

Spilling over deepwater boundaries: evidence of spillover from two deepwater restricted fishing areas in Hawaii

Dana K. Sackett*, Christopher D. Kelley, Jeffrey C. Drazen

Department of Oceanography, University of Hawai'i, Manoa, Honolulu, HI, 96822, USA

ABSTRACT: The net export of adults (spillover) is an important though contentious benefit of marine protected areas (MPAs). Controversy over spillover often exists because it is difficult to discern empirically. In addition, of those studies that have provided empirical evidence, nearly all are from shallow reef ecosystems. Here we examined 2 deepwater MPAs in the main Hawaiian Islands, established to benefit a complex of species called the 'Deep 7.' To study these fishes, we used baited cameras and commercial fishery data. Relative abundance, fish size, and species richness observed using camera data declined with distance from MPAs, signifying that species had begun to spill over the MPA boundaries into fishing grounds. Further, temporal analyses of these spatial trends indicated that they did not always exist but developed in the fifth and sixth years of sampling. Changes in fish size over time supported these results, with asymptotes in fish size seen inside and increases seen outside MPAs in the fifth and sixth years of sampling. Displaced fishing effort may have also caused initial declines in *Etelis coruscans* size and catch data that increased in later years. Further, low sample sizes and public announcements prior to sampling in Year 8 may have contributed to the decline in *E. carbunculus* sizes inside, and spatial trends outside, an MPA that were no longer significant in Year 8. Identifying the ability and time span for an MPA to begin to benefit a fishery and how quickly fishing may remove those benefits is crucial to resolving debates regarding the use of MPAs in fisheries management.

KEY WORDS: Spillover · Deepwater · Marine protected area · Bottomfish restricted fishing area · BRFA · Snapper

— Resale or republication not permitted without written consent of the publisher —

INTRODUCTION

The use of marine protected areas (MPAs), defined here as an area that restricts at least 1 form of fishing to provide lasting protection for at least part of the natural resources therein (Executive Order 13158 [2000]), as spatial management tools to maintain or enhance local fisheries has been extensively debated over the last several decades (Roberts & Polunin 1991, Agardy et al. 2003, Hilborn et al. 2004, Kaiser 2005). Much of this debate focuses on the theory that exploited populations inside an MPA will grow and ultimately export adults ('spillover') and recruits (i.e. larvae and/or juveniles) into surrounding fished

areas, benefiting local fisheries (McClanahan & Mangi 2000, Kerwath et al. 2013). Controversy over spillover often exists because although intuitive arguments and theoretical modeling are prevalent, it is difficult to discern empirically (Roberts & Polunin 1991, Kellner et al. 2007, White & Kendall 2007, Halpern 2014). One of the reasons spillover is difficult to distinguish is that there are numerous other factors that can influence fish populations in open-ocean environments, and distinguishing population changes related to protection alone can be difficult. Further, it often takes several years to decades, depending on the life history of the target species, for spillover to begin and be statistically recognized in

*Corresponding author: danas4@hawaii.edu

monitoring data; this represents a much longer time span than many monitoring programs (Molloy et al. 2009, Russ & Alcala 2010). Protected areas also require a form of data collection that is non-extractive, often relying on diver surveys and baited camera systems to measure relative abundance, which is highly variable and statistically difficult to analyze (Martinez et al. 2011, Smith et al. 2012).

Despite these limitations, studies have shown how relative abundance, size, and biodiversity of exploited species have increased just outside of well-designed and managed MPAs (McClanahan & Mangi 2000, Russ & Alcala 2004). Indeed, Russ & Alcala (2011) demonstrated that after 25 yr of protection, the high level of biodiversity and community complexity inside the Philippines Apo MPA had extended beyond the boundaries into adjacent fished areas due to the spillover of multiple species. Further, while some studies have provided evidence of spillover, few have demonstrated tangible benefits to the fishery (Abesamis et al. 2006, Kerwath et al. 2013), and of those that have, nearly all are from shallow reef ecosystems (McClanahan & Mangi 2000, Russ & Alcala 2004, Abesamis & Russ 2005). Thus, uncertainty still remains over whether spillover from MPAs is a reliable benefit to fisheries management, particularly in environments other than shallow reef ecosystems.

