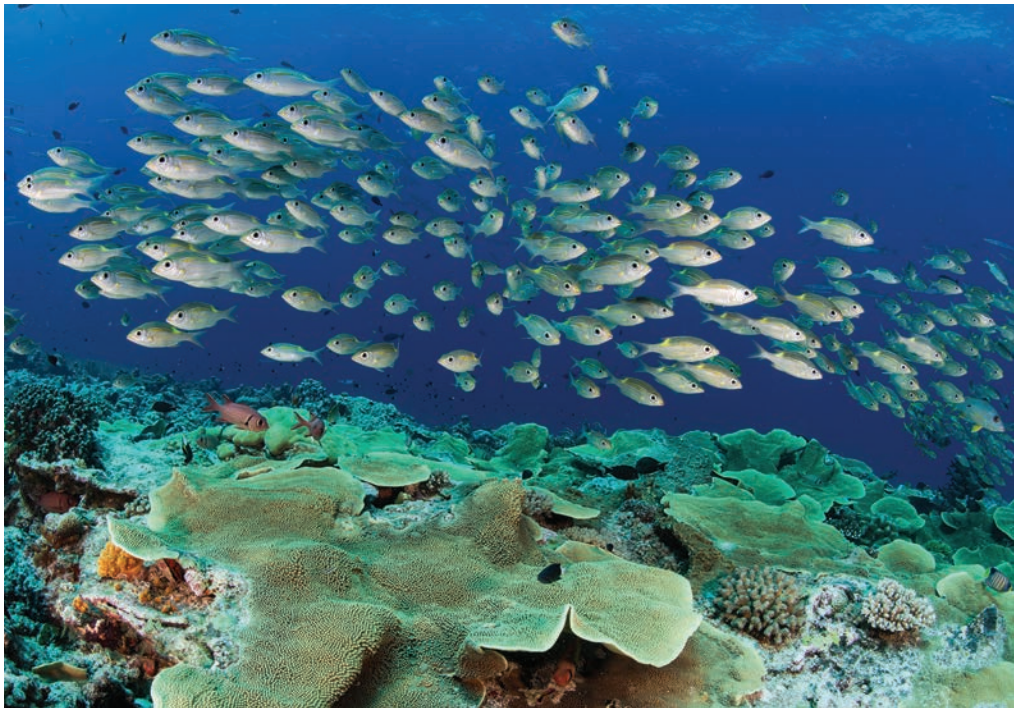


FIGURE 1.

Healthy reef with school of goldlined emperors (chelchelui, *Gnathodentex aureolineatus*).

FIGURE 2.

Top predators such as these giant trevally (cherobk, *Caranx ignobilis*), seen here chasing bluestreak fusiliers (chadins, *Pterocaesio tile*), are more abundant in MPAs than in areas open to fishing.

FIGURE 3.

Charismatic species like the Napoleon Wrasse (maml, *Cheilinus undulates*) are listed as endangered by International Union for the Conservation of Nature, but are common in Palau.

INTRODUCTION

Palau is a world leader in marine conservation, owing to its rich tradition of fisheries management and wise stewardship of its waters (Johannes 1981), including the establishment of the world's first shark sanctuary in 2009. In addition, Palau has placed over 45% of its nearshore waters under some form of protection. The government of Palau was instrumental in establishing the Micronesian Challenge—a regional marine conservation initiative to protect more than 30% of the marine ecosystems of the region through the establishment of local protected area networks (PANs). Today, tourists come to Palau mainly to experience its unique marine ecosystems. In recent years, tourism has contributed about three quarters of GDP growth, more than 80% of exports of goods and services, 15% of total tax revenue, and 40% of total employment (IMF 2014).

Aware of the value of Palau's marine resources and the decline of tuna stocks throughout the Pacific (Ward and Myers 2005, Langley et al. 2009, Bailey et al. 2013), President Remengesau has committed to the creation of a new National Marine Sanctuary. The Sanctuary would ban all foreign fishing for tuna and other pelagic (offshore) fishes, and support the development of a national fishery in 20% of the Exclusive Economic Zone, keeping the other 80% fully protected from any type of extraction. The national pelagic fishery would focus on supplying fresh fish to the domestic market, including in support of tourism.

To assess the benefits of the National Marine Sanctuary to Palau, there is a need to (1) characterize the pelagic and deep marine biodiversity of Palau, and (2) establish a non-destructive, fishery-independent monitoring program to

assess these resources. To these ends, a team of individuals from National Geographic, the Palau International Coral Reef Center, the University of Hawaii, the University of California at Santa Barbara, the University of Western Australia, and Spain's Center for Advanced Studies (Appendix I) collaborated in a three-week Pristine Seas expedition to the Republic of Palau in September 2014. We conducted a fishery-independent assessment of the diversity and abundance of pelagic fish of Palau, and explored deep-sea habitats using National Geographic drop-cams. In addition, we conducted visual surveys of corals, algae, and fishes inside and outside of eight no-take marine protected areas throughout Palau to determine the benefits of current protection efforts (Table 1, Figures 4–5). Appendix II contains a description of all methods used during the expedition.

The ultimate goal of our research is to estimate the value of Palau's marine ecosystem under different levels of protection. This research is motivated by the critical need to develop effective MPA networks that help to conserve ecosystem function while benefiting the local communities and society as a whole.

TABLE 1.

Marine Protected Areas surveyed during the 2014 Pristine Seas Expedition.
PICRC = Palau International Coral Reef Center,
PCS = Palau Conservation Society.

Name	State	Year est.	Size (km^2)	Type	Restrictions
Ebiil	Ngerchelong	1999	37.9	Reef, channel	No fishing
Ngermasech	Ngardmau	1998	3.3	Mangrove, seagrass, coral reef	No entry, no fishing
Ngederrak	Koror	2001	5.9	Seagrass & reef flat	No entry, no fishing
Ngerumekaol	Koror	1976	3.5	Reef	No fishing
Ngemelis	Koror	1995	40.3	Islands & reefs	No fishing
Ngelukes	Ngchesar	2002	1.0	Patch reef	No entry, no fishing
Ileyakl Beluu	Ngardmau	2005	0.4	Reef	No entry, no fishing
Teluleu	Peleliu	2001	0.4	Seagrass & reef flat	No entry, no fishing

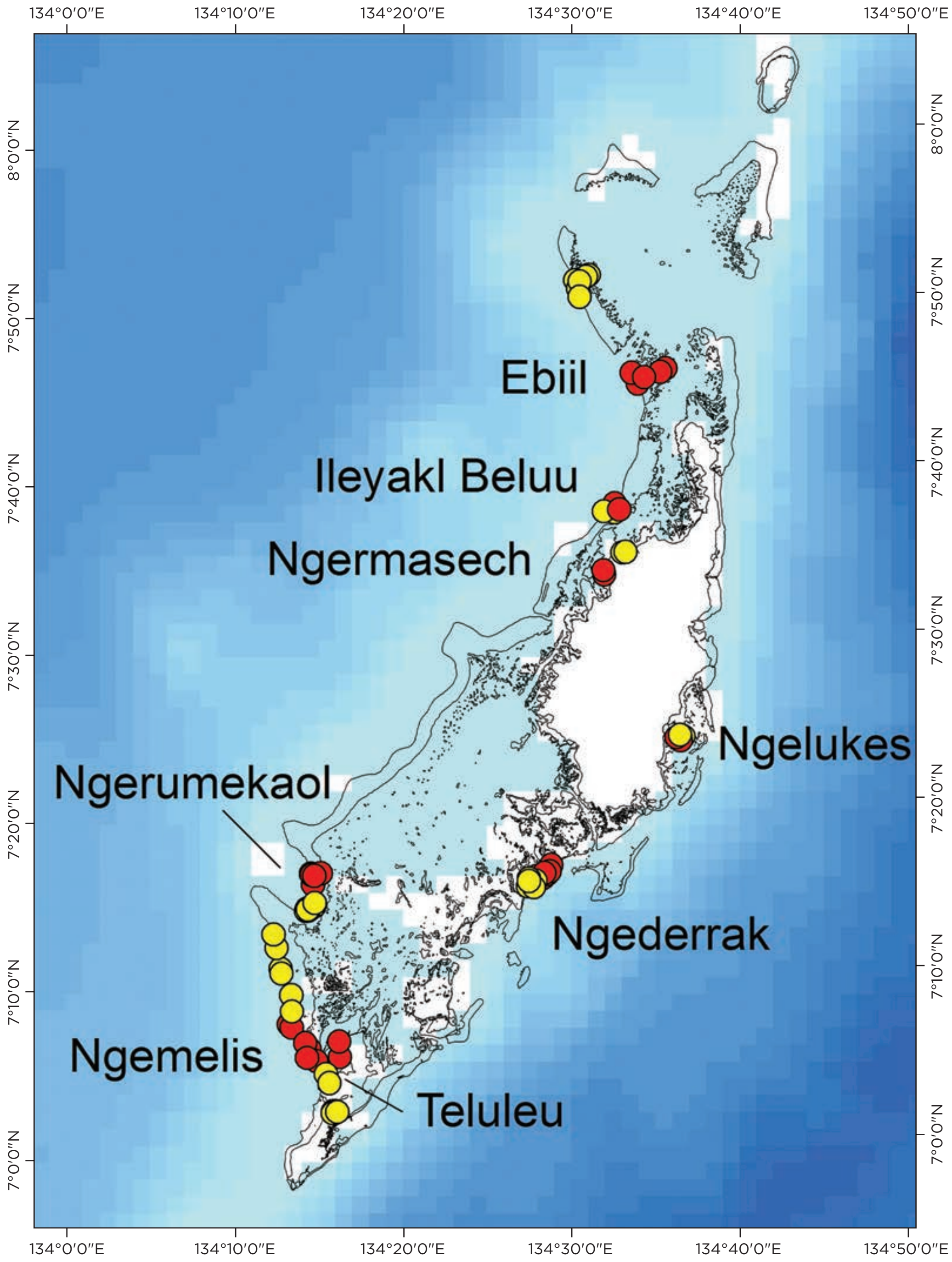


FIGURE 4.

Marine Protected Areas (red) and adjacent control unprotected sites (yellow) surveyed by the Pristine Seas expedition in Palau in September 2014.

