

Marine protected areas for deepwater fish populations: an evaluation of their effects in Hawai'i

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Abstract The success of marine protected areas (MPAs) as a tool for conservation and fisheries management has been well documented. However, these results have typically been seen in shallow water systems and questions remain whether this management strategy could be successfully applied to deepwater ecosystems. Our objectives were to determine the efficacy of four deepwater MPAs called bottomfish restricted fishing areas (BRFAs), with various time spans of protection, monitored at depths between 90 and 310 m from 2007 to 2011 for six species of deepwater snapper and one grouper harvested in the Main Hawaiian Islands. Our results suggested that the duration of protection influenced reserve effects, particularly for target species. Mean fish length, and in some cases abundance, increased for one or more of the most economically important target species inside nearly all tested BRFAs. In addition, more mature fish were seen inside the BRFA with the longest duration of protection (~14 years); species richness increased outside this area while inside it remained the same. Here, we provide the first evidence that deepwater MPAs can have positive effects on deepwater species and

that many protection effects were consistent with results found in shallow water ecosystems. While these findings are novel, additional data over greater temporal scales will be necessary to determine whether these trends will continue and if others will become important over time.

Introduction

Marine protected areas (MPAs; marine areas that exclude some or all forms of harvest) have been used worldwide as a conservation tool and long-term fishery management strategy to benefit fish stocks (Roberts and Polunin 1991; Babcock et al. 2010; Gaines et al. 2010). While there are numerous potential benefits to employing MPAs (e.g., protect biodiversity, habitat, genetic diversity), one of the primary benefits is linked to the exponential increase in fish fecundity with body size (Bohnsack 1994; Roberts and Polunin 1991; Bohnsack 2011). For example, a large female red snapper (*Lutjanus campechanus*; 61 cm) can produce the same number of eggs as 212 smaller female snapper (42 cm; Bohnsack 1994). Ideally, protection of important marine habitats would, therefore, lead to increased fish size inside a protected area, followed by increased recruitment to the whole population (Bohnsack 1994; Pelc et al. 2010). Fish abundance would also ideally increase inside MPAs as fish populations rebuild to unfished levels and density-dependent processes cause adults to emigrate to fished areas (spillover; e.g., Harmelin-Vivien et al. 2008; Stobart et al. 2009; Bohnsack 2011). Previous research has demonstrated these benefits for various exploited species when MPAs are well designed and managed (Halpern and Warner 2003; White and Kendall 2007; White et al. 2008; Lester et al. 2009; Gaines et al. 2010). However, studies on MPAs primarily focus on shallow water reef systems and

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questions remain regarding whether MPAs could be successful in other environments, specifically deepwater habitats and ecosystems.

Understanding whether MPAs could be a useful fishery management tool in deepwater environments is particularly important because fishers have targeted fish stocks in increasingly deeper waters over the last several decades as many shallow water stocks have become depleted (Haedrich et al. 2001; Morato et al. 2006). For example, global trends since the 1950s suggest mean fishing depth has increased from approximately 40–150 m, with an increasing mean rate of 13 m decade⁻¹ in more recent years (Morato et al. 2006). Management measures might therefore be required to replace the natural refuge that depth previously provided. In addition, information on deepwater species ecology suggests that many targeted species are characterized by extended longevity, slow growth rates, late maturity and low rates of natural mortality (Drazen and Haedrich 2012; Williams et al. 2013). As such, deepwater species often have exceptionally low production potential and are, therefore, highly vulnerable to overfishing (Cheung et al. 2005; Morato et al. 2006). These traits suggest deepwater stocks can be rapidly depleted and very slow to recover. Consequently, there is a critical need to apply successful fishery management strategies to deepwater species in a timely manner (Haedrich et al. 2001; Williams et al. 2013). Indeed, fisheries managers have turned to protected area management in deep-sea areas in recent years, often to protect fragile corals and in a few instances to protect fish species (e.g., the protection of a deepwater snapper–grouper complex in the south Atlantic, SAFMC 2013). With the exception of deeper shelf waters (to ~150 m; Harter et al. 2009; Rudershausen et al. 2010), there are no other studies, to our knowledge, which directly evaluate protected area effects on deepwater fished species.

Deepwater fisheries have existed in the Hawaiian Islands for several decades (Grigg 2001; Williams et al. 2013). For instance, deepwater snappers were historically fished by hand by native Hawaiians and have been reported as a commercial fishery since the late 1950s (Hospital and Beavers 2012; Williams et al. 2012). However, the advent of electric reels, advanced fish finders and GPS has increased catch to substantial levels in recent years (Dalzell and Preston 1992; Williams et al. 2012). Further, the spread of these technological advances in the Pacific region suggests that exploitation will grow steadily throughout the range of these species (Dalzell and Preston 1992; Williams et al. 2012). In accordance, there has been a recent request for stock assessments and an evaluation of management strategies for the Pacific region's deepwater snapper stocks (Williams et al. 2012; Williams et al. 2013). Our aim was to evaluate four deepwater MPAs in the Main Hawaiian Islands to determine whether

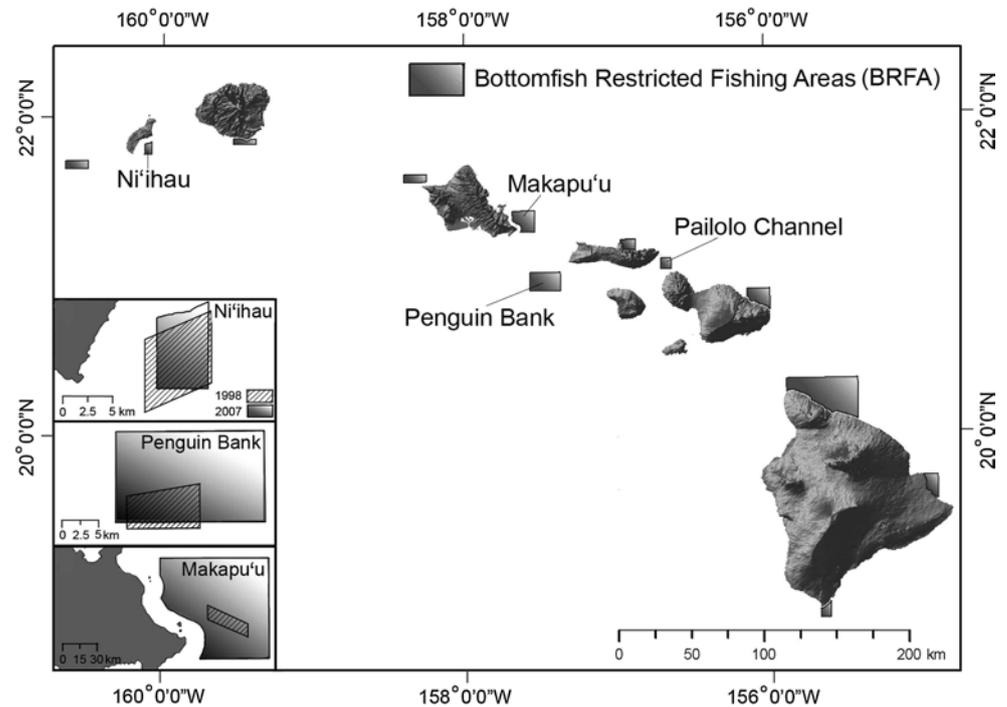
this management strategy could be successfully applied to deepwater snappers.

A particularly important complex of exploited deepwater bottomfish species in Hawai'i is known as the "Deep 7" and comprises six snappers (Lutjanidae) in the subfamily Etelinae: deepwater red snapper *Etelis carbunculus*, deepwater long-tail red snapper *E. coruscans*, crimson jobfish *Pristipomoides filamentosus*, lavender jobfish *P. sieboldii*, oblique-banded snapper *P. zonatus*, rusty jobfish (*Aphareus rutilans*), and one grouper (Serranidae): Hawaiian grouper *Hyporthodus quernus*. Of these, *E. carbunculus*, *E. coruscans* and *P. filamentosus* are the most economically and commercially important in the Main Hawaiian Islands (Haight et al. 1993; Kelley et al. 2006). Although limited, data on life history characteristics for these species indicate that they are generally long lived (20 to 40+ years for some species) and relatively late maturing (≥ 6 years for some species; Andrews et al. 2011, 2012; Kelley and Moriwake 2012). These traits are intermediate to the rapid growth and maturity of many reef fishes and the extreme slow growth and maturity of deep slope or seamount associated fishes (Drazen and Haedrich 2012).

During the 1990s, catch rates and spawning potential ratios of the Deep 7 indicated that their populations had declined, with metrics for *E. carbunculus* and *E. coruscans* generating particular concern. Also, because Deep 7 species are relatively site attached, often forming aggregations around high relief structures such as pinnacles, it was believed that a spatially based management strategy such as a network of MPAs would benefit these fish stocks (Ralston et al. 1986; Haight et al. 1993; Kelley et al. 2006; Parke 2007; Merritt et al. 2011). Therefore, in 1998, the State of Hawai'i, Department of Land and Natural Resources implemented a system of 19 MPAs labeled bottomfish restricted fishing areas (and hereafter referred to as BRFAs) throughout the Main Hawaiian Islands. These BRFAs excluded bottomfish harvest, protecting the deepwater environment and species that reside there while leaving surface waters open to fishing for pelagic species. On June 1, 2007, the system was revised to reduce the overall number to 12, but increased the area protected to include more essential fish habitat (EFH; Rosenberg et al. 2000; Moffitt et al. 2006; Parke 2007; Kelley and Moriwake 2012; Moore et al. 2013; Fig. 1).