Among the main Hawaiian Islands (MHI) there is a system of deepwater MPAs called bottomfish restricted fishing areas (BRFAs) that were initially established in 1998 and substantially revised in 2007 by the State of Hawai'i, Department of Land and Natural Resources. These BRFAs were created in response to declining catch rates and spawning potential ratios of an exploited group of fish called the 'Deep 7' (Ralston et al. 1986, Haight et al. 1993, Kelley et al. 2006, Parke 2007). The Deep 7 refers to a complex of deepwater bottomfish species that are relatively site attached and includes 6 snappers (Lutjanidae) in the subfamily Etelinae: deepwater red snapper *Etelis carbunculus*, deepwater longtail red snapper *E. coruscans*, crimson jobfish *Pristipomoides filamentosus*, lavender jobfish *P. sieboldii*, oblique-banded snapper *P. zonatus*, and rusty jobfish *Apha-reus rutilans*; and 1 grouper (Serranidae): Hawaiian grouper *Hyporthodus quernus* (Haight et al. 1993, Kelley et al. 2006). Of these, the most economically important are *E. carbunculus*, *E. coruscans*, and *P. filamentosus*. These BRFAs restrict bottomfish harvest, both commercial and recreational, and protect the deepwater environment year-round. Surface waters, however, are open to fishing for pelagic species such as tuna. Additionally, other habitat sur-

rounding the MHI outside of these BRFAs are open to bottom-fishing.

Monitoring of the BRFAs began after their revision in 2007. Our previous work analyzing the first 4 yr of monitoring data (2007–2011) from a subset of these BRFAs found that mean fish length, and in some cases abundance, increased for 1 or more of the most economically important Deep 7 species inside, while outside, fish sizes and relative abundance declined or stayed the same (Sackett et al. 2014). Monitoring continued in 2 of the BRFAs following that study. These 2 BRFAs were similar in that both had their boundaries extensively expanded in 2007 (Makapu'u from 10.2 km² to 189.2 km²; Penguin Bank from 54.7 km² to 268.6 km²) because detailed mapping of the seafloor revealed that the original location and size of these BRFAs were insufficient in protecting essential fish habitat for Deep 7 species (Moffitt et al. 2006, Parke 2007, Kelley & Moriwake 2012, Sackett et al. 2014). Data obtained from these 2 BRFAs from 2007 to 2015 were the primary focus of this study. To examine the possibility of Deep 7 spillover from these BRFAs, we investigated the following null hypotheses: (1) fish length did not change over time inside or outside of these BRFAs, (2) economically important Deep 7 fish abundance, fish length, and species richness did not change with distance from the boundary of the BRFAs, (3) these spatial trends also did not change over time, and (4) commercial fishery catch per unit effort (CPUE) in neighboring fished zones did not vary over time after the expansion of the BRFA boundaries. Thus, our predictions for each null hypotheses were that (1) fish length would increase over time both inside and outside protected areas, (2) that economically important Deep 7 fish abundance, fish length, and species richness would decline with distance from the boundary of the BRFAs, signifying more, larger, and a more diverse number of Deep 7 species near the boundary of the BRFAs, (3) that these spatial trends would not always exist but would develop over time after protection, and (4) that commercial fishery CPUE near BRFAs would increase as a result of increased fish abundance and length near BRFAs over time.

MATERIALS AND METHODS

Data collection and synthesis

Data collected in this study were part of a monitoring program examining deepwater bottomfish populations in the MHI using a fishery-independent baited

stereo-video camera system (BotCam). Detailed data collection methods, video analysis methods, and sampling strategies were previously described by Moore et al. (2013), Misa et al. (2013), and Sackett et al. (2014). Briefly, the camera system used 2 paired ultralow-light video cameras that enabled accurate fish identification and length measurements under ambient light conditions to a depth of 310 m (Shortis et al. 2008, Watson et al. 2010). In addition, 0.04 km² (200 m × 200 m) sample grid cells created in and around the 2 BRFAs (Penguin Bank and Makapu'u; Fig. 1) were randomly chosen and stratified by level of protection (fished/unprotected or unfished/protected) and habitat. The camera system was left to record 3 m above the sea floor for approximately 40 min at each sample site. These specifications allowed our system to target the Deep 7, which are closely associated with the benthos and/or school in the water column above it (Sackett et al. 2014). Habitat designations were classified by slope (high: ≥20°; low: <20°) and substrate type (hard: consolidated hard rocky substrate; soft: unconsolidated soft substrate) for every 0.04 km² area based on multibeam

bathymetry and backscatter data (Misa et al. 2013). While more detailed habitat designations may be useful, these habitat designations have been used extensively in the past for Deep 7 species and have been seen to explain much of the variation in Deep 7 distributions (Kelley et al. 2006, Parke 2007, Misa et al. 2013, Sackett et al. 2014).