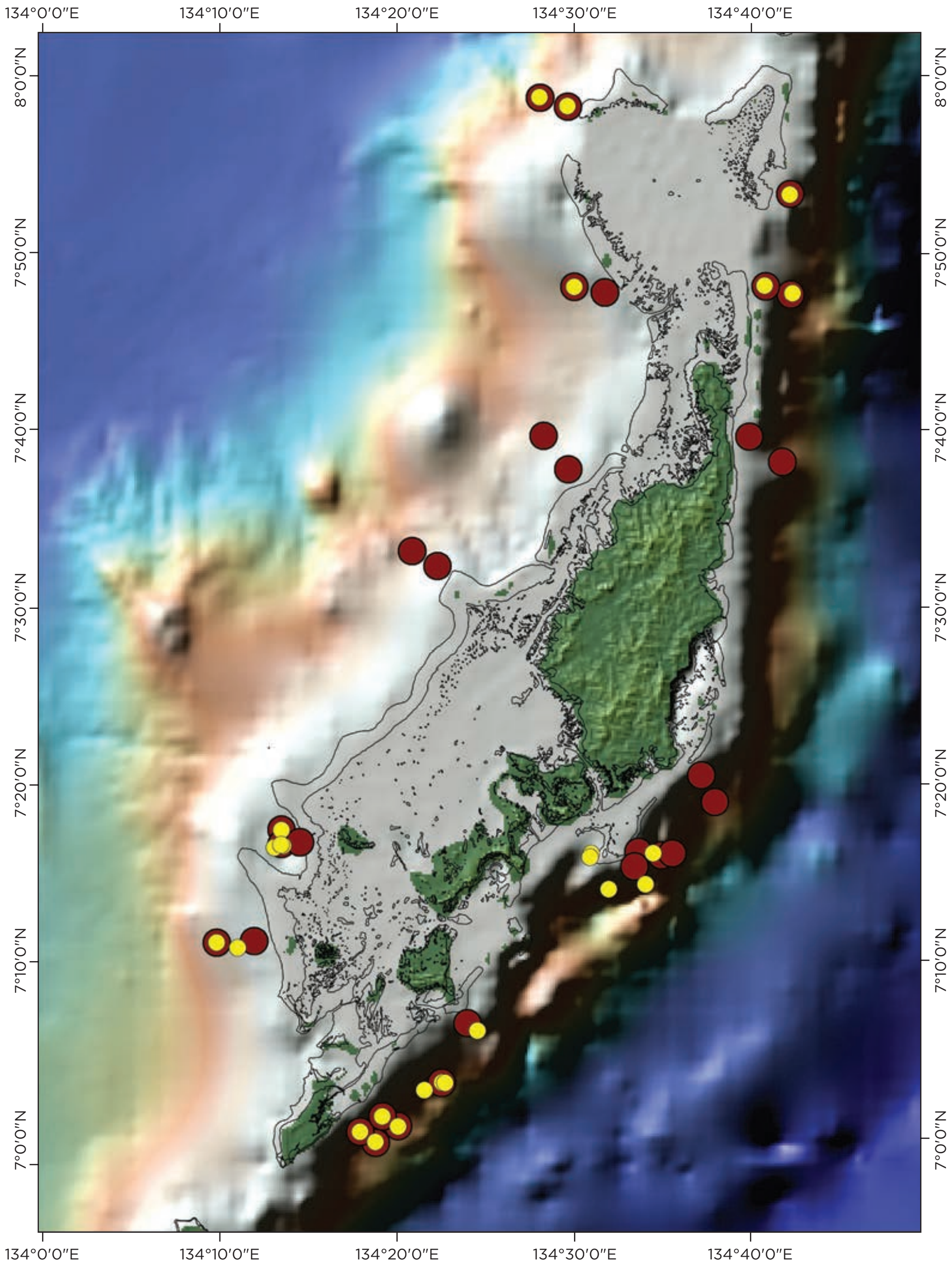


FIGURE 5.

Locations of pelagic camera (red) and drop-cam (yellow) deployments.

RESULTS

Coral Reefs

Based on satellite-derived habitat maps (Battista et al. 2007), approximately 45% of the areas within the MPAs consisted of sand, followed by reef pavement (33%), patch reefs (5.7%) and aggregated reef (5.3%) (Figure 6). Maps of habitat types and sampling locations show wide variation in habitats among MPAs (Appendix III).

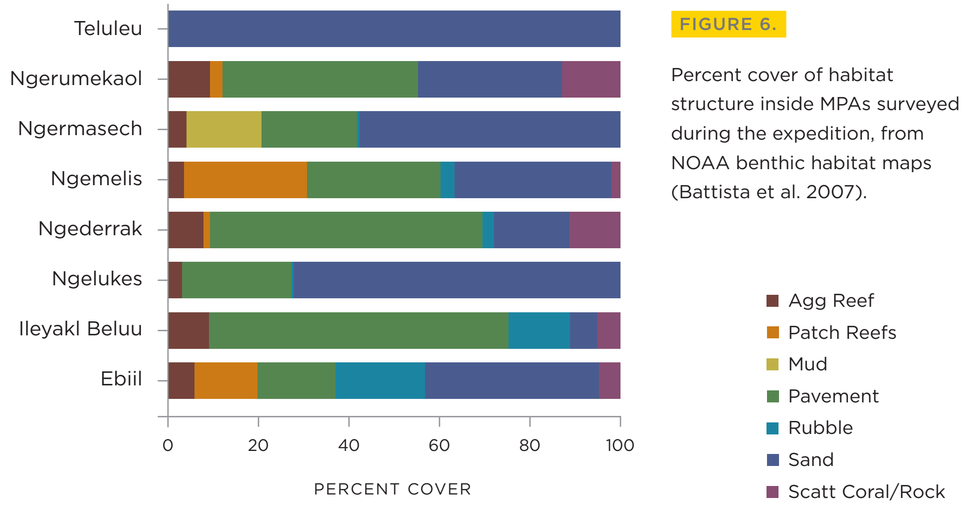


FIGURE 6.

Percent cover of habitat structure inside MPAs surveyed during the expedition, from NOAA benthic habitat maps (Battista et al. 2007).

The coral reefs surveyed around Palau during the Pristine Seas expedition ranged from degraded to very healthy (Figure 7). Hard corals accounted for 50% of the total cover on average across all locations. This percentage of coral cover can be considered high, relative to other locations worldwide (e.g. average coral cover in the Caribbean is less than 10%; Gardner et al. 2003, Alvarez-Filip et al. 2009).

Coral cover was not significantly different between Marine Protected Areas (MPAs) and adjacent unprotected sites, except for the Ngelukes MPA, which had coral cover nearly two times higher than the adjacent unprotected area. We found the highest coral cover in the MPAs of Ngerumekaol, Ileyakl Beluu, and Ngemelis (55% for all) (Figure 10). The lowest coral cover was in the Ngederrak MPA, which may have been affected more severely by the typhoon in 2013 than the adjacent open area.

FIGURE 7.

Complex branching corals support a wide range of species in the shallows.

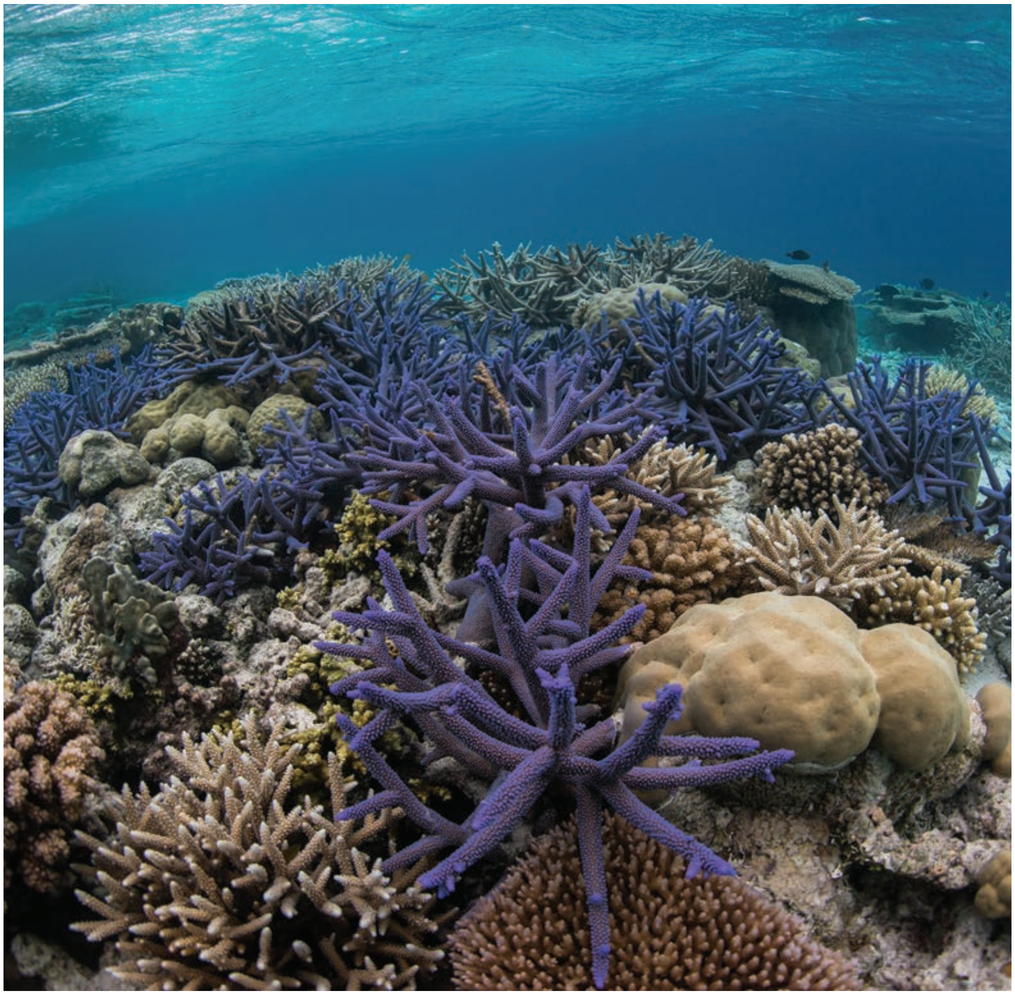


FIGURE 8.

Tube coral (*Tubastrea micrantha*) and encrusting sponges with a swarm of swallowtail cardinalfish (*Rhabdamia cypselura*).

FIGURE 9.

Whip corals on a forereef slope.

FIGURE 10.

Coral cover (mean ± standard error) in Marine Protected Areas (MPAs) and adjacent open access areas. Asterisk denotes MPA/control pair that is significantly different (t-test, $p < 0.05$).

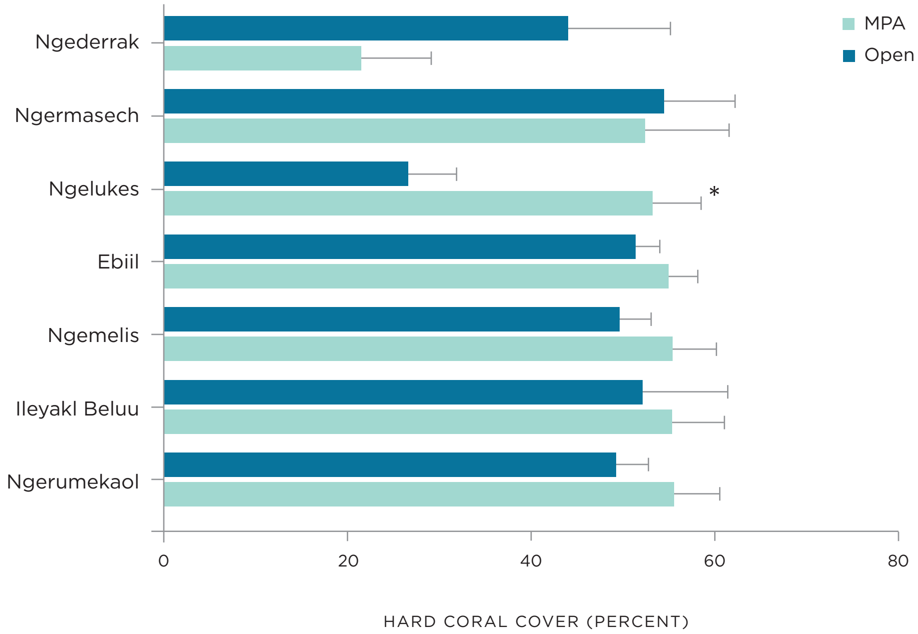
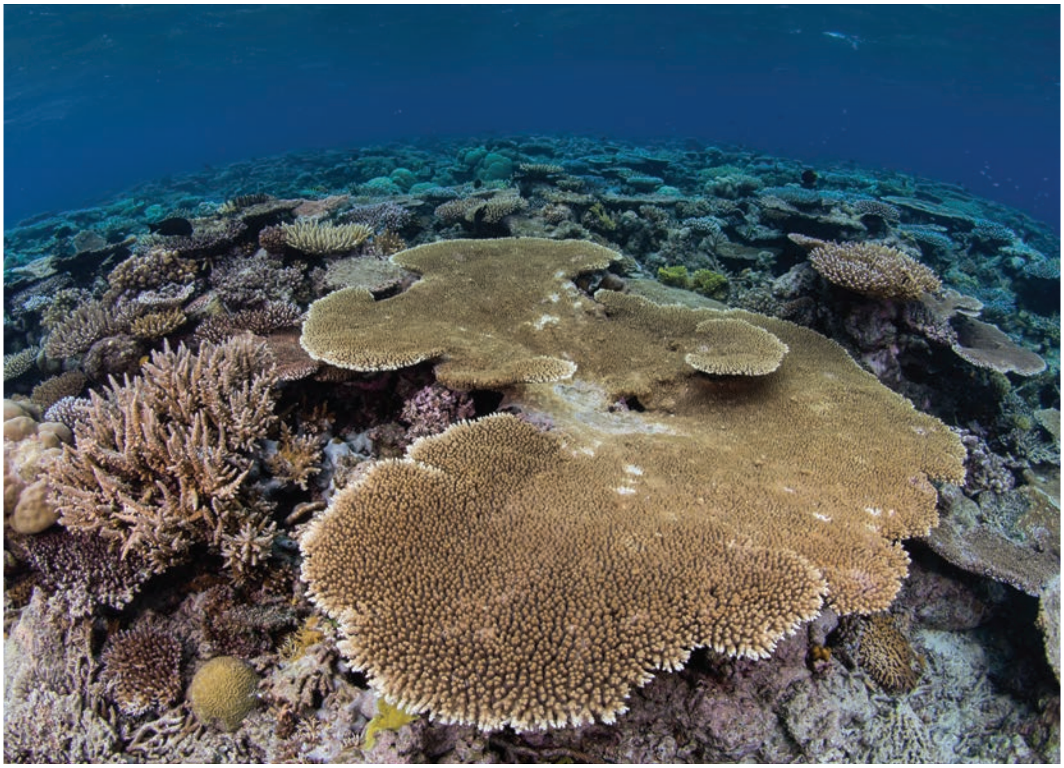