Here, we examined whether relative abundance, mean length and species richness of the Deep 7 complex increased inside BRFAs compared to adjacent fished areas using data acquired from a baited camera system from 2007, when the revised BRFAs were established, to 2011. Further, because some BRFAs remained unchanged after they were revised in 2007 while others were expanded or newly created, we were able to compare BRFAs with different time spans of protection to examine the potential

Fig. 1 In 1998, 19 deepwater marine protected areas called bottomfish restricted fishing areas (BRFAs) were implemented throughout the Main Hawaiian Islands and later revised on June 1, 2007, reducing the overall number to 12 (revised BRFAs depicted with gradient fill). Our study sites included four BRFAs, one had boundaries similar to the original 1998 BRFAs (original BRFAs depicted with diagonal hatching in *insets*) and thus had been protected for approximately 14 years (Ni'i'hau), two encompassed smaller pre-existing closed areas (Penguin Bank and Makapu'u), and one was newly closed in 2007 (Pailolo Channel)



progress of protection effects beyond when monitoring began.

Materials and methods

Data collection

The sampling design and technique used here have been described previously by Moore et al. (2013). Briefly, our baited stereo-video camera system (BotCam) was specifically designed as a fishery-independent tool to monitor Hawaiian deepwater bottomfish and their habitat (Merritt et al. 2011). The system employed two ultralow-light video cameras that recorded under ambient light to a depth of 310 m, used a light diode to synchronize the stereo-video pair and enabled accurate fish length measurements (Harvey and Shortis 1995; Shortis et al. 2008; Watson et al. 2010). BotCam floated approximately 3 m above the seafloor to optimize the field of view for our targeted species. For instance, those Deep 7 species closely associated with the seafloor (e.g., *P. zonatus*) and those that resided higher in the water column (e.g., *E. coruscans*) were both visible in the field of view. Bait was kept in a plastic mesh bait canister in view of both cameras and consisted of approximately 800 g of chopped and frozen anchovy (*Engraulis mordax*) and squid (*Loligo opalescens*). Local commercial anglers also use this bait on hooks and in chum bags while fishing.

We used BotCam to conduct paired sampling inside and outside of four BRFAs in the Main Hawaiian Islands from approximately 90 to 310 m (Fig. 1). Of these four BRFAs, one had boundaries similar to the original 1998 BRFAs (Ni'i'hau) and thus had been protected for approximately 14 years, two encompassed smaller pre-existing closed areas (Penguin Bank and Makapu'u), and one was newly closed in 2007 (Pailolo Channel; Fig. 1). Data were collected from May 2007 to June 2011. Sample sites were selected using a stratified random sampling protocol with strata based on protection and habitat. An equal number of samples were targeted inside and outside but adjacent to each BRFA with the same habitat designations. Habitat designations were classified as high slope ($\geq 20^\circ$) or low slope ($< 20^\circ$) and as consolidated hard substrate or unconsolidated soft substrate for every 200 m² area based on multibeam bathymetry and backscatter data. These habitat classifications resulted in four possible designations: hard-high, hard-low, soft-high and soft-low (Moore et al. 2013; Misa et al. 2013). The 200 m² grid-cell size was chosen to reflect the area where fish would likely be drawn by bait and large enough to provide an adequate target for the deployment of BotCam. At each sample site, BotCam was deployed and left to record for 45 min before being retrieved, a time previously noted for optimizing peak feeding activity using bait (Harvey and Cappo 2001). In addition, BotCam units deployed concurrently were placed at a minimum of 400 m apart to reduce if not prevent bait plume overlap and sampling the same fish by both systems (Moore et al. 2013).

Video analysis

All fish within a single video were identified to the lowest taxonomic unit, commonly species. Relative abundance was recorded as the maximum number of each species observed in a single frame of video (MaxN; Parrish 1989; Priede et al. 1994; Cappelletti et al. 2003). Species not seen in the video were given a value of zero. Because of the high number of zeros in the MaxN datasets for each species and because not all species occupy the entire depth range sampled, we included only those data from a preferred depth range for each of our target species. These preferred depth ranges were previously determined by Misa et al. (2013) using a Euclidean distance matrix and pair-wise PERMANOVA of MaxN data in 30-m depth bins for four of the Deep 7 and are as follows: 210–310 m for *E. carbunculus* and *E. coruscans*, 90–210 m for *P. filamentosus* and 180–270 m for *P. sieboldii*. We calculated the preferred depth ranges for the remaining three species using the same method as Misa et al. (2013): 150–270 m for *P. zonatus*, 120–240 m for *H. quernus* and 90–240 m for *A. rutilans*. More than 90 % of the mean relative abundance for each species was within the specified depth ranges and allowed for more robust statistical analyses by reducing the number of zeros in each species' dataset. Fork lengths (mm) were also taken only one time in a single video to avoid measuring the same fish more than once. These measurements were recorded when the highest number of measurable fish (the entire fish was visible in both cameras) was seen and computed using one of three stereo-photometric programs (Visual Measurement System version 7.5, Geomsoft, Victoria, Australia; PhotoMeasure version 1.74, SeaGIS Pty Ltd; EventMeasure Stereo version 3.32, SeaGIS Pty Ltd). Approximately, five replicate measurements were also taken for each individual to increase precision and accuracy. In addition, we used species richness, a count of the number of Deep 7 species that were present in a single video, as a measure of biodiversity (e.g., if all Deep 7 species were viewed in a single 45 min video the species richness value would be seven).

Statistical analysis

To analyze factors that affected relative fish abundance and size structure for all seven species from each BRFA, we ran a series of seven candidate models for both MaxN and fish length for each species and BRFA and ranked them with Akaike's information criterion (AIC_c ; Burnham and Anderson 1998; Table 1). Factors included sampling year, protection (inside or outside the BRFA), habitat designations (hard-high, hard-low, soft-high and soft-low), and the interaction between protection and sampling year (year*protection). Model selection was based on available

Table 1 Seven candidate models tested to explain MaxN and fish length data for each species in each BRFA

Candidate models
habitat
protection
year
year*protection
year*protection, habitat
year*protection, protection
year*protection, protection, habitat

Candidate models were also tested to explain species richness data in each BRFA. The best of the seven models tested for each analysis was determined using Akaike's information criterion (AIC_c ; Burnham and Anderson 1998)

* Represents an interaction between the two parameters

factors, the sample size of the dataset and to answer specific questions about the data. For instance, the interaction between protection and sampling year was tested to determine whether there were different trends in fish length or abundance over time inside versus outside each BRFA (i.e., the slopes of the regression lines inside and outside were significantly different). In all cases, sample depth was treated as a random effect to address potential bias in our model results because samples were not stratified by depth until year 4, and then, stratification was very broad (above and below 200 m depth). MaxN data were analyzed using generalized linear mixed models (GLMM) with a negative binomial distribution to account for the hyperdispersed nature of count data. This method has been successfully used in previous studies with similar datasets (Martinez et al. 2011; Smith et al. 2012). Because length data met assumptions of normality, we used standard least squares multiple regression models for these analyses. Model probability weights (W_i) were used to examine the strength of evidence for each model (W_i indicates the probability that a model is the best of the set of models tested; Burnham and Anderson 1998). Here, we display only the top ranked model, using AIC_c for each species, BRFA and analysis (MaxN and fish length; Tables 2, 3).

To examine factors that best explained the variation in species richness data, we used the same series of seven candidate models and ranked them with AIC_c (Table 1). All significant ($P < 0.05$) factor effects in our weighted models were further investigated using adjusted means and mean predicted values from model output because these measures take other model effects into account. The percent of mature fish inside and outside each BRFA was also compared (sizes at maturity were *E. carbunculus* = 279 mm (DeMartini and Lau 1999), *E. coruscans* = 700 mm (Everson et al. 1989), *P. filamentosus* = 450 mm (Ralston and Miyamoto 1983), *P. sieboldii* = 290 mm (DeMartini and

Table 2 Top ranked generalized linear mixed models for explaining MaxN data for each species in each BRFA using Akaike's information criterion (AIC_c; Burnham and Anderson 1998)

BRFA	Species	Top model	<i>P</i>	<i>N</i>	<i>W_i</i>	Models tested
Ni'ihau	<i>E. carbunculus</i>	year*protection, protection, habitat	0.73	90	0.90	7
	<i>E. coruscans</i>	year*protection, protection, habitat	0.87	90	0.83	7
	<i>P. filamentosus</i>	year*protection, protection	0.35	102	1.00	7
	<i>P. sieboldii</i>	year*protection, protection, habitat	0.22	90	0.92	7
	<i>P. zonatus</i>	year*protection, protection, habitat	0.63	123	0.99	7
	<i>H. quernus</i>	protection	0.27	116	0.99	7
	<i>A. rutilans</i>	–	–	128	–	0
Penguin Bank	<i>E. carbunculus</i>	protection	0.37	140	0.62	7
	<i>E. coruscans</i>	year*protection [#] , protection [#] , habitat ^{##}	0.01	140	0.99	7
	<i>P. filamentosus</i>	year*protection, protection, habitat	0.22	105	0.96	7
	<i>P. sieboldii</i>	habitat	0.51	145	0.81	7
	<i>P. zonatus</i>	year*protection, protection, habitat	0.76	175	1.00	3
	<i>H. quernus</i>	protection	0.27	153	1.00	7
	<i>A. rutilans</i>	year*protection, protection, habitat	0.99	168	0.89	6
Makapu'u	<i>E. carbunculus</i>	year*protection, protection, habitat	0.71	72	0.82	7
	<i>E. coruscans</i>	year*protection, protection, habitat	0.19	72	0.93	5
	<i>P. filamentosus</i>	year*protection ^{##} , habitat ^{##}	0.00	123	1.00	6
	<i>P. sieboldii</i>	protection	0.99	76	1.00	1
	<i>P. zonatus</i>	habitat	0.99	125	0.93	7
	<i>H. quernus</i>	habitat	0.45	131	0.93	7
	<i>A. rutilans</i>	year*protection	0.23	148	0.88	4
Pailolo Channel	<i>E. carbunculus</i>	year	0.76	142	0.47	7
	<i>E. coruscans</i>	year*protection, protection ^{##} , habitat ^{##}	0.07	142	1.00	7
	<i>P. filamentosus</i>	habitat	0.41	51	0.94	2
	<i>P. sieboldii</i>	year*protection, protection, habitat	0.61	122	1.00	6
	<i>P. zonatus</i>	–	–	135	–	0
	<i>H. quernus</i>	year	0.34	111	1.00	7
	<i>A. rutilans</i>	–	–	113	–	0

Model probability weights (*W_i*) indicated the probability that a model is the best of the set of models tested. The full scientific name for each species is *Etelis carbunculus*, *E. coruscans*, *Pristipomoides filamentosus*, *P. sieboldii*, *P. zonatus*, *Hyporthodus quernus* and *Aphareus rutilans*. # indicates a marginally significant model effect (0.05 < *P* < 0.10); ## indicates a significant model effect (*P* < 0.05).