Relative abundance data for each sample was recorded using the MaxN metric: the maximum number of fish observed in a single frame of the video (Parrish 1989, Priede et al. 1994, Moore et al. 2013). Species not seen were given a value of 0. In addition, because each species does not occupy the entire depth range sampled (90–310 m), data collected outside of a species' preferred depth range were excluded from the MaxN database (Misa et al. 2013, Sackett et al. 2014). Fork lengths for a single species were also measured only once during a video, when the most measurable fish were visible on both cameras. Species richness was measured by a count of the number of Deep 7 species present in a single video. These data were collected from 2007 to 2013 in and around Makapu'u BRFA and from 2007 to

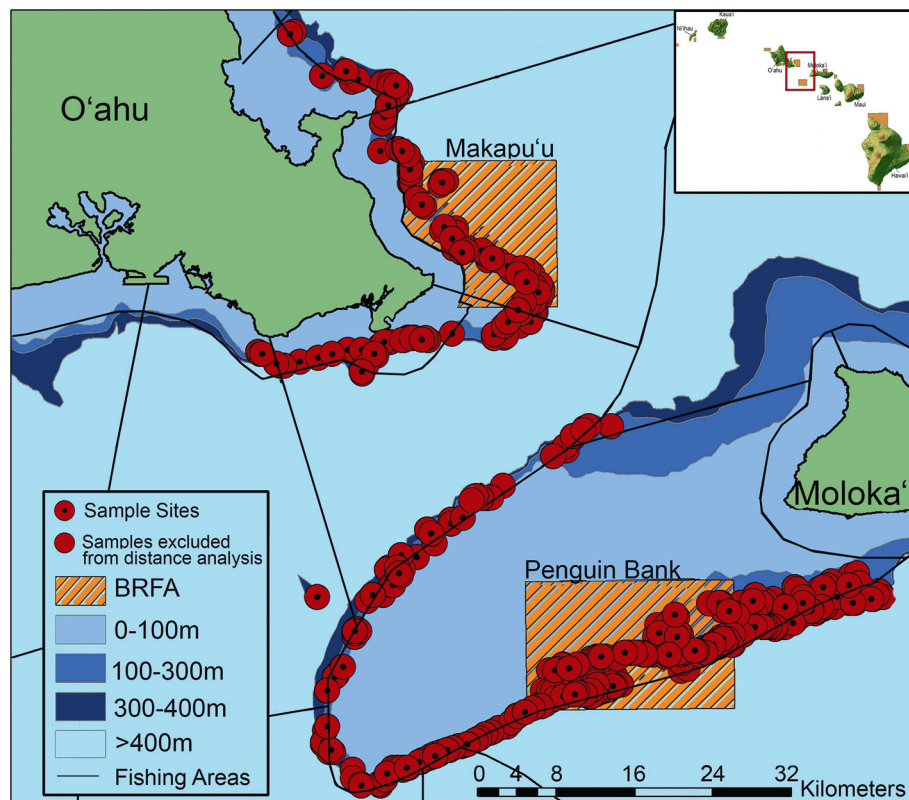


Fig. 1. Two out of a system of 12 deepwater marine protected areas called bottomfish restricted fishing areas (BRFAs) in the main Hawaiian Islands, and sample sites inside and outside each BRFA. Depth contours from 100 to 400 m and fishing zones for the bottomfish fishery are delineated on the map. Data excluded from our spatial analyses using distance from Penguin Bank BRFA are also indicated on the map

2015 in and around Penguin Bank BRFA. Additionally, because fish in this study were not removed from the water or physically handled and only recorded on video, no express permission to sample in and around the BRFAs was necessary. This work was approved by the University of Hawaii's Institutional Animal Care and Use Committee (IACUC 14-1934).