FIGURE 11.

Diverse forereef coral reef community.



Benthic community composition was similar between MPAs and adjacent open areas (PERMANOVA pseudo-$F_{1,127}$ = 1.76, p = 0.14, average dissimilarity = 16.9%). Forereef MPAs and adjacent open areas clustered together in ordination space and had similar benthic community composition (Figure 12). Inshore areas (e.g., Ngelukes, Ngermasech, and Ngederrak) were distinct from the forereef areas and from each other. Benthic communities were similar between MPAs and adjacent open areas at Ngermasech and Ngelukes, but the communities at Ngederrak were highly dissimilar (average dissimilarity = 57.5%), which was driven mainly by higher coral cover in the open area and a barer substrate in the MPA. Hard and soft corals, as well as crustose coralline algae (CCA), drove the clustering of the forereef locations, while algae, substrate, and sediment drove the differences in the inshore sites (Figure 11).

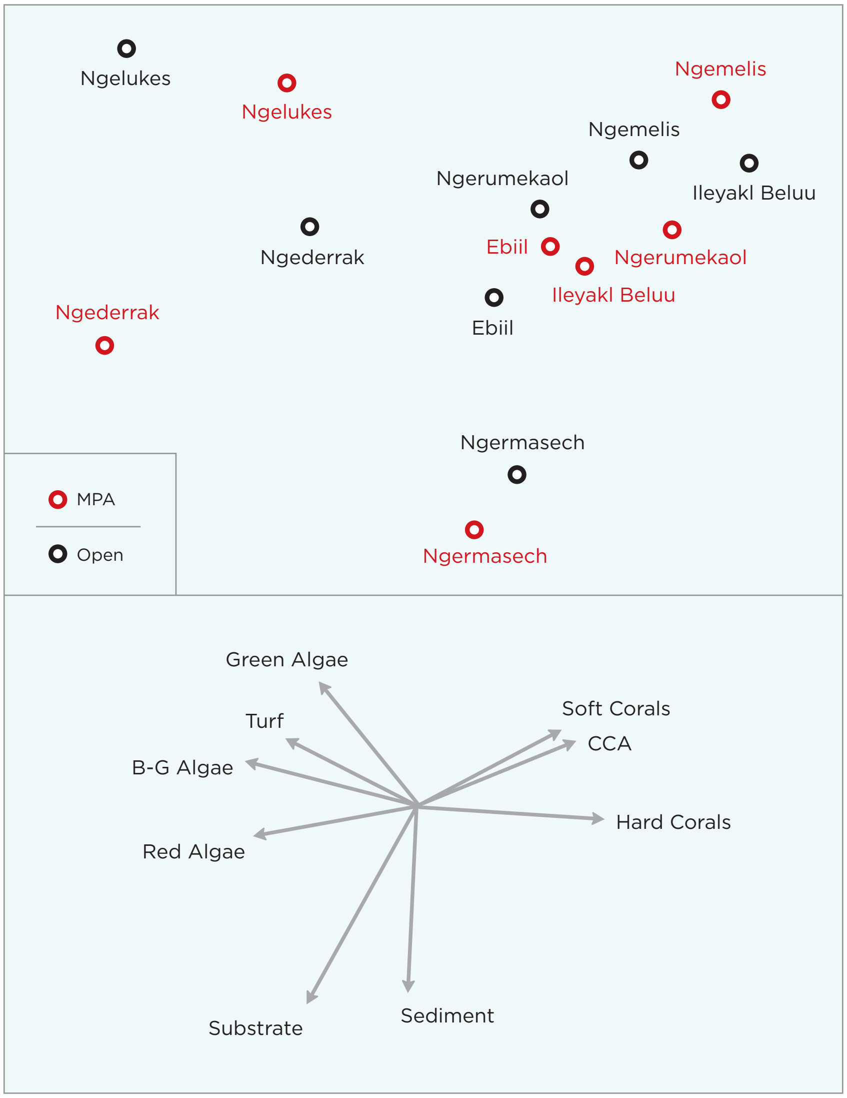


FIGURE 12.

Nonmetric multidimensional scaling plot of benthic cover by location. Stress = 0.07. Vectors are the primary taxa driving the ordination (Pearson Product movement correlations ≥ 0.5).

A total of 109 species of marine algae and seagrass were identified during the expedition, including 47 species of red algae, 43 species of green algae, 13 species of brown algae, and six species of seagrass (Appendix IV). Corals were identified to genus and growth form (e.g. branching, columnar, corymbose digitate, encrusting, foliose, free living, laminar, massive, submassive, tabular), resulting a total of 76 taxa of corals being identified during the expedition (Figure 13).

FIGURE 13.

Massive *Porites* spp. grow with a mix of other corals on a shallow reef flat.

Fishes

The MPAs we surveyed in Palau harbor more and larger fishes than unprotected areas nearby. ‘Resource species’ (i.e. those preferentially targeted by fishers) accounted for 78% of the total biomass sampled within MPAs, but only 63% in the unprotected areas. Resource fish biomass in Ngemelis (over 3 tonnes ha^{-1}, Figure 17) is comparable to that of pristine sites elsewhere in the Pacific (Knowlton and Jackson 2008, Sandin et al. 2008). Total resource fish biomass was, on average, twice as high in all MPAs relative to control areas, but three and a half times higher at the Ngermasech MPA than at its control, and three times higher in the Ngerumekaol MPA (Figure 18). Fish assemblage structure showed strong gradients, increasing dramatically in biomass and dominance of top predators from inshore to offshore, and from unprotected to MPAs (Figure 19).

Trophic Structure – The most striking difference in trophic (food web) structure between MPAs and open areas was that biomass of top predators was five times larger in the MPAs than at the control areas (Figure 21). Top predators accounted for 31% of the biomass in MPAs but only 10% in adjacent open areas (Figure 14). Secondary consumers and

FIGURE 14.

Predators like this red snapper (kedesau, *Lutjanus bohar*) are conspicuous inside MPAs.

herbivores had similar biomass within MPAs—accounting for 26% and 25%, respectively—and were not significantly different from open areas, although biomass was nearly one third larger for both trophic groups inside the MPAs compared to adjacent areas open to fishing. Planktivores comprised 18% of the biomass within MPAs and nearly 30% in open areas, although these differences were not significant (Figures 15, 16).

FIGURE 15.

Black-and-white snapper (kelalk, *Macolor niger*) feeding on plankton in German Channel.

FIGURE 16.

Mantas (choklemedaol, *Manta birostris*) and scissortail fusiliers (chadins, *Caesio caerulaurea*) feed on rich plankton soup.

Comparison of MPAs – We conducted an ordination (unconstrained PCA) of fish trophic biomass by MPA and overlaid MPA characteristics (e.g. MPA age, size, inshore vs. offshore, percent coral cover) over this ordination plot to examine the characteristics of these MPAs that explained their distribution in ordination space (Figure 22). Based on this analysis, age of the MPA was the most important variable in explaining the observed distribution, followed by size and whether it was inshore or offshore (Figure 20).

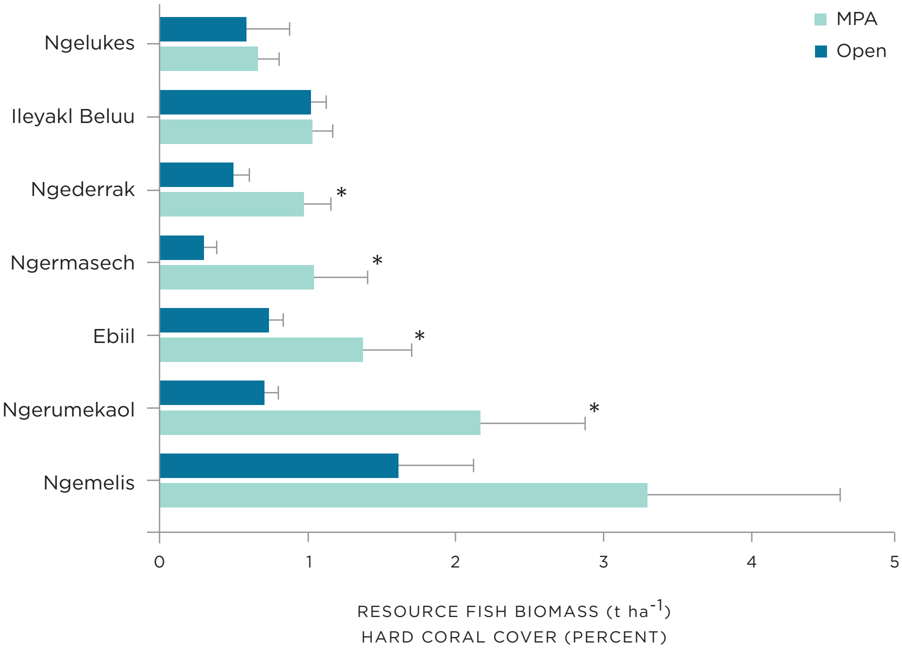


FIGURE 17.

Comparison of resource fish biomass (tonnes ha^{-1}, mean ± standard error) inside and outside Marine Protected Areas (MPAs). Asterisks denote MPA/control pairs that are significantly different.

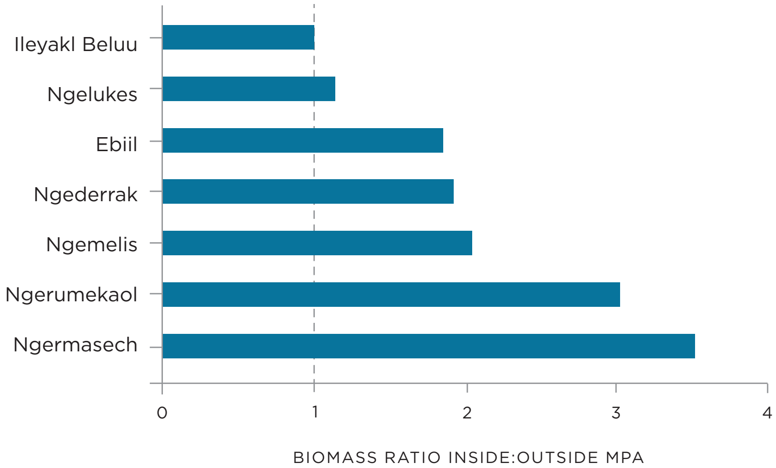


FIGURE 18.