Lau 1999) and *H. quernus* = 580 mm (DeMartini et al. 2011)). *H. quernus* are protogynous hermaphrodites, and while we used the 580 mm size at which females reach maturity for our analyses, we also summed the number of fish sampled that were large enough to be male (895 mm; DeMartini et al. 2011). All analyses were conducted using JMP 9.0.2 (2010 SAS Institute Inc.) and SPSS 21 (2012 IMB Corp.).

Results

Our results showed that the same model was ranked as best among nearly all BRFAs and species for explaining the variation in relative abundance (MaxN) and fish length data (Tables 2, 3). Factors in this model included year*protection, protection and habitat. The strength (*W_i*) of the best and significant (*P* < 0.05) models in explaining MaxN and fish length data ranged from 0.90 to 1.00. Of the significant (*P* < 0.05) weighted models,

not all factors included in the models had significant effects. For instance, although year*protection, protection and habitat were all in the top model for *P. filamentosus* length data in Makapu'u BRFA, the protection factor (comparing mean length inside to outside with years pooled; adjusted mean length inside = 495 mm, outside = 479 mm) was not significant (*P* = 0.22) while year*protection and habitat factors were significant (*P* < 0.01). Also, among BRFAs and species, small sample sizes, especially among explanatory variable categories, resulted in a loss of power to run all seven models. At least six models could be run for 20 of the 28 tests for MaxN data (Table 2) and 13 of the 28 tests for length data (Table 3). This limitation reduced our ability to examine protection effects for all species in all BRFAs. Overall, however, changes in length and relative abundance over time occurred for one or more of the most economically important and abundant target species (*E. carbunculus*, *E. coruscans*, *P. filamentosus*; Table 4) in nearly all tested BRFAs. Results for other species

Table 3 Top ranked standard least squares models for explaining fish length data for each species in each BRFA using Akaike's information criterion (AIC_c; Burnham and Anderson 1998)

BRFA	Species	Top model	<i>P</i>	<i>R</i> ²	<i>N</i>	<i>W</i> _{<i>i</i>}	Models tested
Ni'ihau	<i>E. carbunculus</i>	year*protection, protection, habitat ^{##}	0.01	0.34	42	0.95	7
	<i>E. coruscans</i>	year*protection, protection ^{##} , habitat	0.04	0.13	92	1.00	4
	<i>P. filamentosus</i>	year*protection, protection ^{##} , habitat	0.01	0.31	61	1.00	7
	<i>P. sieboldii</i>	year*protection ^{##} , protection ^{##} , habitat ^{##}	0.00	0.18	244	1.00	7
	<i>P. zonatus</i>	–	–	–	9	–	0
	<i>H. quernus</i>	year*protection, protection, habitat	0.17	0.31	31	0.93	5
	<i>A. rutilans</i>	–	–	–	2	–	0
Penguin Bank	<i>E. carbunculus</i>	year*protection ^{##} , protection ^{##} , habitat	0.03	0.13	158	0.98	7
	<i>E. coruscans</i>	year*protection ^{##} , protection ^{##} , habitat	0.00	0.21	118	1.00	5
	<i>P. filamentosus</i>	year*protection ^{##} , protection ^{##} , habitat ^{##}	0.00	0.42	230	0.95	7
	<i>P. sieboldii</i>	year*protection ^{##} , protection ^{##} , habitat ^{##}	0.00	0.21	312	1.00	7
	<i>P. zonatus</i>	year*protection, protection, habitat	0.07	0.27	28	0.90	6
	<i>H. quernus</i>	year*protection, protection, habitat	0.69	0.33	17	0.96	7
	<i>A. rutilans</i>	year*protection, protection ^{##} , habitat	0.02	0.41	29	1.00	6
Makapu'u	<i>E. carbunculus</i>	year*protection, protection, habitat	0.31	0.42	37	0.96	7
	<i>E. coruscans</i>	year*protection, protection	0.86	0.70	10	0.46	6
	<i>P. filamentosus</i>	year*protection ^{##} , protection, habitat ^{##}	0.00	0.44	215	0.92	7
	<i>P. sieboldii</i>	habitat	0.12	0.88	5	1.00	1
	<i>P. zonatus</i>	year	0.98	0.40	3	1.00	1
	<i>H. quernus</i>	–	–	–	4	–	0
	<i>A. rutilans</i>	year	0.41	0.65	3	1.00	1
Pailolo Channel	<i>E. carbunculus</i>	year*protection, protection	0.09	0.06	289	0.48	4
	<i>E. coruscans</i>	year*protection [#] , protection ^{##}	0.00	0.22	166	0.97	4
	<i>P. filamentosus</i>	year*protection, protection ^{##} , habitat	0.00	0.49	76	0.95	7
	<i>P. sieboldii</i>	year*protection, protection ^{##}	0.00	0.12	95	0.90	3
	<i>P. zonatus</i>	–	–	–	1	–	0
	<i>H. quernus</i>	year*protection, protection	0.15	0.07	34	0.95	4
	<i>A. rutilans</i>	–	–	–	0	–	0

Model probability weights (*W*_{*i*}) indicate the probability that a model is the best of the set of models tested. The full scientific name for each species is *Etelis carbunculus*, *E. coruscans*, *Pristipomoides filamentosus*, *P. sieboldii*, *P. zonatus*, *Hyporthodus quernus*, and *Aphareus rutilans*

[#] indicates a marginally significant model effect (0.05 < *P* < 0.10); ^{##} indicates a significant model effect (*P* < 0.05)

were limited due to sample size. Indeed, significant results were only found when samples sizes were greater than approximately 100 for length data, and the percent of samples in which a particular species was present was greater than 40 % (Table 4).

Site with the longest duration of protection

The BRFA with the longest duration of protection, Ni'ihau BRFA, showed no significant effects for MaxN data for any of the models tested (Table 2). This may have been the result of the smaller fraction of deployments in which a particular species was observed (nonzero MaxN data <35 %) in this BRFA (Table 4). Conversely, our length analysis showed significant results for three species. *P. filamentosus* inside Ni'ihau BRFA were larger compared

to outside, while the opposite was seen for *E. coruscans* and *P. sieboldii* (Fig. 2a). Over time mean predicted lengths decreased significantly inside for *P. sieboldii* and increased significantly outside (*P* < 0.05; Fig. 3a). Similar trends for *E. coruscans* and *P. filamentosus* were not significant (*P*_{year*protection} = 0.17; *P*_{year*protection} = 0.14). Diversity (species richness) of our target species increased outside this BRFA (*P*_{year*protection} = 0.01; *P*_{out} = 0.01), although it remained unchanged inside (*P*_{in} = 0.33; Table 4c). There were also higher percentages of mature fish inside Ni'ihau BRFA than outside for each species examined, with the exception of *P. filamentosus* where 100 % of the fish seen inside and outside the BRFA were mature (Fig. 4a). In addition, for *H. quernus*, which undergo a sex change from female to male at approximately 895 mm (DeMartini et al. 2011), none of the fish

Table 4 A summary of significant ($P < 0.05$, bold) and marginally significant ($0.05 < P < 0.10$, italics) trends in (a) length (b) relative abundance and (c) species richness data over time inside and outside protected areas (year*protection)

a. Length	Ni'ihau			Penguin Bank			Makapu'u			Pailolo Channel			
	Species	N	In	Out	N	In	Out	N	In	Out	N	In	Out
<i>E. carbunculus</i>	42			158	↑	↓	37				289		
<i>E. coruscans</i>	92			118	↑	↓	10				166	↑	↓
<i>P. filamentosus</i>	61			230	↑	–	215	↑	–		76		
<i>P. sieboldii</i>	244	↓	↑	312	↓	↑	5				95		
<i>P. zonatus</i>	9			28			3				1		
<i>H. quernus</i>	31			17			4				34		
<i>A. rutilans</i>	2			29			3				0		

b. MaxN	Ni'ihau			Penguin Bank			Makapu'u			Pailolo Channel			
	Species	Presence*	In	Out	Presence*	In	Out	Presence*	In	Out	Presence*	In	Out
<i>E. carbunculus</i>	0.20 (90)			0.48 (140)			0.19 (72)				0.77 (142)		
<i>E. coruscans</i>	0.31 (90)			0.44 (140)	↑	–	0.13 (72)				0.48 (142)		
<i>P. filamentosus</i>	0.24 (102)			0.53 (105)			0.47 (123)	↑	↓		0.43 (51)		
<i>P. sieboldii</i>	0.32 (90)			0.34 (145)			0.04 (76)				0.23 (122)		
<i>P. zonatus</i>	0.12 (123)			0.16 (175)			0.07 (125)				0.01 (135)		
<i>H. quernus</i>	0.14 (116)			0.10 (153)			0.04 (131)				0.17 (111)		
<i>A. rutilans</i>	0.01 (128)			0.14 (168)			0.01 (148)				0.00 (113)		

c. Species richness	Ni'ihau			Penguin Bank			Makapu'u			Pailolo Channel			
	Species	Presence*	In	Out	Presence*	In	Out	Presence*	In	Out	Presence*	In	Out
Deep 7		0.45 (190)	–	↑	0.70 (244)			0.44 (192)			0.75 (190)		

↑ signifies an increase over time, – signifies no change over time and ↓ signifies a decrease over time. The full scientific names for each species that make up the Deep 7 are *Etelis carbunculus*, *E. coruscans*, *Pristipomoides filamentosus*, *P. sieboldii*, *P. zonatus*, *Hyporthodus quernus* and *Aphareus rutilans*

* The percent of nonzero data in each database with the sample size in parentheses

measured were large enough to be male inside the BRFA, and only one of 15 was large enough to be male outside the BRFA.

Significant habitat associations occurred for only two species in Ni'ihau BRFA, *E. carbunculus* and *P. sieboldii*, and only with length ($P \leq 0.01$) and species richness data ($P < 0.01$). Mean predicted lengths of *E. carbunculus* were largest in soft-low habitats (532 ± 43 mm SE) and smaller in hard-high and hard-low habitats (392 ± 15 mm, 385 ± 17 mm). There were no length measurements taken in soft-high habitats for this species. The largest *P. sieboldii* were in soft-high habitats (379 ± 12 mm), followed by hard-high and hard-low (351 ± 3 mm, 342 ± 6 mm), with the smallest fish found in soft-low habitats (289 ± 12 mm). Habitat associations with species richness in this BRFA indicated that hard-high and hard-low habitat types had the highest mean number of target species in a single deployment (1.14 ± 0.06 , 0.91 ± 0.04) followed by soft-low (0.52 ± 0.04) and then soft-high habitats (0.28 ± 0.01).

Sites with an intermediate duration of protection

The Penguin Bank and Makapu'u BRFAs were expanded from their original 1998 boundaries in 2007 to include previously unprotected areas. As a consequence of the blend of newly protected sections and those sections protected since 1998 inside these BRFAs, we defined the time span of protection intermediate compared to the others we tested. Protection of the area influenced relative fish abundance and fish length in both BRFAs. At Penguin Bank mean predicted MaxN for *E. coruscans* was higher inside the BRFA compared to outside, though this result was only marginally significant ($0.05 < P < 0.10$; Fig. 5a). Adjusted mean length was also higher in this BRFA for four species (*E. carbunculus*, *E. coruscans*, *P. filamentosus*, *P. sieboldii*) while the opposite was seen for *A. rutilans* (Fig. 2b). Higher percentages of mature fish were also noted inside compared to outside Penguin Bank BRFA for *E. coruscans*, *P. sieboldii* and *H. quernus*, while results were approximately even for *E. carbunculus* and opposite for *P. filamentosus*

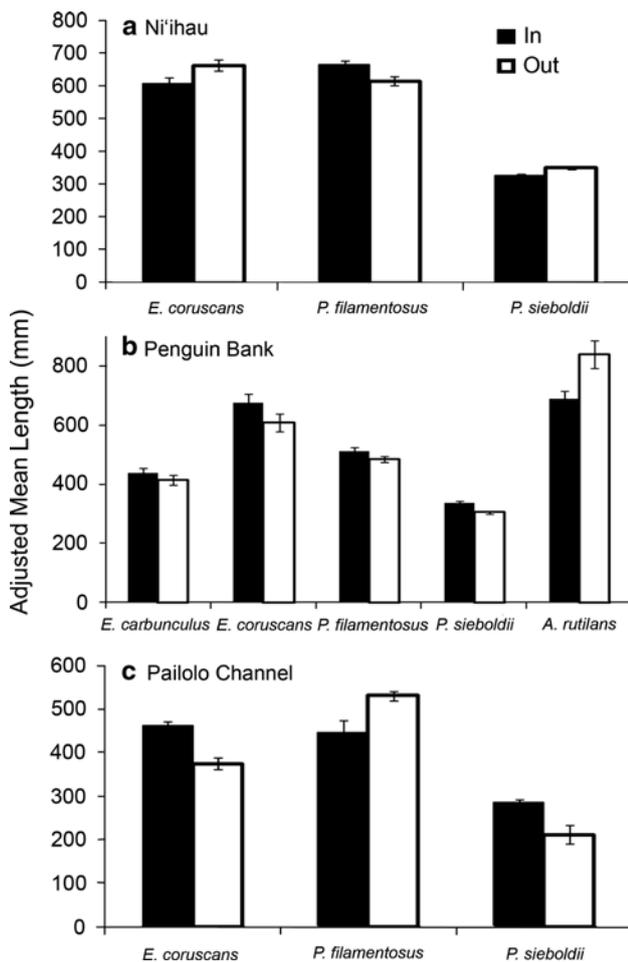


Fig. 2 Significant ($P < 0.05$) fish length model effects for the factor protection (differences in length inside and outside BRFAs; see Table 3). The genera for displayed species are *Etelis*, *Pristipomoides* and *Aphareus*

(Fig. 4b). Maturity results were also varied in Makapu'u BRFA, where more mature *E. coruscans* were inside the BRFA and more mature *E. carbunculus* were outside the BRFA (Fig. 4c). Furthermore, none of the measured *H. quernus* inside Penguin Bank BRFA or outside Makapu'u BRFA (*H. quernus* were only measured outside Makapu'u BRFA) were large enough to be male. Outside Penguin Bank BRFA, two of nine measured *H. quernus* were large enough to be male.

In both the Penguin Bank and Makapu'u BRFAs protection also influenced relative fish abundance and fish length for a few species over time. As such, there was a significant increase in *E. coruscans* mean predicted MaxN inside Penguin Bank BRFA, while outside MaxN remained unchanged (Fig. 6a). Although the difference in slope of these regressions (year*protection) was only marginally significant ($0.05 < P < 0.10$) in the top ranked model, in the second best model for the same species and BRFA,

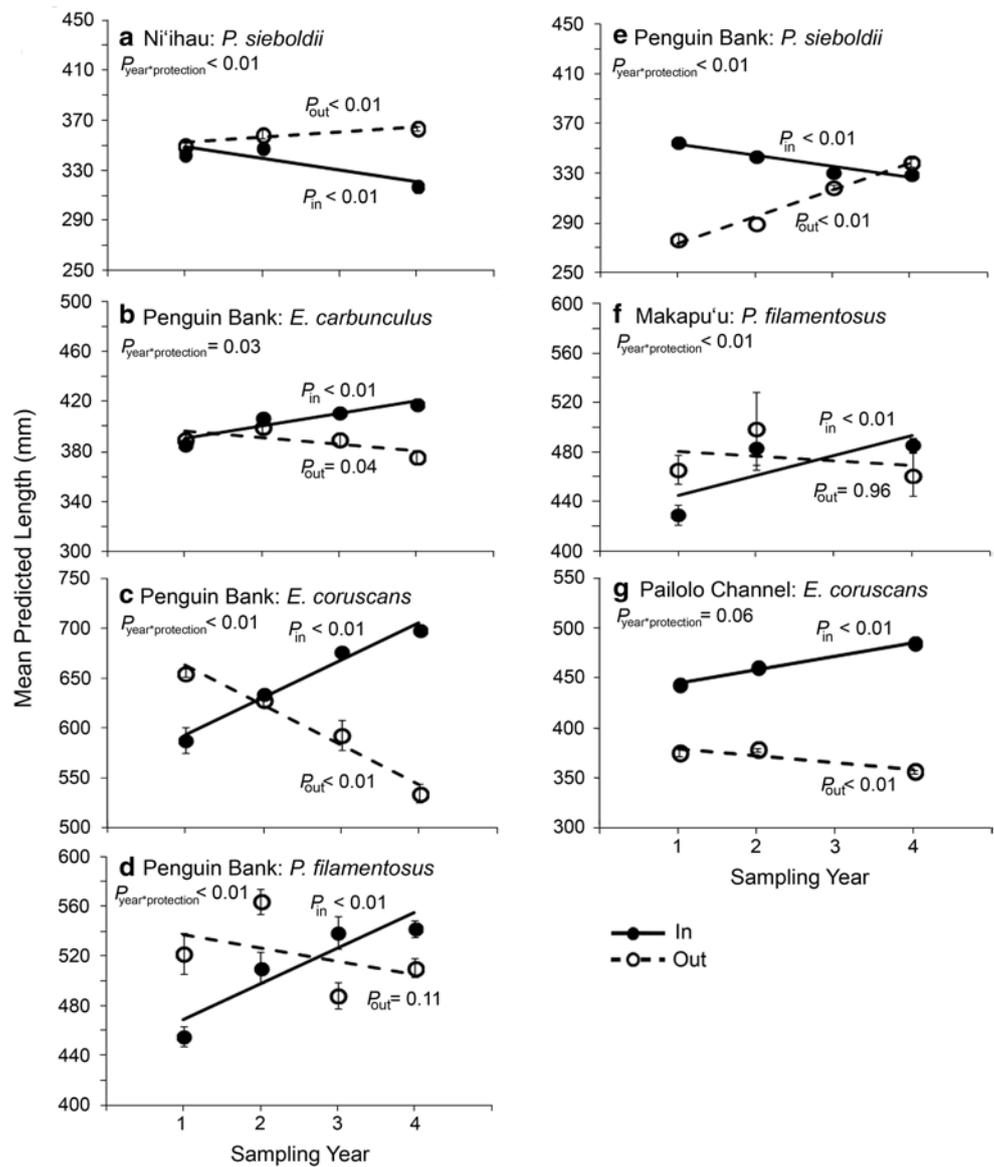
the slopes of these regressions were significantly different ($P_{\text{year*protection}} = 0.02$, $P_{\text{in}} = 0.03$, $P_{\text{out}} = 0.97$) and showed the same trends over time. For *P. filamentosus* in Makapu'u BRFA, the slopes of the MaxN regressions over time inside and outside the BRFA were significantly different with an increasing trend occurring inside and a decreasing trend occurring outside the BRFA (Fig. 6b). However, the individual regressions were not significant. Mean predicted lengths increased inside and decreased or showed no change over time outside Penguin Bank BRFA for *E. carbunculus*, *E. coruscans* and *P. filamentosus* (Fig. 3b–d). *P. sieboldii* displayed an opposite trend in Penguin Bank BRFA (Fig. 3e). In Makapu'u BRFA, mean fish length increased inside and showed no significant change outside for *P. filamentosus* over time (Fig. 3f).