Ratio of resource fish biomass inside/outside MPAs.

FIGURE 19.

Nonmetric multidimensional scaling plot of mean fish biomass for each MPA and adjacent open areas. Arrows denote the direction and magnitude from open area MPA in ordination space. Stress = 0.11.

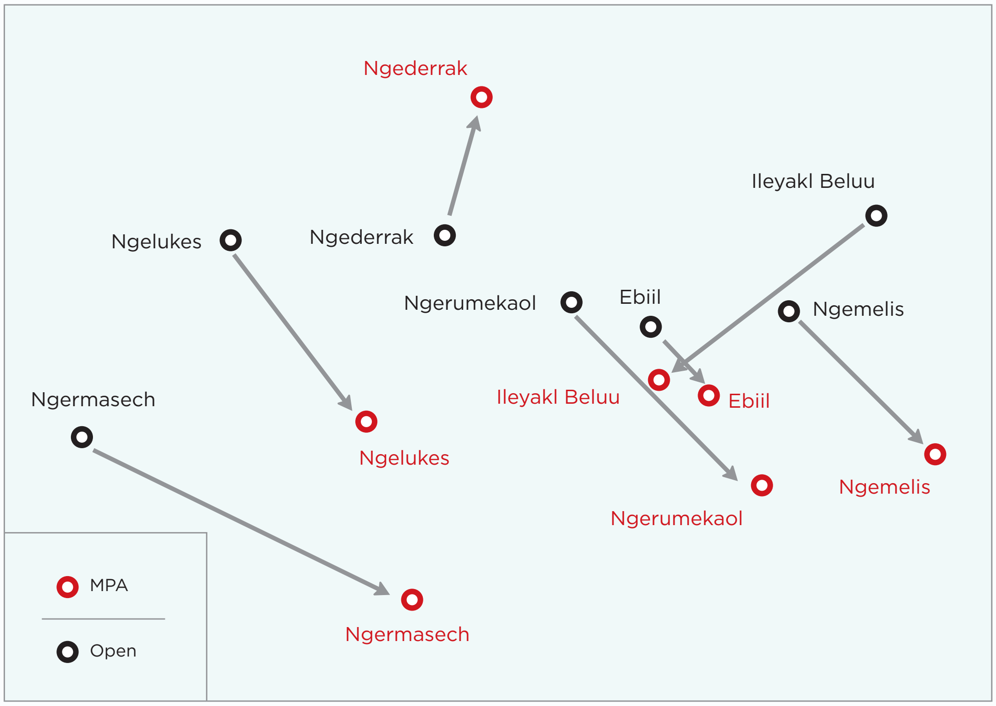


FIGURE 20.

The MPAs are home to abundant and diverse fish life. Here, a school of scissortail fusiliers (chadins, *Caesio caerulaurea*) swims above black-and-white snappers (kelalk, *Macolor niger*), rudderfishes (*komud, Kyphosus* spp.), and a grey reef shark (mederart, *Carcharhinus amblyrhynchos*).

FIGURE 21.

Biomass (t ha-1, mean ± standard error) by fish groups and conservation level (open to fishing and MPA) at the MPA surveyed during our expedition. The asterisk identifies significant changes between MPA and the unprotected area nearby.

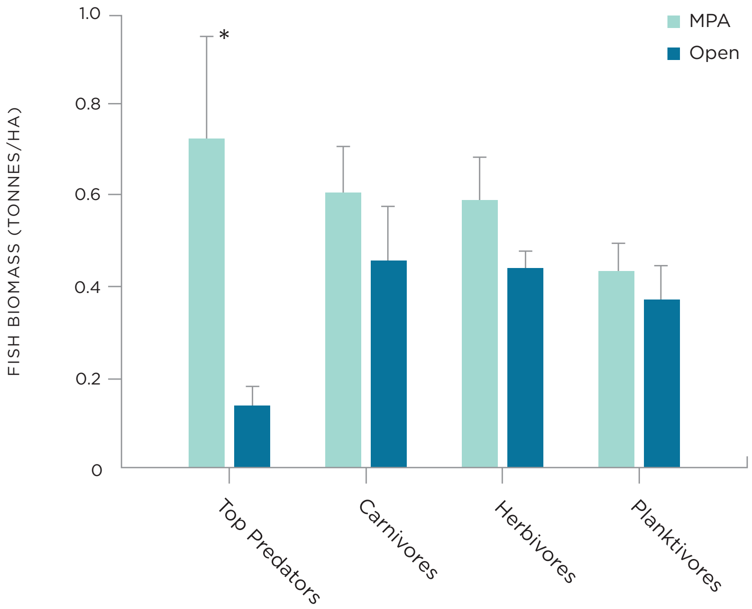
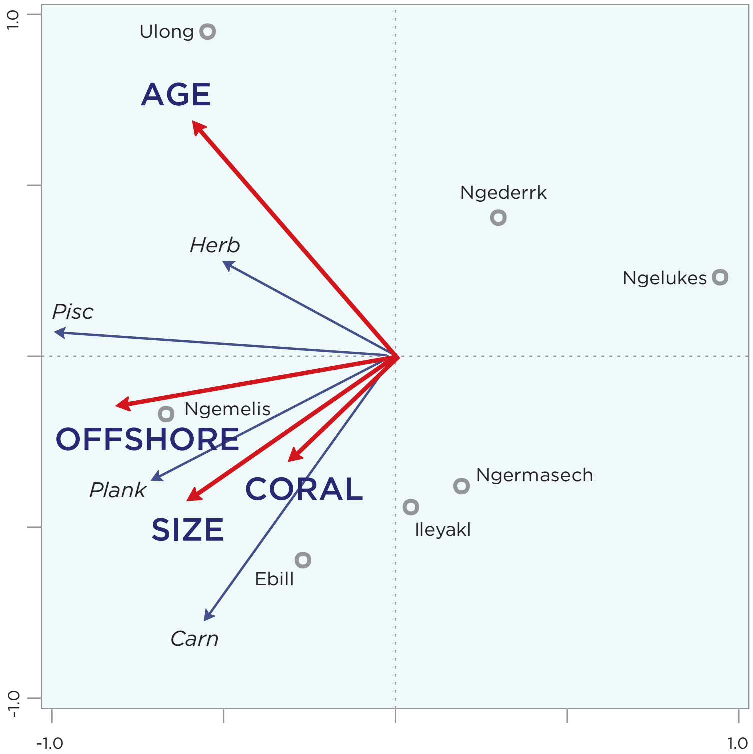


FIGURE 22.

Unconstrained PCA on fish trophic biomass by MPA and overlaid MPA characteristics (e.g. MPA age, size, inshore vs. offshore, percent coral cover).



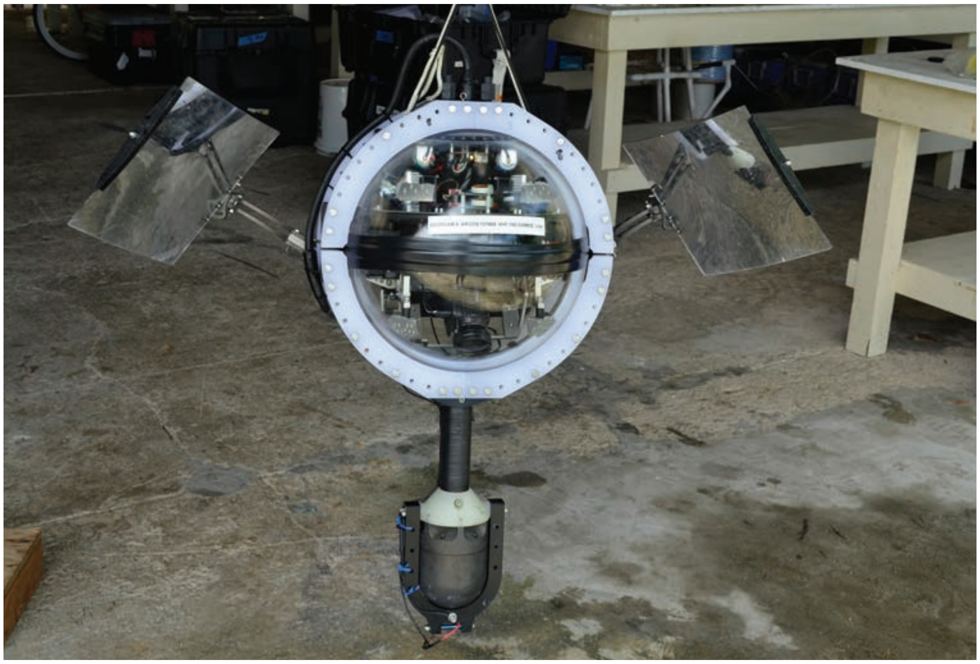
The Deep Sea

To explore the deep-sea life around Palau we used the National Geographic “drop-cams.” These are high-definition cameras encased in a boro-silicate sphere, which can be dropped off the side of a small boat. Inside the ball there is a computer that is programmed to film for a set amount of time, and then return to the surface. Drop-cams were deployed for three hours at a time, recording for 20 continuous minutes, followed by 40 minutes without lights and recording, for a total of three filming intervals per deployment. Drop-cams were baited with 1 kg of crushed bonito. A total of 26 deployments were conducted around Palau during the expedition (Figure 5) at an average depth of 1,125 m (range: 260–3,500 m).

A wide range of fish species were observed on the deep drop cameras including sharks, eels, rattails, and chimeras (Figure 24), with a total of 26 fish taxa from 19 families recorded during the expedition (Appendix V). Cutthroat eels (family Synaphobranchidae) were the most common and numerous fishes, occurring in 65% of the

FIGURE 23.

A National Geographic drop-cam, which allows for exploration of the deep sea to full ocean depth.



samples and accounting for nearly half of all the fishes observed. Rattails (family Macrouridae) were the second most common fish family, being present in 46% of the camera drops. In addition, we observed a wide range of mobile and sessile invertebrates from five different phyla, with Arthropoda (e.g. shrimps and crabs) being the most diverse and numerous (Appendix VI).

FIGURE 24.

Sample of deep-sea species filmed by drop cameras in Palau in September 2014. A: Spiny dogfish, 526 m depth. B: Rattail, 637 m. C: Tiger shark, 515 m. D: Cutthroat eels, 927 m.

The Offshore Environment

From our boat we observed pilot whales (*Globicephala* spp.), spinner dolphins (*Stenella longirostris*), seabirds (primarily sooty terns - *Onychoprion fuscatus*), a whale shark (*Rhincodon typus*), silky sharks (*Carcharhinus falciformis*), and mahi-mahi (*Coryphaena hippurus*). We observed fishes on 86% of pelagic camera deployments, from 16 families and 34 taxonomic groups (Appendix VII). Jacks (Carangidae) were the most common family, accounting for 80% of all fishes, followed by tunas and mackerels (Scombidae, 5%), and sharks (Carcharhinidae, 3%). Overall, 347 sharks were observed, comprising 16% of the observed pelagic fishes. Sharks were observed at 76% of all sites. Examples of species observed on pelagic cameras appear in Figure 25.

There were strong effects of both distance from the coast (inshore vs. offshore) and coast (east vs. west) on characteristics of the pelagic fish assemblages. Mean species richness was significantly higher on west coast than on the east coast, and offshore compared to inshore locations (Table 2). Mean total abundance of all fishes per deployment was nearly twice higher

TABLE 2.