Habitat associations with MaxN data varied by species and were only significant in Penguin Bank BRFA for *E. coruscans* ($P = 0.01$) and *E. carbunculus* ($P < 0.01$) and in Makapu'u BRFA for *P. filamentosus* ($P < 0.01$). *E. carbunculus* had the highest mean predicted MaxN in hard-high and soft-high habitats (2.99 ± 0.15 SE, 2.81 ± 0.21) followed by hard-low (1.78 ± 0.15) and then soft-low (0.12 ± 0.01), which had the lowest predicted MaxN. *E. coruscans* had the highest predicted mean MaxN in hard-high and hard-low habitats (3.89 ± 0.32 , 4.13 ± 0.57) followed by soft-high (2.11 ± 0.29), then soft-low (0.64 ± 0.10). *P. filamentosus* had the highest predicted MaxN in hard-low and soft-low habitats (5.45 ± 0.52 , 6.98 ± 1.07) followed by hard-high (2.78 ± 0.23) and then soft-high (1.02 ± 0.07). Habitat associations with length data were only significant for *P. filamentosus* in Penguin Bank and Makapu'u BRFAs and *P. sieboldii* in Penguin Bank BRFA. In both Penguin Bank and Makapu'u BRFAs, the largest *P. filamentosus* were in soft-high habitats (569 ± 11 mm, 582 ± 19 mm) followed by hard-high habitats (508 ± 11 mm, 523 ± 10 mm), while smaller *P. filamentosus* were in hard-low (470 ± 10 mm, 415 ± 8 mm) and soft-low habitats (441 ± 35 mm, 428 ± 26 mm). The largest *P. sieboldii* in Penguin Bank BRFA were in hard-high and hard-low habitats (330 ± 5 mm, 333 ± 8 mm) followed by soft-high habitats (301 ± 6 mm).

Site with the shortest duration of protection

Pailolo Channel BRFA was newly created in 2007 and thus had the shortest duration of protection compared to the others tested. In this BRFA, larger and more *E. coruscans* were found inside compared to outside the reserve (Figs. 2c, 5b). Larger *P. sieboldii* were also found inside this BRFA compared to outside, though the opposite was seen for *P. filamentosus* (Fig. 2c). Maturity results varied among species in Pailolo Channel BRFA, with more mature *E. coruscans*

Fig. 3 Significant ($P < 0.05$) and marginally significant ($0.05 < P < 0.10$) fish length model effects for the interaction between year and protection (differences in the trends seen over time inside and outside BRFAs; see Table 3). The genera for displayed species are *Etelis* and *Pristipomoides*



and *P. sieboldii* inside the BRFA and more mature *E. carbunculus*, *P. filamentosus* and *H. quernus* outside (Fig. 4d). In addition, only one of eight measured *H. quernus* inside and only two of 26 outside this BRFA were large enough to be male. Over time, there was a slight trend of increasing fish length for *E. coruscans* inside the BRFA; however, the difference in the slopes of these regressions inside and outside the BRFA was only marginally significant ($0.05 < P < 0.10$; Fig. 3g).

Species richness in Pailolo Channel BRFA was significantly ($P < 0.01$) associated with habitat; hard-low habitats had higher species richness (1.59 ± 0.01 SE) than soft-low habitats (0.38 ± 0.01). Fish length and relative abundance were not significantly associated with habitat for any species in this BRFA, though only two habitat types were present (hard-low and soft-low).

Discussion

Our study used data collected inside and outside of four deepwater MPAs (BRFAs) in the Main Hawaiian Islands and provided evidence that this strategy can benefit deepwater fish populations similar to shallow water MPAs. For instance, studies on the efficacy of shallow water MPAs have demonstrated increased length and abundance of targeted fish inside protected areas relative to areas that remained open to fishing (Russ and Alcala 1996; Friedlander et al. 2003). We show that mean fish length, and in some cases abundance, increased for one or more of the most economically important deepwater bottomfish species (*E. coruscans*, *E. carbunculus* and *P. filamentosus*) inside nearly all tested deepwater BRFAs (Table 4). However, the strength and number of significant protection effects

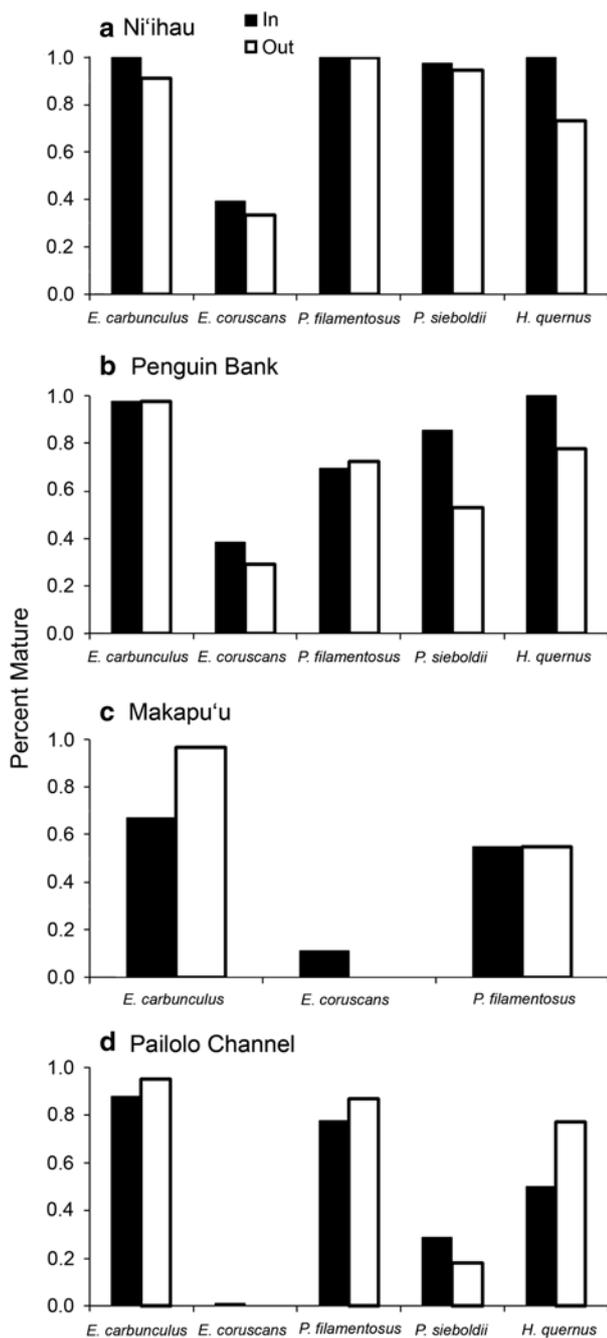


Fig. 4 The percentage of mature fish inside and outside BRFAs for each species with enough data to make a comparison. Sizes at maturity were *Etelis carbunculus* = 279 mm (DeMartini and Lau 1999), *E. coruscans* = 700 mm (Everson et al. 1989), *Pristipomoides filamentosus* = 450 mm (Ralston and Miyamoto 1983), *P. sieboldii* = 290 mm (DeMartini and Lau 1999) and *Hyporthodus quernus* = 580 mm (DeMartini et al. 2011)

varied among BRFAs and were likely a consequence of the time span of protection, potential poaching inside some BRFAs, small sample sizes for length and MaxN data and the inherent variability of MaxN data (i.e., hyperdispersed

count data with excess zeros; Martinez et al. 2011; Smith et al. 2012). For instance, only 86 *H. quernus* were measured in all four BRFAs over 4 years of data collection and even more, only six of those were large enough to be male (>895 mm; DeMartini et al. 2011). Despite these effects, our results suggest that a spatial management strategy such as a network of MPAs can benefit deepwater fish populations, many of which are in need of sustainable fisheries management (Haedrich et al. 2001; Morato et al. 2006; Baker et al. 2009; Williams et al. 2012, 2013).

Typical reserve effects (e.g., increased fish length and abundance inside the MPA; White and Kendall 2007; White et al. 2008; Lester et al. 2009; Gaines et al. 2010) were most often present in Penguin Bank and Makapu'u BRFAs. These BRFAs were intermediate in the duration of protection compared to the others tested because they included a blend of newly protected habitat (starting in 2007) and habitat that had been protected since 1998 (Moffitt et al. 2006; Kelley and Moriwake 2012). For instance, the three most economically important species in the fishery (*E. carbunculus*, *E. coruscans* and *P. filamentosus*; Haight et al. 1993; Kelley et al. 2006) were larger inside Penguin Bank BRFA compared to outside the reserve, with increases in length occurring over time inside and decreases or no change observed outside the BRFA. Further, increases in fish size seen over time were equivalent to approximately 1–3 years of growth (Smith and Kostlan 1991; Williams and Lowe 1997; Andrews et al. 2012). *E. coruscans* relative abundance also increased inside and showed no change over time outside the BRFA. Similar results were evident in Makapu'u BRFA, but only for a single species, *P. filamentosus*. The lack of significant length and abundance results for other species in Makapu'u BRFA was likely due to very low sample sizes (Table 4). This area has been anecdotally labeled as a fishing ground for *P. filamentosus* and *E. coruscans* by local anglers and, as expected, *P. filamentosus* was the most abundant species in this area while unexpectedly *E. coruscans* were rarely sampled. Conversely, *P. sieboldii*, which are generally not targeted by commercial fishers because of their small body size (Kelley et al. 2006), showed the opposite trend in Penguin Bank BRFA, increases in fish length outside and decreases inside the BRFA over time. The decline in mean length seen inside this BRFA may be the result of larger target species out-competing this smaller non-target species inside the BRFA (Sanchez Lizaso et al. 2000).

While decreased fish length in fished areas adjacent to Penguin Bank BRFA for *E. carbunculus* and *E. coruscans* may indicate displaced fishing effort, fish abundance did not change over time outside the reserve. In previous studies, evidence of displaced fishing effort included decreases in fish catch and abundance adjacent to the MPA (Greenstreet et al. 2009; Halpern et al. 2004). Decreased mean

Fig. 5 Significant ($P < 0.05$) and marginally significant ($0.05 < P < 0.10$) MaxN model effects for the factor protection (differences in MaxN inside and outside BRFA; see Table 2). The genus for displayed species is *Etelis*

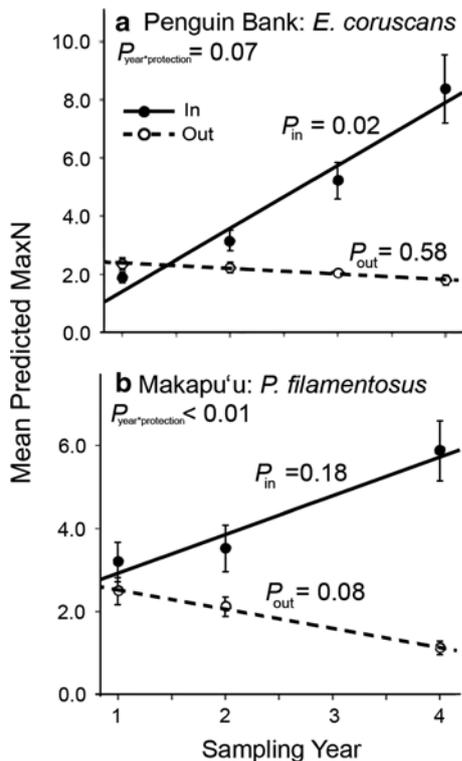
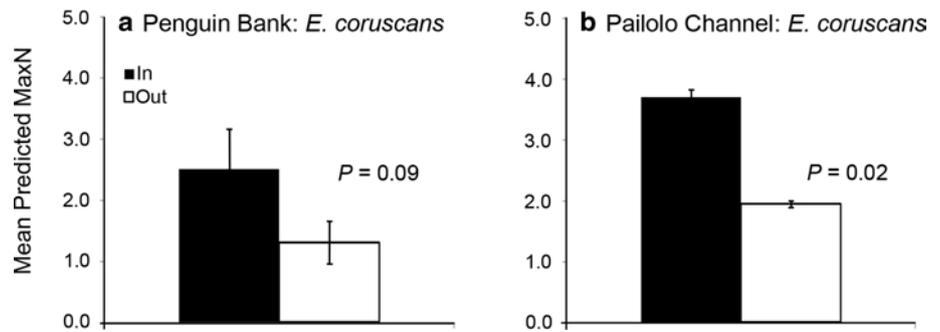


Fig. 6 Significant ($P < 0.05$) and marginally significant ($0.05 < P < 0.10$) MaxN model effects for the interaction between year and protection (differences in the trends seen over time inside and outside BRFA; see Table 2). The genera for displayed species are *Etelis* and *Pristipomoides*

fish length in fished areas could also be from the larger and more productive spawning stock inside the reserve increasing recruitment to fished areas along with continual fishing pressure selectively removing large individuals from the population (Bohnsack 1994; Halpern and Warner 2003; Pelc et al. 2010). In keeping with this hypothesis, Vaz et al. (in review) modeled egg dispersal of Deep 7 species inside the BRFA among the Main Hawaiian Islands and showed the majority of eggs spawned in deepwater BRFA would disperse to fished areas. In addition, Halpern et al. (2004) evaluated the affects of displaced fishing

effort and reported that exported production from reserves can supply and sustain fisheries at current or higher levels, compensating anglers for the closure of fishing grounds (Pelc et al. 2010). While this is clearly an objective of using MPAs for fisheries management, we currently do not have the data necessary to evaluate exported production from the BRFA.

Consistent and significant positive effects from protection were seen less often in Pailolo Channel BRFA, as expected, given that this BRFA had the shortest period of protection in our study (from 2007). Although significant differences in mean fish length and relative abundance occurred inside compared to outside, results were mixed and many did not change significantly over time. Previous research has indicated that direct effects on target species as a result of protection first appear, on average, within 5 years (Babcock et al. 2010). Although life history data for our target species are limited, studies suggest they are generally long lived (20 to 40+ years for some species; Andrews et al. 2011, 2012; Kelley and Moriwake 2012), with slower growth than many reef fishes, such as those studied in Babcock et al. (2010). Consequently, it would likely take more than 4 years for protection effects demonstrated in other shallow water MPAs to develop for deep-water species (Haedrich et al. 2001; Morato et al. 2006; Baker et al. 2009). Another possible reason for inconsistent results among species in this BRFA compared to others was that only two types of habitat were available, hard-low and soft-low. The limited available habitat in this reserve could affect species composition compared to other BRFA, particularly because both *E. carbunculus* and small *E. coruscans* prefer hard-low habitat types (Misa et al. 2013). Additionally, previous research has indicated that this area may be a nursery ground for *E. coruscans*, in which case changes in fish lengths may not be expected (Misa et al. 2013). As such, the slight increase in mean predicted fish length seen in this BRFA for *E. coruscans* did not exceed the estimated size at maturity (700 mm, Everson et al. 1989) and may indicate that fish leave this area when they reach maturity. Because there are no minimum size regulations for non-commercial fishers for any of the Deep 7,

protecting nursery habitat should still provide benefits to the population and fishery.

The boundaries of Ni'ihau BRFA have changed very little since 1998, providing nearly 14 years of protection to this area. In accordance, our maturity results suggested that long-term protection in this BRFA had benefits not seen in other BRFAs. For instance, across all years each species in Ni'ihau BRFA had a higher percent of mature fish inside the reserve compared to outside (with the exception of *P. filamentosus* where all of the fish sampled inside and out were mature), a result not yet seen in the other analyzed BRFAs, which had shorter durations of protection. In addition, Niihau BRFA was the only area where four of the five species tested had >98 % maturity inside the BRFA. Further, this BRFA was the only one tested to show any changes in species richness over time, with increases occurring in adjacent fished habitats and no changes occurring inside Ni'ihau BRFA; a result that may indicate a spillover effect. A study by Russ and Alcala (1996) indicated that an increase in species richness of large predators, including Lutjanid and Serranid species, also increased with reserve age and suggested that the increase seen outside the reserve was due to spillover. However, they also hypothesized that increased species richness outside the reserve could be caused by successful recruitment. Other studies have indicated that initial signs of spillover are generally evident after approximately 15 years of protection (Abesamis and Russ 2005; Molloy et al. 2009). In addition, a previous examination of this BRFA to establish baseline data in the first year of monitoring (9 years after reserve creation) demonstrated that mean *E. coruscans* and *P. filamentosus* lengths were significantly larger inside the reserve; this difference was equivalent to ~10 years of growth for *P. filamentosus* (Moore et al. 2013). These results suggest that an increase in fish length had occurred for these species over the first 10 years of protection inside the reserve. Our results were consistent with this analysis, demonstrating that in the first year of monitoring there were larger *E. coruscans* and *P. filamentosus* inside the BRFA compared to outside; however, for *E. coruscans*, the opposite trend was seen when all 4 years were averaged together. This difference was likely due to a decline in mean fish length that seemed to occur inside and an increase that seemed to occur outside the reserve for *E. coruscans*. However, these trends over time were not significant ($P = 0.17$). Indeed, no changes in fish size or abundance over time were noted in this BRFA for any tested species, with the exception of *P. sieboldii*, a predominantly schooling non-target species that many commercial anglers avoid due to their small body size (Kelley et al. 2006).

The lack of significant changes in fish size and relative abundance over time inside Ni'ihau BRFA may be the result of small sample sizes, and high variance in the data

that increases in fish length and abundance has reached an asymptote, or due to an increase in poaching inside the BRFA in recent years. While other studies have indicated that an asymptote in fish length and abundance is often seen around 15 years of protection (Abesamis and Russ 2005; Molloy et al. 2009), small sample sizes may be a likely explanation for our lack of significant results. There were fewer length data for all but *P. sieboldii*, in Ni'ihau BRFA in comparison with situations where significant trends were found ($N \sim 100$; Table 4). In addition, the percent of nonzero data in datasets from Ni'ihau BRFA were <35 %, also lower than those that had significant results (~40 %; Table 4). However, previous research has demonstrated that using a GLMM with a negative binomial distribution, as we did, is likely to have reduced this possibility for our relative abundance data (Martinez et al. 2011; Smith et al. 2012). The lack of changes with time in Ni'ihau BRFA could also be due to a recent increase in anglers disregarding the boundaries of the BRFA and bottomfishing inside the reserve. While anecdotal evidence and a survey of fishers have suggested that poaching in BRFAs has occurred (Hospital and Beavers 2011), the local population near this BRFA is small and unlikely to have had a major impact on the bottomfish populations inside the BRFA. Ni'ihau is a small private island with a very small population of approximately 170 individuals living as ancestral Hawaiians did, without power boats or most modern technology (Hawaii State Data Center 2011). Instead, there is a relatively small community of non-local fishers using this area from neighboring islands. This community has changed during the years we monitored Ni'ihau BRFA with at least one commercial fisher that respected the boundaries of the BRFA retiring during this period. This BRFA is the most remote and therefore most difficult to monitor, so community enforcement is important. Further, previous research has demonstrated that even a small degree of fishing inside a MPA can result in little to no positive reserve effects (Denny and Babcock 2004; Shears et al. 2006). Despite this, positive effects of protection were demonstrated in Penguin Bank, Makapu'u and Pailolo Channel BRFAs, where poaching has been reported (Hospital and Beavers 2011).