Comparisons of species richness between coasts and distance from shore from pelagic camera stations.
Statistical results 2-way ANOVA with interactions. Test ratio = $F_{3,29}$ for full model and t-test for individual factors and interaction.

Term	Test Ratio	P	Multiple Comparisons	% diff.
Full model	4.80	0.009		
Distance from shore	2.33	0.028	Offshore > Inshore	54.7
Coast	2.60	0.015	West > East	61.7
Distance x coast	0.68	0.503		

TABLE 3.

Comparisons of total fish abundance between coasts and distance from shore from pelagic camera stations.
Statistical results of Generalized Linear Model with a Poisson distribution.

Term	X^2 Test Ratio	P	Multiple Comparisons	% diff.
Full model	115.9	<0.001		
Distance from shore	109.1	<0.001	Offshore > Inshore	186.9
Coast	4.3	0.038	West > East	27.7
Distance x coast	3.0	0.081		

at the offshore sites than at inshore sites, and 28% higher on the west coast compared the east coast (Figure 26, Table 3). During our expedition, the east coast was predominately protected from the main winds, while the west coast was more exposed to westerly trade winds. However, this pattern reverses during the year, so our spatial patterns may not be consistent over time.

FIGURE 25.

A. Pelagic camera bait arm attracting rainbow runners and silky sharks, B. Great Hammerhead (*Sphyrna mokarran*)

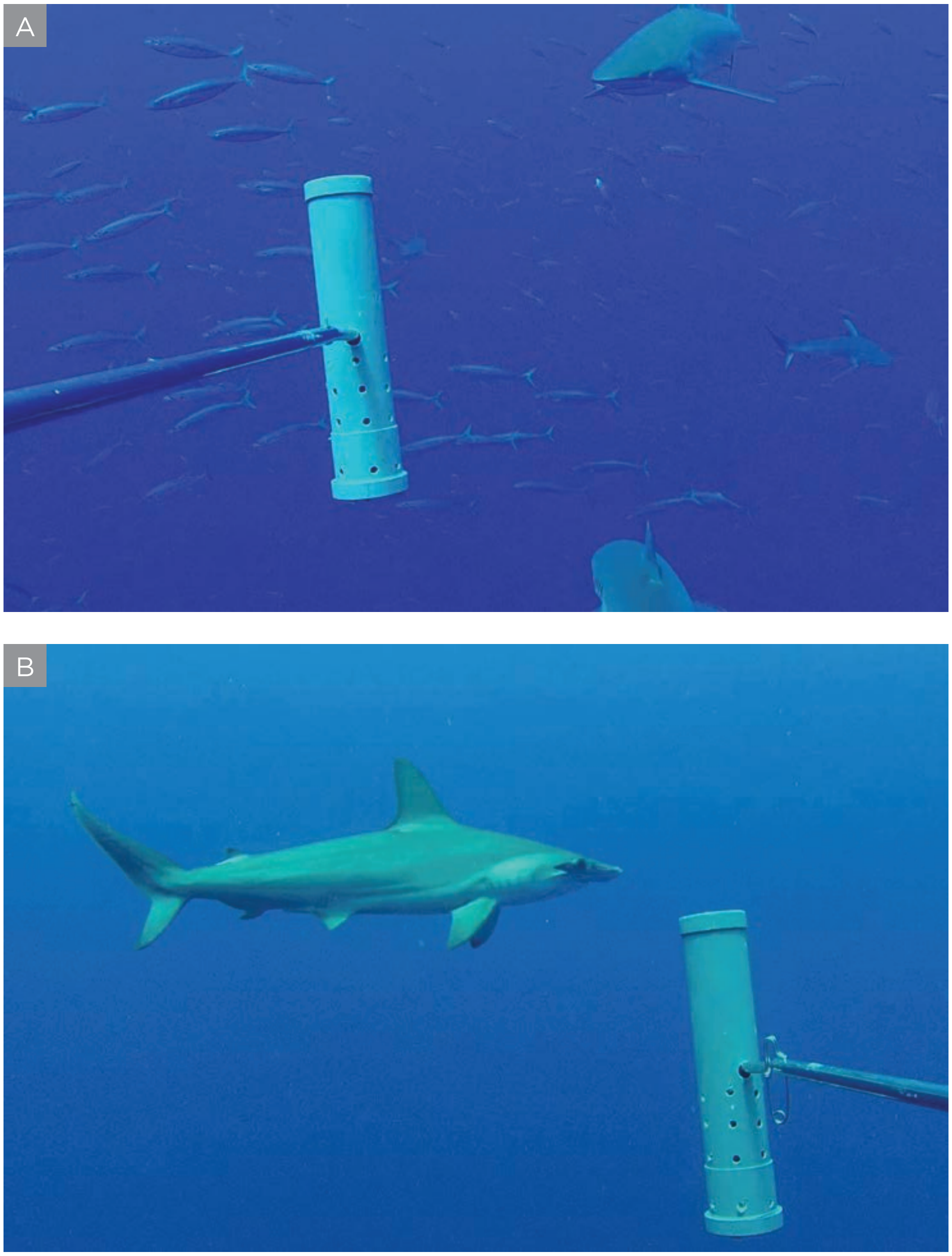
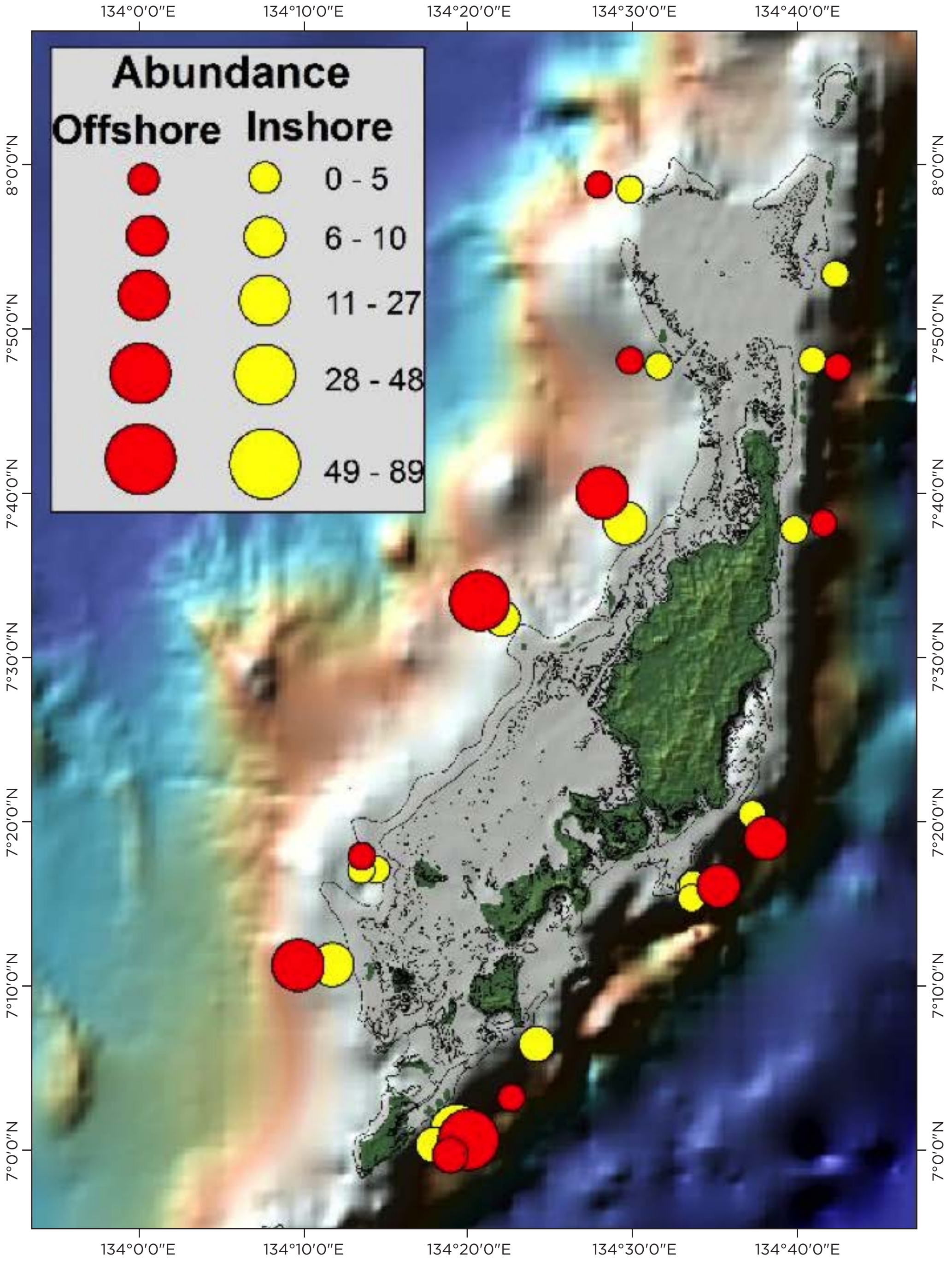


FIGURE 26.

Mean abundance of all fishes observed on pelagic cameras.



Microplastics Sampling

Given the increasing levels of plastic pollution in the ocean (Cózar et al. 2014, Jambeck et al. 2015), it is important to better understand the impact of microplastics in the ocean food web. To begin to do that, it is necessary to assess the amount and spatial distribution of plastics. We collected water samples at the surface (n = 12) and at 5 m (n = 10) and found that every sample contained plastic (16 pieces l^{-1} on average), with 19 pieces l^{-1} at 5 m depth and 12 pieces l^{-1} at the surface (Figure 26). Density of microplastics was more than twice as high in the lagoon (19 pieces l^{-1}) compared to windward locations (9 pieces l^{-1}), with leeward areas intermediate (15 pieces l^{-1}) (Figure 27).

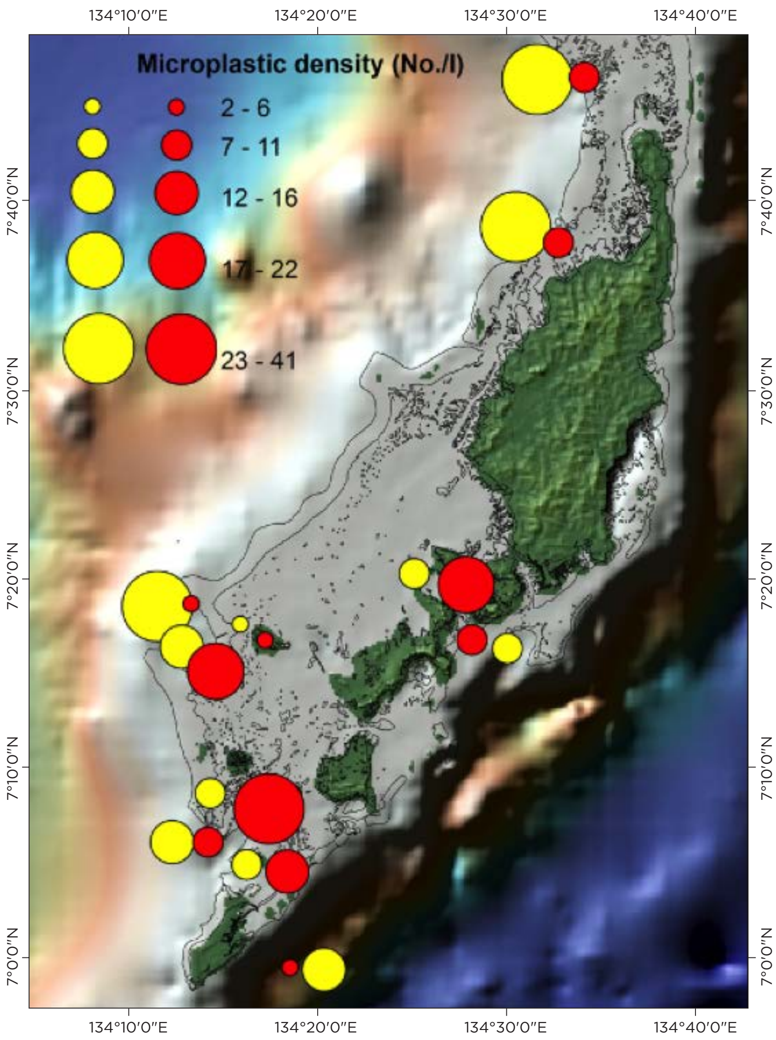


FIGURE 27.

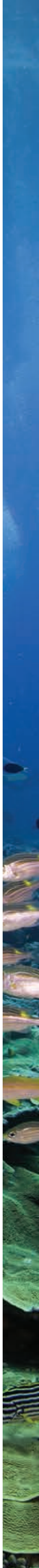
Distribution of microplastics around Palau. Red circles represent samples taken at the surface. Yellow circles represent samples taken at 5 m depth.

We collected microplastics data in Palau's waters in partnership with the Adventurers and Scientists for Conservation's Global Microplastics Project.

DISCUSSION & CONCLUSIONS

Palau possesses some of the best-preserved coral reefs remaining in Coral Triangle, where much of the world's marine biodiversity lies (Figure 28). The majority of the MPAs in Palau surveyed during our expedition are effective in conserving resource fish biomass relative to adjacent unprotected sites. Resource fishes were significantly more abundant and larger within MPAs compared to unprotected areas nearby. There were no differences in coral cover and benthic community structure between MPAs and adjacent unprotected areas, therefore the greater abundance of resource fish inside MPAs is likely due to protection and not to differences in the state of the coral community.

The most striking difference in the fish assemblages between MPAs and unprotected areas was that of top predator biomass, which was five times larger inside the MPAs than at unprotected sites; top predators accounted for a third of the fish biomass in MPAs, but only one tenth of that in adjacent unprotected areas. This clearly indicates that no-take MPAs in Palau are meeting their goals of conservation of resource fish. The level of enforcement of the MPAs is high by most standards due to local community support and patrolling. Conservation rangers were present at every MPA we surveyed and we were told that compliance is high. MPAs benefit adjacent fisheries by protecting large spawning individuals and through the spillover of adults into fished areas (Russ et al. 2003 and 2004, Tupper 2007, Harmelin-Vivien et al. 2008, Stamoulis and Friedlander 2013). The effectiveness of Palau's extensive network of MPAs is therefore likely benefiting the nearshore fisheries of the entire country.



The deep-sea biota around Palau was relatively unknown prior to our expedition and this research therefore serves as a valuable baseline for future investigations. We encountered a diverse assemblage of fishes, including numerous deep-water sharks, rattails, and eels, and we are currently working with deep-sea specialists at the University of Hawaii to identify these taxa to the highest taxonomic resolution possible.

Palau's pelagic fauna is diverse and rich. The number of species and individuals observed per sample were comparable to those observed in the Chagos Marine Reserve, currently the third largest marine protected area in the world at 640,000 km^2 (Meeuwig, unpubl. data). Clear spatial patterns in both coasts and distance from shore highlight significant spatial structure in pelagic populations. Such patterns have implications for large-scale protection that will need to ensure that representative areas of these locations are included.

Although the protection of far-ranging species presents a major challenge for spatial management, there is good evidence that open ocean MPAs have the potential to dramatically reduce the overall mortality of these species by protecting critical areas necessary for reproduction and feeding (Norse et al. 2005, Game et al. 2009). Despite the ability of many pelagic species to move great distances, some individuals will likely spend their entire life inside the new sanctuary, thus increasing the density of marine life inside the sanctuary, boosting genetic diversity, and increasing local reproductive output, which will in turn benefit adjacent fisheries (Hooker and Gerber 2004, Pala 2009, Grüss et al. 2011).

FIGURE 28.

From the coasts to the open ocean and from small to large organisms, Palau's marine ecosystems are unlike anywhere else on Earth. *(Photo at right and page 28)*

Researchers in the western Pacific previously found that half of the skipjack tuna spend their entire lives within a radius of 675–750 km, and yellowfin tuna were found to have even smaller ranges (Sibert and Hampton 2003). Therefore Palau can achieve benefits from domestic conservation and fishery development policies, although international cooperation will also be necessary. The long reach of global fishing fleets have eliminated nearly all natural refugia, and as a result we urgently need to protect large areas of the ocean in order to achieve sustainable ecosystems.

Climate change is predicted to redistribute the world's fisheries in a dramatic way over the coming decades (Cheung et al. 2008). Palau is projected to lose 25% of its fisheries catch potential by 2050 because of climate change alone (Cheung et al. 2010). This large-scale loss of catch will have major implications for the economy of Palau.

A major question is whether a large fishing closure as part of the Palau National Marine Sanctuary would benefit local fisheries. Recent research shows that closing the high seas to fishing would increase fisheries yield in countries' exclusive economic zones by 30%, and fisheries profit by more than 100% (White and Costello 2014). That would also increase the social equitability of fishing, by shifting benefits to local fishers away from large foreign fleets fishing pelagic migratory species (Sumaila et al. 2015). An increasing body of research worldwide also shows that no-take marine reserves result in improved, more stable, and more profitable fisheries around the reserves (e.g. Sala et al. 2013). These results suggest that the proposed closure to fishing of 80% of Palau's EEZ may benefit fishing of migratory species such as tuna in waters nearer to shore by local Palauan fishers.

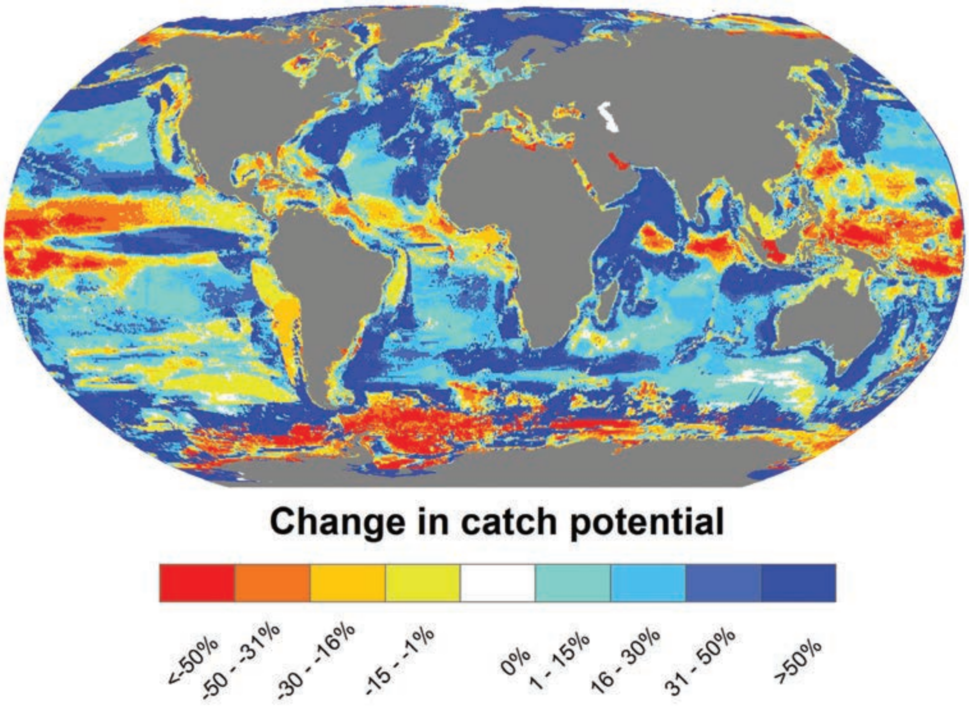


FIGURE 29.

Change in maximum catch potential (10-year average) from 2005 to 2055. IPCC Emission Scenarios A1B (from Cheung et al. 2010).

A recent economic study in Palau showed that divers would be willing to pay more for diving in no-take marine reserves because of more and larger fishes (Koike et al. 2014, Figure 30). The economic benefits of more protection of just two charismatic species (Napoleon wrasse [*maml*] and bumphead parrotfish [*kemedukl*], currently protected in Palau) would be 100 to 1,000 times greater than the market value if those species were fished. In addition, the value of live sharks in the water brings in $1.9 million to Palau's economy through dive tourism, compared to $10,800 if these sharks were killed for sale (Vianna et al. 2012). These results suggest that greater levels of protection may bring greater economic revenue to Palau (Figure 31).

With a longstanding tradition of fisheries management and the thoughtful stewardship of its waters, Palau has already established itself as a world leader in marine conservation. We believe that the creation of a large sanctuary around Palau will benefit the entire country through increased tourism revenues, improvement of local fisheries, and long-term sustainability of marine resources.

FIGURE 30.

Healthy reefs are Palau's major economic and cultural asset.

FIGURE 31.

Jellyfish Lake is a major contributor to Palau's tourist economy.

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APPENDICES

Appendix 1.

Expedition Team

Name	Role	Institution
Enric Sala	Expedition leader	National Geographic Society
Alan Friedlander	Chief Scientist - fishes	National Geographic Society/U Hawaii
Jennifer Caselle	Fishes	U California, Santa Barbara
Kike Ballesteros	Algae/benthos	Centre d'Estudis Avançats, Spain
Yimnang Golbuu	Corals	Palau International Coral Reef Center
Marine Gouezo	Corals	Palau International Coral Reef Center
Dawnette Olsudong	Corals	Palau International Coral Reef Center
Jessica Meeuwig	Pelagic cameras	Centre for Marine Futures, U Western Australia
Tom Letessier	Pelagic cameras	Centre for Marine Futures, U Western Australia
Manu San Felix	UW camera	National Geographic Society
Nathan Lefevre	UW assistant	National Geographic Society
Dave McAloney	Dive safety officer	National Geographic Society
Neil Gelinas	Producer/camera	National Geographic Society
Jesse Goldberg	Cameraman	National Geographic Society
Alan Turchik	Drop camera	National Geographic Society

Appendix II.

Methods

We conducted surveys of nearshore Marine Protected Areas (MPAs), offshore pelagic fishes, and deep benthos over the course of the expedition.

Marine Protected Areas Surveyed

We examined a subset of MPAs within the Palau PAN and compared ecosystem function within these areas to adjacent habitats. These areas range in age from 38 years of protection (Ngerumekaol Spawning Area) to Ileyakl Beluu, which was created in 2005, and ranged in size from 0.5 km^{-2} (Ngelukes Conservation Area) to 40 km^{-2} (Ngemelis Island Complex) (Table 1). Although PICRC is currently monitoring some of these MPAs, we used comprehensive integrated survey methods conducted at the same time, therefore adding value to the information that is currently being collected by PICRC and others.

Benthos - Characterization of the benthos was conducted along a 50 m-long transect parallel to the shoreline at each sampling depth strata. For algae, corals, and other sessile invertebrates we used a line-point intercept methodology along transects, recording the species or taxa found every 20 cm on the measuring tape.

Fishes - At each depth stratum within a site, divers counted and estimated lengths for all fishes encountered within fixed-length (25-m) belt transects whose widths differed depending on direction of swim. All fish ≥ 20 cm total length (TL) were tallied within a 4 m wide strip surveyed on an initial “swim-out” as the transect line was laid (transect area = 100 m^2). All fishes < 20 cm TL were tallied within a 2 m wide strip surveyed on the return swim back along the laid transect line (transect area = 50 m^2).