Previously reported habitat associations for Hawaiian bottomfish have suggested they are generally found in hard bottom habitat types, particularly hard-high habitat (Parke 2007). In accordance with these findings, species richness was highest in hard habitat types in two of our research areas (Ni'ihau and Pailolo Channel BRFAs). However, significant relative abundance and mean fish length results were inconsistent with previously reported habitat associations in a few instances, and varied among BRFAs and species. For example, both juvenile and adult *E. carbunculus* have been reported to inhabit hard habitat types because

they are smaller than most bottomfish and use rocky substrate as cover from predation (Kelley et al. 2006; Misa et al. 2013). While the smallest *E. carbunculus* were found in hard habitat types in Ni'ihau BRFA, the largest individuals were found in soft-low habitats. A previous study by Misa et al. (2013) into habitat associations for Hawaiian bottomfish showed no ontogenetic shifts in habitat preference for *E. carbunculus*, however, very few juveniles were observed. Conversely, habitat associations for *P. sieboldii* were generally in agreement with previous research. Misa et al. (2013) suggested *P. sieboldii* have no significant habitat preferences, possibly as a result of their reliance on schooling rather than habitat for protection against predators. Our results were in agreement as *P. sieboldii* had different habitat preferences among Ni'ihau and Penguin Bank BRFAs. Lastly, most *P. filamentosus* in Makapu'u BRFA were found in low habitat types with the largest fish in soft-high habitats followed by hard-high habitats in both Penguin Bank and Makapu'u BRFAs. Soft-low habitat preferences have been reported for juvenile *P. filamentosus* (Moffitt and Parrish 1996, Parrish et al. 1997) and an ontogenetic shift from soft-low to hard-low (transition) and finally hard-high habitat was also recently reported to occur as fish size increases (Misa et al. 2013). Our results, therefore, suggested that many *P. filamentosus* from these areas (Penguin Bank and Makapu'u BRFAs) were juveniles. However, the largest *P. filamentosus* were associated with soft-high habitats, which was inconsistent with previously reported patterns. Overall, our results indicate that these species are responding to their habitat in a more complex manner than previously thought, that there are species-specific differences in habitat preferences and that ontogenetic shifts in habitat preferences are occurring for many species as proposed (Misa et al. 2013). Habitat classifications used here were broad, based on the dominant habitat within a 200 m² grid, to classify the area of bait attraction for target species (Moore et al. 2013). While this approach was the most appropriate with our current understanding of species–habitat associations and proved useful in establishing protection effects, a more detailed understanding of species–habitat associations is needed.

Conclusions

Differences among our BRFAs were likely influenced by the age of the BRFA. For instance, the oldest BRFA (Ni'ihau, protected approximately 14 years) showed more mature fish inside compared to outside the reserve for each species examined, and species richness in adjacent fished habitats increased while remaining unchanged inside the reserve, possibly due to spillover. Those with an intermediate duration of protection (Penguin Bank and Makapu'u)

had positive protection effects (i.e., increases in mean fish lengths and relative abundance), and the youngest BRFA (Pailolo Channel, protected approximately 4 years) showed little change over the duration of protection. Similarly, Molloy et al. (2009), reported that protection effects were positive but less reliable in “new” reserves (<5 years), young reserves (5 and 10 years) showed positive effects, established reserves (10–15 years) showed no change in relative fish density, and old reserves (>15 years) showed the most benefits to protection (consistently higher fish densities inside the reserve and overall relative fish densities reliably increased at ~5 % per annum). Our results follow this trend assuming Penguin Bank and Ni'ihau BRFAs were equivalent to approximately 5–10 years of protection. These authors and others also suggest that at least 15 years of protection are necessary to see reliable benefits of protection (Molloy et al. 2009; Russ and Alcala 2010). Accordingly, our data suggested that it may take a decade or more for target species to reach an equilibrium and spillover into adjacent fished areas. Importantly, though differences among BRFAs may be due to differences in the age of each BRFA, the degree of compliance among local anglers, initial fish population size inside the reserve, degree of fishing mortality reduction inside the reserve, local human population size, the extent of nearby fishing pressure, differences in fish biology, differences in habitat and smaller-scale habitat preferences may have also influenced our results (Mosqueira et al. 2000; Tetreault and Ambrose 2007; Gaines et al. 2010). Nonetheless, the predominant finding of larger more mature fishes inside the BRFAs and increases in abundance and size inside versus outside of these zones strongly suggests that the BRFAs can benefit Hawai'i's deepwater fish populations. While the results of this study are unique and provide evidence of the potential success of MPAs for deepwater species, additional data over greater temporal scales will be necessary to determine whether these trends will continue and if others will become important over time (Molloy et al. 2009). Deep water habitats and species are notoriously difficult to study and scientists' knowledge of deep-sea fish stocks frequently lags far behind fisheries exploitation (Haedrich et al. 2001). Using the precautionary principle, Lauck et al. (1998) suggested that MPAs are the best solution to protect fishery resources and enhance long-term sustainability in the face of data deficient and uncertain traditional management approaches. A network of moderately sized reserves that protect a diverse complex of species, as seen here and in other studies, may be the best strategy for deepwater species (Halpern and Warner 2003; Gaines et al. 2010).

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Conflict of interest The authors declare that they have no conflict of interest.

References

- Abesamis RA, Russ GR (2005) Density-dependent spillover from a marine reserve: long-term evidence. *Ecol Appl* 15:1798–1812
- Andrews AH, Humphreys RL, DeMartini EE, Nichols RS, Brodziak J (2011) Bomb radiocarbon and lead-radium dating of opakapaka (*Pristipomoides filamentosus*). *Pacific Islands Fish Sci Cent Natl Mar Fish Serv, NOAA, Honolulu, HI 96822-2396*. Pacific Islands Fish Sci Cent Admin Rep H-11-07, 58p
- Andrews AH, DeMartini EE, Brodziak J, Nichols RS, Humphreys RL (2012) A long-lived life history for tropical, deepwater snapper (*Pristipomoides filamentosus*): bomb radiocarbon and lead-radium dating as extensions of daily increment analyses in otoliths. *Can J Fish Aquat Sci* 69:1850–1869. doi:10.1139/f2012-109
- Babcock RC, Shears NT, Alcalá AC, Barrett NS, Edgar GJ, Lafferty KD, McClanahan TR, Russ GR (2010) Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. *PNAS* 107:18256–18261. doi:10.1073/pnas.0908012107
- Baker KD, Devine JA, Haedrich RL (2009) Deep-sea fishes in Canada's Atlantic: population declines and predicted recovery times. *Environ Biol Fish* 85:79–88. doi:10.1007/s10641-009-9465-8
- Bohnsack JA (1994) How marine fishery reserves can improve reef fisheries. *Proc Gulf Carib Fish Inst* 43:217–241
- Bohnsack JA (2011) Impacts of Florida coastal protected areas on recreational world records for spotted seatrout, red drum, black drum, and common snook. *Bull Mar Sci* 87:939–970. doi:10.5343/bms2010.1072
- Burnham KP, Anderson DR (1998) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. New York, New York
- Cappo M, Harvey ES, Malcolm H, Speare P (2003) Advantages and applications of novel “video-fishing” techniques to design and monitor Marine Protected Areas. In: Beumer JP, Grant A, Smith DC (eds) Aquatic protected areas—what works best and how do we know? Proceedings of the world congress on aquatic protected areas, Cairns, Australia, August, 2002, pp 455–464
- Cheung WWL, Pitcher TJ, Pauly D (2005) A fuzzy logic expert system to estimate intrinsic extinction vulnerabilities of marine fishes to fishing. *Biol Conserv* 124:97–111
- Dalzell P, Preston GL (1992) Deep reef slope fishery resources of the south Pacific: a summary and analysis of the dropline fishing survey data generated by the activities of the SPC Fisheries Programme between 1974 and 1988. *Tech Doc South Pac Comm, Inshore Fish Res Project 2*
- DeMartini EE, Lau BB (1999) Morphometric criteria for estimating sexual maturity in two snappers, *Etelis carbunculus* and *Pristipomoides sieboldii*. *Fish Bull* 97:449–458
- DeMartini EE, Everson AR, Nichols RS (2011) Estimates of body sizes at maturation and at sex change, and the spawning seasonality and sex ratio of the endemic Hawaiian grouper (*Hyporthodus quernus*, *F. Epinephelidae*). *Fish Bull* 109:123–134
- Denny CM, Babcock RC (2004) Do partial marine reserves protect reef fish assemblages? *Biol Conserv* 116:119–129. doi:10.1016/S0006-3207(03)00183-6
- Drazen JC, Haedrich RL (2012) A continuum of life histories in deep-sea demersal fishes. *Deep-Sea Res I* 61:34–42
- Everson AR, Williams HA, Ito BM (1989) Maturation and reproduction in two Hawaiian eteline snappers, uku, *Aprion virescens*, and onaga, *Etelis coruscans*. *Fish Bull* 87:877–888
- Friedlander AM, Brown EK, Jokiel PL, Smith WR, Rodgers KS (2003) Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. *Coral Reefs* 22:291–305. doi:10.1007/s00338-003-0317-2
- Gaines SD, Lester SE, Grorud-Colvert K, Costello C, Pollnac R (2010) Evolving science of marine reserves: new developments and emerging research frontiers. *PNAS* 107:18251–18255. doi:10.1073/pnas.1002098107
- Greenstreet SPR, Fraser HM, Piet GJ (2009) Using MPAs to address regional-scale ecological objectives in the North Sea: modeling the effects of fishing effort displacement. *ICES J Mar Sci* 66:90–100. doi:10.1093/icesjms/fsn214
- Grigg RW (2001) Black coral: history of a sustainable fishery in Hawai'i. *Pac Sci* 55:291–299
- Haedrich RL, Merrett NR, O'Dea NR (2001) Can ecological knowledge catch up with deep-water fishing? A North Atlantic perspective. *Fish Res* 51:113–122
- Haight WR, Parrish JD, Hayes TA (1993) Feeding ecology of deepwater Lutjanid snappers at Penguin Bank, Hawaii. *TAFS* 122:328–347
- Halpern BS, Warner RR (2003) Matching marine reserve design to reserve objectives. *Proc R Soc Lond B* 270:1871–1878. doi:10.1098/rspb.2003.2405
- Halpern BS, Gaines SD, Warner RR (2004) Confounding effects of the export of production and the displacement of fishing effort from marine reserves. *Ecol Appl* 14:1248–1256
- Harmelin-Vivien M, Le Direach L, Bayle-Sempere J, Charbonnel E, Garcia-Charton JA, Ody D, Perez-Ruzafa A, Renones O, Sanchez-Jerez P, Valle C (2008) Gradients of abundance and biomass across reserve boundaries in six Mediterranean marine protected areas: evidence of fish spillover? *Biol Conserv* 141:1829–1839. doi:10.1016/j.biocon.2008.04.029
- Harter SL, Ribera MM, Shepard AN, Reed JK (2009) Assessment of fish populations and habitat on Oculina Bank, a deep-sea coral marine protected area off eastern Florida. *Fish Bull* 107:195–206
- Harvey E, Cappo M (2001) Direct sensing of the size frequency and abundance of target and non-target fauna in Australian fisheries. 4–7 September 2000, Rottnest Island, Western Australia. Fisheries Research and Development Corporation
- Harvey E, Shortis M (1995) A system for stereo-video measurement of subtidal organisms. *Mar Technol Soc J* 29:10–22
- Hawaii State Data Center (2011) Island population and housing units, state of Hawaii: 2010. Hawaii Dept of Business, Economic Development and Tourism, Research and Economic Analysis Division, Statistics and Data Support Branch, Hawaii State data Center Rep 2010-3
- Hospital J, Beavers C (2011) Management of the Main Hawaiian Islands bottomfish fishery: fishers' attitudes, perceptions, and comments. *Pacific Islands Fish Sci Cent, Natl Mar Fish Serv, NOAA, Honolulu, HI 96822-2396*. Pacific Islands Fish Sci Cent Admin Rep H-11-06, 46 p
- Hospital J, Beavers C (2012) Economic and social characteristics of bottomfish fishing in the Main Hawaiian Islands. *Pacific Islands Fish Sci Cent, Natl Mar Fish Serv, NOAA, Honolulu, HI 96822-2396*. Pacific Islands Fish Sci Cent Admin Rep H-12-01, 44 p
- Kelley CD, Moriwake VN (2012) Appendix 3: essential fish habitat descriptions, Part 1: bottomfish. In: WPRFMC (ed) Final fishery management plan for coral reef ecosystems of the western 596 Pacific region, volume III, Essential Fish Habitat for Management Unit Species, p 597