Pelagic Cameras

We used mid-water Baited Remote Underwater Video Stations (BRUVS) to survey the pelagic fish and shark assemblage of Palau, and to determine how mid-water fish assemblages vary with distance from reef edge and as a function of geographic location (Letessier *et al*., 2013). Each rig consisted of a bar with two GoPro cameras 80 cm apart with an inward convergent angle of 8°. Five units were deployed concurrently and separated by 200 m of surface line (800 m in total). The first and last camera rigs had GPS trackers to document the path of the drifting long line. The long line was deployed perpendicular to the current, which was predominantly longshore in either a southerly or northerly direction. Rigs were baited with approximately 800 g of mashed bonito and deployed twice daily, with a minimum filming time of two hours. The soak time is consistent with Letessier et al (2013) and reflected logistical constraints of the expedition.

Paired sites were sampled at 15 locations around Palau (Fig. 2). At each location, the long line was deployed ca. 1 nm from the reef with a second site approximately 3.5 nm offshore. A total of 29 sites were sampled, with one location having only a single site due to weather conditions. More than 600 hours of video imagery was collected.

Deep Drop-camera Surveys

National Geographic's Remote Imaging Team developed deep ocean drop-cams, which are high definition cameras encased in a borosilicate glass sphere that are rated to 10,000 m depth. Drop-cams have an onboard VHF transmitter that allows for recovery using locating antennae with backup location achieved via communication with the ARGOS satellite system. We deployed drop-cameras on seamounts and other unique geological features on an opportunistic basis, and replied on bathymetry charts and local knowledge for optimal deployment locations. Deep-water drop-cam deployments were co-located at 11 of the 15 locations sampled by pelagic cameras, generating paired benthic and pelagic observations along with accurate depth measurements.

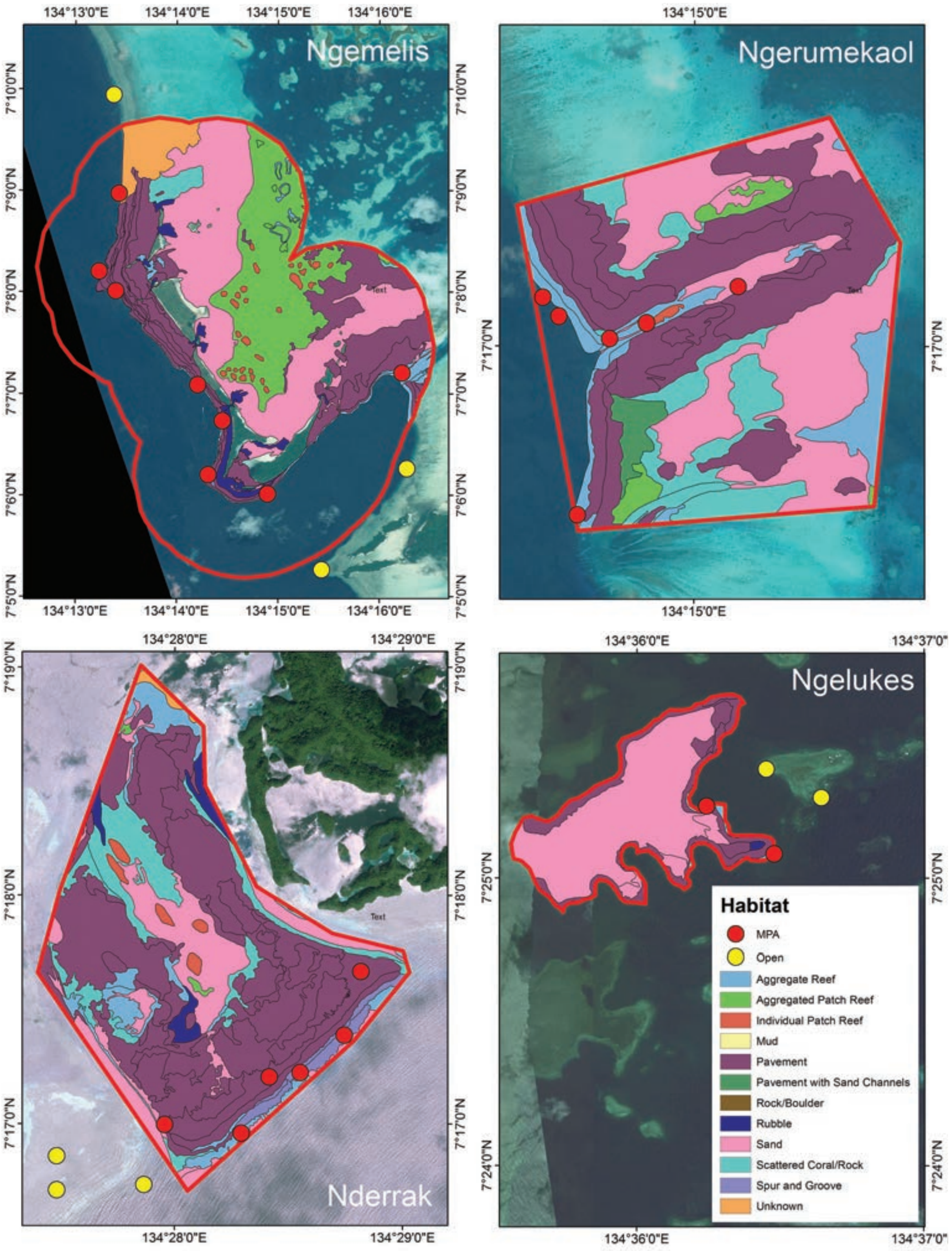
Statistical Analyses

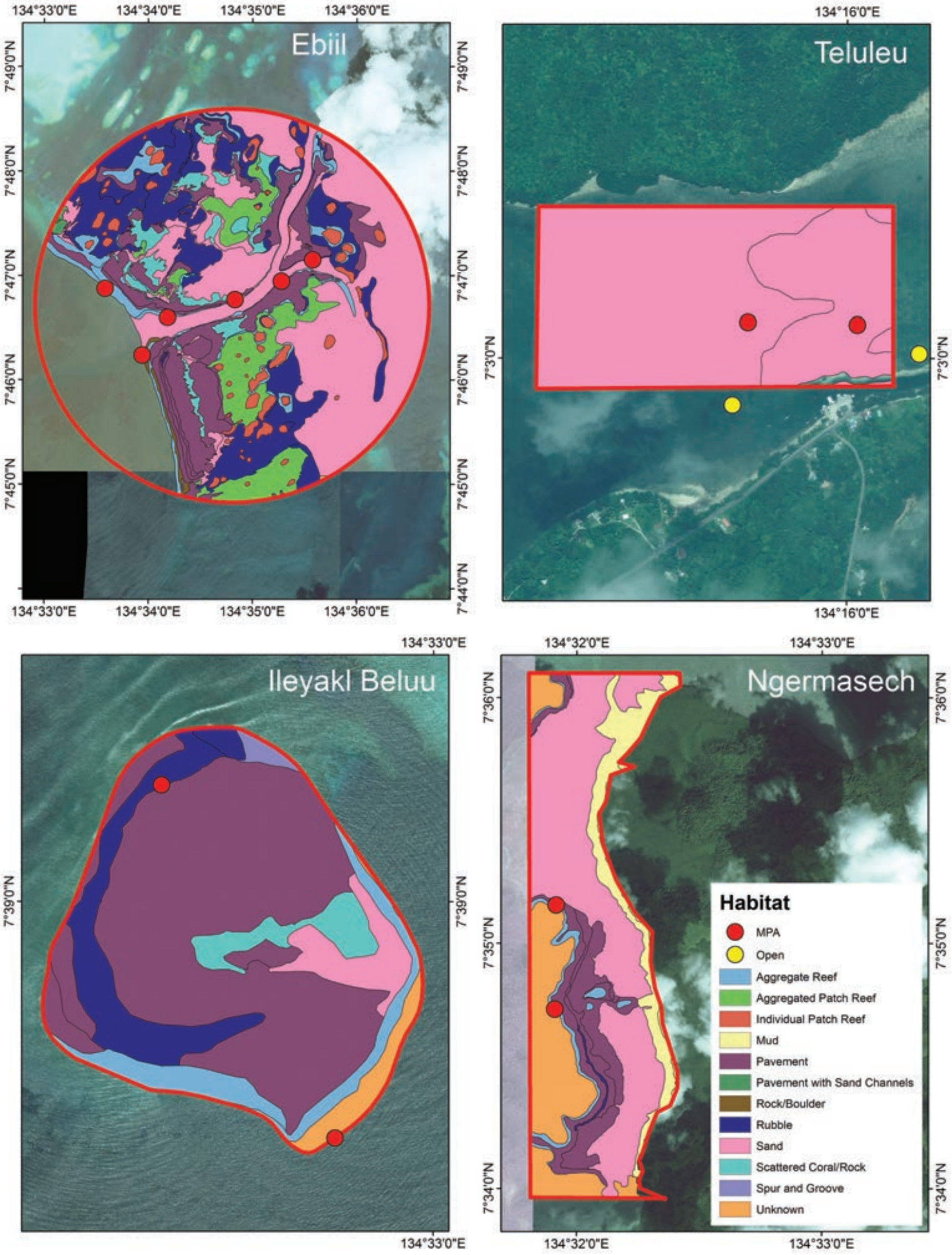
Benthic community composition among MPAs and adjacent open areas was compared using PERMANOVA. Comparisons of coral cover between MPAs and adjacent areas were conducted using Student's t-test. Non-metric multi-dimensional scaling (nMDS) analysis, coupled with an analysis of similarities (ANOSIM) test, was conducted using PRIMER v6 to examine differences in benthic communities and fish assemblage structure between MPAs and adjacent open areas. A Bray–Curtis similarity matrix was created for percent cover of major benthic components and biomass of fish species. Prior to conducting the nMDS, benthic data were arcsin square root transformed and fish biomass data were ln(x+1) transformed. The benthic nMDS plot was overlaid with the primary component vectors driving the ordination using a Pearson correlation at $p > 0.5$.

Fish species richness was estimated as the total number of species observed per station by the pair of divers. Species diversity was calculated from the Shannon-Weaver Diversity Index (Ludwig and Reynolds 1988): $H'=-\sum (p_i 1n(p_i)$, where p_i is the proportion of all individuals counted that were of species i. Fish assemblage characteristics (e.g., species richness, numerical abundance, biomass, and diversity) were compared among locations using One-way ANOVA. Unplanned comparisons between pairs were examined using the Tukey-Kramer HSD. Fish trophic biomass among locations was compared using a Kruskal-Wallis rank sum test with Dunn's test for unplanned multiple comparisons. Unconstrained PCA on fish trophic biomass by MPA and overlaid MPA characteristics (e.g., MPA age, size, inshore vs. offshore, percent coral cover).

Appendix III.

Habitat maps and sampling locations




Ebiil
134°33'0"E
134°34'0"E
134°35'0"E
134°36'0"E
7°49'0"N
7°48'0"N
7°47'0"N
7°46'0"N
7°45'0"N
7°44'0"N
Teluleu
134°16'0"E
7°3'0"N
Ileyakl Beluu
134°33'0"E
7°39'0"N
Ngermasech
134°32'0"E
134°33'0"E
7°36'0"N
7°35'0"N
7°34'0"N
Habitat
MPA
Open
Aggregate Reef
Aggregated Patch Reef
Individual Patch Reef
Mud
Pavement
Pavement with Sand Channels
Rock/Boulder
Rubble
Sand
Scattered Coral/Rock
Spur and Groove
Unknown

Appendix IV.

Algal species observed during the expedition

J-fish = Jellyfish lake, Omed = Omedes (Geruherugairu Passage).