- Kelley C, Moffitt R, Smith JR (2006) Mega- to micro-scale classification and description of bottomfish essential fish habitat on four banks in the Northwestern Hawaiian Islands. *Atoll Res Bull* 543:319–332
- Lauck T, Clark CW, Mangel M, Munro GR (1998) Implementing the precautionary principle in fisheries management through marine reserves. *Ecol Appl* 8:S72–S78
- Lester SE, Halpern BS, Grorud-Colvert K, Lubchenco J, Ruttenberg BI, Gaines SD, Airame S, Warner RR (2009) Biological effects within no-take marine reserves: a global synthesis. *Mar Ecol Prog Ser* 384:33–46. doi:10.3354/meps08029
- Martinez I, Jones EG, Davie SL, Neat FC, Wigham BD, Priede IG (2011) Variability in behaviour of four fish species attracted to baited underwater cameras in the North Sea. *Hydrobiol* 670:23–34. doi:10.1007/s10750-011-0672-x
- Merritt D, Donovan MK, Kelley C, Waterhouse L, Parke M, Wong K, Drazen JC (2011) BotCam: a baited camera system developed for non-extractive monitoring of bottomfish species. *Fish Bull* 109:56–67
- Misa WFXE, Drazen JC, Kelley CCD, Moriwake VN (2013) Establishing species–habitat associations for 4 eteline snappers with the use of a baited stereo-video camera system. *Fish Bull* 111:293–308. doi:10.7755/FB.111.4.1
- Moffitt RB, Parrish FA (1996) Habitat and life history of juvenile Hawaiian pink snapper, *Pristipomoides filamentosus*. *Pac Sci* 50:371–381
- Moffitt R, Kobayashi D, Dinardo G (2006) Status of the Hawaiian bottomfish stocks, 2004 Admin Rep H-06-01, Pacific Islands Fish Sci Cent, Natl Mar Fish Serv, NOAA, Honolulu, HI
- Molloy PP, McLean IB, Cote IM (2009) Effects of marine reserve age on fish populations: a global meta-analysis. *J Appl Ecol* 46:743–751. doi:10.1111/j.1365-2664.2009.01662.x
- Moore CH, Drazen JC, Kelley CD, Misa WFXE (2013) Deepwater marine protected areas of the main Hawaiian Islands: establishing baselines for commercially valuable bottomfish populations. *Mar Ecol Prog Ser* 476:167–183. doi:10.3354/meps10132
- Morato T, Watson R, Pitcher TJ, Pauly D (2006) Fishing down the deep. *Fish Fish* 7:24–34
- Mosqueira I, Cote I, Jennings S, Reynolds JD (2000) Conservation benefits of marine reserves for fish populations. *Animal Conserv* 4:321–332
- Parke M (2007) Linking Hawaii fisherman reported commercial bottomfish catch data to potential bottomfish habitat and proposed restricted fishing areas using GIS and spatial analysis. US Dep Commer, NOAA Tech Memo, NOAA-TM-NMFS-PIFSC-11, 38 p
- Parrish FA (1989) Identification of habitat of juvenile snappers in Hawaii. *Fish Bull* 87:1001–1005
- Parrish FA, DeMartini EE, Ellis DM (1997) Nursery habitat in relation to production of juvenile pink snapper, *Pristipomoides filamentosus*, in the Hawaiian Archipelago. *Fish Bull* 95:137–148
- Pelc RA, Warner RR, Gaines SD, Paris CB (2010) Detecting larval export from marine reserves. *PNAS* 107:18266–18271. doi:10.1073/pnas.0907368107
- Priede IG, Bagley PM, Smith A, Creasey S, Merrett NR (1994) Scavenging deep demersal fishes of the Porcupine Seabight, north-east Atlantic: observations by baited camera, trap and trawl. *J Mar Biol Assoc UK* 74:481–498
- Ralston S, Miyamoto GT (1983) Analyzing the width of daily otolith increments to age the Hawaiian snapper, *Pristipomoides filamentosus*. *Fish Bull* 81:523–535
- Ralston S, Gooding RM, Ludwig GM (1986) An ecological survey and comparison of bottom fish resource assessments (submersible versus handline fishing) at Johnston Atoll. *Fish Bull* 84:141–155
- Roberts CM, Polunin NVC (1991) Are marine reserves effective in management of reef fisheries? *Rev Fish Biol Fish* 1:65–91
- Rosenberg A, Bigford TE, Leathery S, Hill RL, Bickers K (2000) Ecosystem approaches to fishery management through essential fish habitat. *Bull Mar Sci* 66:535–542
- Rudershausen PJ, Mitchell WA, Buckel JA, Williams EH, Hazen E (2010) Developing a two-step fishery-independent design to estimate the relative abundance of deepwater reef fish: application to a marine protected area off the southeastern United States coast. *Fish Res* 105:254–260
- Russ GR, Alcala AC (1996) Do marine reserves export adult fish biomass? Evidence from Apo Island, Central Philippines. *Mar Ecol Prog Ser* 132:1–9
- Russ GR, Alcala AC (2010) Decadal-scale rebuilding of predator biomass in Philippine marine reserves. *Oecologia* 163:1103–1106. doi:10.1007/s00442-010-1692-3
- SAFMC (2013) Deepwater MPAs. South Atlantic Fishery Management Council online: <http://www.safmc.net/MPAInformationPage/tabid/469/Default.aspx>. Accessed 18 July 2013
- Sanchez Lizaso JL, Goni R, Renones O, Garcia Charton JA, Galzin R, Bayle JT, Sanchez Jerez P, Perez Ruzafa A, Ramos AA (2000) Density dependence in marine protected populations: a review. *Environ Conserv* 27:144–158
- Shears NT, Grace RV, Usmar NR, Kerr V, Babcock RC (2006) Long-term trends in lobster populations in a partially protected vs. no-take Marine Park. *Biol Conserv* 132:222–231. doi:10.1016/j.biocon.2006.04.001
- Shortis MR, Seager JW, Williams A, Barker BA, Sherlock M (2008) Using stereo-video for deep water benthic habitat surveys. *Mar Technol Soc J* 42:28–37
- Smith MK, Kostlan E (1991) Estimates of age and growth of ehu *Etelis carbunculus* in four regions of the Pacific from density of daily increments in otoliths. *Fish Bull* 89:461–472
- Smith ANH, Anderson MJ, Millar RB (2012) Incorporating the intraspecific occupancy-abundance relationship into zero-inflated models. *Ecology* 93:2526–2532
- Stobart B, Warwick R, Gonzalez C, Mallol S, Diaz D, Renones O, Goni R (2009) Long-term and spillover effects of a marine protected area on an exploited fish community. *Mar Ecol Prog Ser* 384:47–60. doi:10.3354/meps08007
- Tetreault I, Ambrose RF (2007) Temperate marine reserves enhance targeted but not untargeted fishes in multiple no-take MPAs. *Ecol Appl* 17:2251–2267
- Watson DL, Harvey ES, Fitzpatrick BM, Langlois TJ, Shedrawi G (2010) Assessing reef fish assemblage structure: how do different stereo-video techniques compare? *Mar Biol* 157:1237–1250
- White C, Kendall BE (2007) A reassessment of equivalence in yield from marine reserves and traditional fisheries management. *Oikos* 116:2039–2043. doi:10.1111/j.2007.0030-1299.16167.x
- White C, Kendall BE, Gaines S, Siegel DA, Costello C (2008) Marine reserve effects on fishery profit. *Ecol Lett* 11:370–379. doi:10.1111/j.1461-0248.2007.01151.x
- Williams HA, Lowe MK (1997) Growth rates of four Hawaiian deep slope fishes: a comparison of methods for estimating age and growth from otolith microincrement widths. *Can J Fish Aquat Sci* 54:126–136
- Williams AJ, Nicol SJ, Bentley N, Starr PJ, Newman SJ, McCoy MA, Kinch J, Williams PG, Magron F, Pilling GM, Bertram I, Batty M (2012) International workshop on developing strategies for monitoring data-limited deepwater demersal line fisheries in the Pacific Ocean. *Rev Fish Biol Fish* 22:527–531. doi:10.1007/s11160-011-9234-6
- Williams AJ, Loeun K, Nicol SJ, Chavance P, Ducrocq M, Harley SJ, Pilling GM, Allain V, Mellin C, Bradshaw CJA (2013) Population biology and vulnerability to fishing of deep-water Eteline snappers. *J Appl Ichthyol* 29:395–403. doi:10.1111/jai.12123