Species Name	1	2-6	7-12	13-28	J-fish	29-40	Ulong	41-52	53-56	57-60	61-64	Omed	65-68
Phaeophyceae													
Dictyopteris repens								x				x	
Dictyota bartayresiana	x	x					x						x
Dictyota canaliculata											x		
Dictyota friabilis		x	x					x		x			
Dictyota grossidentata	x												
Lobophora variegata		x	x	x		x		x	x	x	x	x	
Padina australis												x	
Padina cf. pavonica			x				x				x		x
Sargassum ilicifolium							x			x			
Stypopodium zonale											x		
Turbinaria conoides							x						
Turbinaria decurrens		x											
Turbinaria ornata				x		x	x						
Chlorophyta													
Anadyomene wrightii				x									
Avrainvillea amadelpha				x		x							
Avrainvillea lacerata				x	x								
Boergesenia forbesii												x	x
Boodlea composita												x	
Bornetella sphaerica			x				x						
Caulerpa brachypus									x			x	
Caulerpa cf. fastigiata					x								
Caulerpa macrodisca												x	
Caulerpa macrophysa			x			x							
Caulerpa opposita						x							
Caulerpa peltata												x	
Caulerpa racemosa												x	x
Caulerpa racemosa v. lamourouxii												x	
Caulerpa serrulata		x	x				x			x		x	x
Caulerpa sertularioides							x						
Caulerpa urvilleana													x
Caulerpa verticillata					x							x	

APPENDIX IV. CONTINUED.

Species Name	1	2–6	7–12	13–28	J-fish	29–40	Ulong	41–52	53–56	57–60	61–64	Omed	65–68
Chlorodesmis fastigiata	x		x	x		x		x					
Dictyospheria versluysii				x		x		x					
Halimeda cuneata f. undulata		x	x			x		x	x				
Halimeda cylindracea							x						x
Halimeda hederacea		x	x	x		x	x	x	x	x	x	x	
Halimeda incrassata			x	x					x				
Halimeda macroloba							x					x	x
Halimeda macrophysa				x		x		x	x				
Halimeda micronesica				x		x		x	x				
Halimeda minima				x		x		x		x			
Halimeda opuntia			x			x	x	x	x			x	x
Halimeda simulans												x	x
Halimeda taenicola				x		x			x				
Neomeris vanbosseae		x	x	x		x	x	x				x	
Rhipilia orientalis												x	
Rhipilia sinuosa			x	x		x		x	x	x			
Spongocladia dichotoma												x	
Spongocladia vaucheriaeformis						x							
Tydemania expeditionis			x			x					x		
Udotea argentea				x									x
Udotea geppii												x	
Valonia fastigiata						x							
Valonia ventricosa			x	x		x		x	x		x	x	
Valoniaceae unidentified						x							
Rhodophyta													
Actinotrichia fragilis				x		x		x		x	x	x	
Amphiroa foliacea								x	x	x			
Amphiroa fragilissima						x	x			x	x	x	
Amphiroa tribulus						x	x	x	x	x	x		
Ceratodictyon spongiosum													x
Cryptonemia sp.												x	
Dasyphila plumarioides				x									
Dudresnaya hawaiiensis									x				
Ganonema farinosum						x		x					
Gelidiopsis intricata						x							
Gibsmithia hawaiiensis				x		x		x	x				
Gracilaria salicornia												x	
Haematocelis sp.		x	x	x		x		x	x				
Halichrysis coalescens												x	
Haloplegma duperreyi								x					

APPENDIX IV. CONTINUED.

Species Name	1	2–6	7–12	13–28	J-fish	29–40	Ulong	41–52	53–56	57–60	61–64	Omed	65–68
Halymenia dilatata												x	
Halymenia durvillei												x	
Halymenia maculata									x			x	
Heterosiphonia crispella													x
Hydrolithon farinosum	x	x	x	x		x		x	x		x	x	
Hydrolithon gardineri						x							
Hydrolithon onkodes	x	x	x	x		x		x	x	x	x		
Hydrolithon reinboldii	x	x	x	x		x		x		x		x	
Hydrolithon samoense				x				x		x			
Hypnea pannosa								x					
Laurencia tronoi	x							x					
Lithophyllum bamleri		x	x			x		x					
Lithophyllum okamurae												x	
Lithophyllum pygmaeum			x					x		x			
Lithothamnion orthoblastum				x		x							
Martensia elegans								x					
Mastophora pacifica						x		x					
Mesophyllum erubescens				x									
Neogoniolithon fosliei				x		x							
Neogoniolithon frutescens							x						
Peyssonnelia boergesenii				x		x		x		x	x		
Peyssonnelia caulifera												x	
Peyssonnelia obscura									x		x		
Peyssonnelia orientalis				x				x					
Peyssonnelia sp.			x	x		x							
Portieria hornemanni								x					
Titanophora cf. pikeana									x				
Tolypiocladia calodictyon													x
Tricleocarpa cylindrica			x										
Tricleocarpa fragilis		x	x										
Vanvoorstia spectabilis										x			
Zellera tawallina			x	x		x							
Seagrasses													
Cymodocea serrulata	x											x	x
Enhalus acoroides												x	x
Halophila minor							x						x
Halophila ovalis	x												x
Syringodium isoetifolium	x												
Thalassia hemprichii	x												x

Appendix V.

Fish taxa observed on deep sea drop camera deployments

Nmax = the average of the maximum number of individuals of that species observed per video frame.
% Freq = percent frequency of occurrence (N = 26 deployments). % Nmax = percentage of total Nmax for all species combined.

Family	Common Name	Taxa	N_{max}	% Freq	% N_{max}	Depth range (m)
Argentinidae	Smelt		0.23	7.69	4.44	(645)
Ateleopodidae	Tadpole fishes		0.08	7.69	1.48	(1016-1652)
Carangidae	Jacks	*Caranx lugubris*	0.04	3.85	0.74	(178)
Carcharhinidae	Tiger shark	*Galeocerdo cuvier*	0.04	3.85	0.74	(516-516)
Centrophoridae	Gulper Sharks	*Centrophoris* sp.	0.12	11.54	2.22	(547-744)
Chimaeridae	Chimeras	*Hydrolagus* sp.	0.04	3.85	0.74	(1580)
Congridae	Conger eel		0.27	23.08	5.19	(526-1413)
Dalatiidae	Kitefin shark	*Dalatius* sp.	0.15	7.69	2.96	(1172-1652)
Dasyatidae	Rays		0.04	3.85	0.74	(2400)
Epigonidae	Deepwater Cardinalfish	*Epigonus* sp.	0.04	3.85	0.74	(516-516)
Etmopteridae	Lantern shark	*Etmopterus* sp.	0.38	23.08	7.41	(1413-1738)
Gempylidae	Oilfish	*Ruvettus pretiosus*	0.08	7.69	1.48	(526)
Hexanchidae	6-gill shark	*Hexanchus griseus*	0.08	7.69	1.48	(744)
Macrouridae	Rattails	*Bathygadinae*	0.08	3.85	1.48	(526)
		Coelorinchus sp.	0.15	11.54	2.96	(637-643)
		Gadomus sp.1	0.04	3.85	0.74	(645)
		Macrourinae	0.04	3.85	0.74	(637)
		Others	0.31	26.92	5.93	(1288)
Moridae	Codlings	*Antimora* sp.	0.19	15.38	3.70	(637)
Ophidiidae	Cusk eel		0.23	15.38	4.44	(972)
Pseudotriakidae	False Catshark	*Pseudotriakis microdon*	0.04	3.85	0.74	(1652)
Squalidae	Dogfishes	*Squalus mitsukurii*	0.08	7.69	1.48	(1108-1738)
		Squalus sp.	0.04	3.85	0.74	(1016-1016)
Synaphobranchidae	Cutthroat eel	*Histiobranchus* sp.	0.12	3.85	2.22	(645)
		Synaphobranchus sp.	1.23	46.15	23.70	(526-590)
		Others	1.08	26.92	20.74	(645-645)

Appendix VI.

Invertebrate taxa observed on deep sea drop camera deployments

Phylum	Class	Order	Family	Taxa	Common name
Porifera					Sponge
Cnidaria	Anthozoa	Pennatulacea			Sea pen
Cnidaria	Anthozoa	Actiniaria	Actiniidae		Sea anemone
Cnidaria	Anthozoa	Alcyonacea	Alcyoniidae		Soft corals
Cnidaria	Anthozoa	Alcyonacea	Acanthogorgiidae		Gorgonians
Arthropoda	Malacostraca	Decapoda	Aristeidae		Deep sea shrimp
Arthropoda	Malacostraca	Decapoda	Xanthidae		Mud crab
Arthropoda	Malacostraca	Decapoda	Pandalidae	*Heterocarpus* sp.	Deep sea shrimp
Arthropoda	Malacostraca	Decapoda	Mathildellidae		Deep sea crab
Arthropoda	Malacostraca	Decapoda	Pandalidae		Pandalid shrimp
Arthropoda	Malacostraca	Decapoda	Homolidae		Carrier crab
Arthropoda	Malacostraca	Decapoda	Leucosiidae		Crab
Arthropoda	Malacostraca	Decapoda	Lithodidae		King crab
Arthropoda	Malacostraca	Decapoda	Inachidae		Arrow crab
Arthropoda	Malacostraca	Decapoda	Pandalidae	*Plesionika* sp.	Pandalid shrimp
Mollusca	Cephalopoda	Nautilida	Nautilidae	Nautilus pompilius	Chambered Nautilus
Echinodermata	Echinoidea				Sea urchins
Echinodermata	Holothuroidea				

Appendix VII.

Family, taxa, and total relative abundance observed on mid-water Baited Remote Underwater Video Stations (BRUVS)

Family	Taxon	Common name	Total
Acanthuridae	*Naso* sp.	Unicornfish	1
	Naso vlamingii	Bignose unicornfish	3
Balistidae	*Pseudobalistes flavimarginatus*	Yellowmargin triggerfish	1
	Pseudobalistes fuscus	Bluestriped triggerfish	5
Blenniidae	*Aspidontus* sp.	Cleaner mimic blenny	4
	Aspidontus taeniatus	Cleaner mimic blenny	16
Carangidae	*Carangoides ferdau*	Barred jack	1
	Caranx sexfasciatus	Bigeye trevally	154
	Decapterus macarellus	Mackerel scad	435
	Decapterus sp.	Mackerel scad	969
	Elagatis bipinnulata	Rainbow runner	45
	Naucrates ductor	Pilotfish	1
Carcharhinidae	*Carcharhinus amblyrhynchos*	Gray reef shark	15
	Carcharhinus falciformis	Silky shark	55
	Carcharhinus limbatus	Blacktip shark	2
	Galeocerdo cuvier	Tiger shark	1
Centrolophidae	*Seriolella* sp.	Medusafish	151
Coryphaenidae	*Coryphaena hippurus*	Dolphinfish	26
Echeneidae	*Echeneis naucrates*	Sharksucker	15
Ephippidae	*Platax teira*	Blunthead batfish	6
Fistulariidae	*Fistularia commersonii*	Coronetfish	17
Istiophoridae	*Istiompax indica*	Black marlin	2
Molidae	*Mola mola*	Ocean sunfish	1
Monacanthidae	*Aluterus scriptus*	Scrawled filefish	1
	Monacanthidae sp.	Filefish	69
Priacanthidae	*Priacanthus* sp.	Bigeye	5
Scombridae	*Acanthocybium solandri*	Wahoo	8
	Euthynnus affinis	Mackerel tuna	5
	Sarda sp.	Bonito	17
	Scombridae sp.	Mackerel-tuna-bonito	1
	Thunnus alalunga	Albacore tuna	78
Sphyraenidae	*Sphyraena barracuda*	Great barracuda	3
Sphyrnidae	*Sphyrna lewini*	Scalloped hammerhead shark	1
	Sphyrna sp.	Hammerhead shark	1
Unidentified	Unidentified		16
Grand Total			2131

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