Statistical approach

We focused much of our analyses on the 3 most economically important and abundant of the com-

plex of deep-dwelling bottomfish species called the Deep 7 (*Etelis carbunculus*, *E. coruscans*, and *Pristipomoides filamentosus*; Haight et al. 1993, Kelley et al. 2006, Sackett et al. 2014). Where data were sufficient, results for other Deep 7 species are briefly presented as well (Table 1). To address our first null hypothesis, that fish length did not change over time inside or outside of these BRFAs, we analyzed fish length data collected by our camera system using non-linear (degree 2 polynomial fit) regression both inside and outside of protected areas. A nonlinear approach was chosen to ensure asymptotes and changes in data direction over time would be accounted for in our analyses. Further, as MaxN and

Table 1. Sample sizes for (a) fish length data and (b,c) MaxN (maximum number of fish observed in a single frame of video) data collected within the preferred depth range of each species for sampling Years 1 and 2, 3 and 4, 5 and 6, and Year 8 in 2 protected areas (Penguin Bank and Makapu'u). Data are from 2007–2015 (Years 1–8) from inside and outside each protected area and for each of the 'Deep 7' species. Genera in the table are *Etelis*, *Pristipomoides*, *Hyporthodus*, and *Aphareus*. In (b) and (c), percentages shown are % of the data that were non-zero

Species	Years 1–2				Years 3–4				Years 5–6				Year 8			
	Penguin Bank		Makapu'u		Penguin Bank		Makapu'u		Penguin Bank		Makapu'u		Penguin Bank			
	In	Out	In	Out	In	Out	In	Out	In	Out	In	Out	In	Out		
(a) Length																
<i>E. carbunculus</i>	34	39	5	7	43	43	4	21	71	29	11	8	26	40		
<i>E. coruscans</i>	67	30	7	1	39	18	2	0	93	36	15	4	30	10		
<i>P. filamentosus</i>	82	39	59	41	67	62	111	10	153	90	83	31	54	57		
<i>P. sieboldii</i>	81	77	5	0	110	73	0	0	141	99	18	0	100	96		
<i>P. zonatus</i>	6	3	0	1	8	12	0	2	15	5	1	3	7	9		
<i>H. quernus</i>	4	2	0	4	4	7	0	0	12	1	0	0	7	1		
<i>A. rutilans</i>	13	3	0	1	8	6	0	2	17	20	0	0	2	7		
(b) MaxN Makapu'u																
	Years 1–2				Years 3–4				Years 5–6							
	In		Out		In		Out		In		Out					
	N	%	N	%	N	%	N	%	N	%	N	%				
<i>E. carbunculus</i>	20	15	32	16	5	40	15	27	25	20	29	10				
<i>E. coruscans</i>	20	20	32	9	5	40	15	0	25	24	29	10				
<i>P. filamentosus</i>	44	41	34	53	27	59	17	35	39	54	35	37				
<i>P. sieboldii</i>	19	11	34	3	6	0	17	0	27	4	30	0				
<i>P. zonatus</i>	40	0	41	10	19	5	25	16	39	3	43	9				
<i>H. quernus</i>	45	0	38	13	24	0	24	0	40	0	43	2				
<i>A. rutilans</i>	51	0	44	2	29	0	24	4	49	0	46	4				
(c) MaxN Penguin Bank																
	Years 1–2				Years 3–4				Years 5–6				Year 8			
	In		Out		In		Out		In		Out		In		Out	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
<i>E. carbunculus</i>	34	53	43	35	29	55	34	53	56	46	54	33	30	43	29	55
<i>E. coruscans</i>	34	50	43	40	29	41	34	44	56	46	54	35	30	40	29	31
<i>P. filamentosus</i>	27	59	17	41	34	53	27	56	69	51	70	47	33	52	34	50
<i>P. sieboldii</i>	32	28	41	27	27	44	45	40	63	33	60	18	29	28	35	34
<i>P. zonatus</i>	41	12	44	7	39	26	51	20	84	15	80	11	40	18	45	29
<i>H. quernus</i>	34	12	37	5	42	12	39	13	73	16	78	1	39	15	44	5
<i>A. rutilans</i>	40	23	41	10	46	15	41	7	86	12	88	10	41	5	49	14

species richness data were hyperdispersed count data with excess zeroes (Sackett et al. 2014), they were not appropriate for these parametric tests. We ran these analyses for Penguin Bank BRFA in both Years 1 through 6 and Years 1 through 8 separately to demonstrate how the trajectory of our analyses was changed by including data from Year 8. We also examined the proportion of immature (*E. carbunculus* <279 mm, DeMartini & Lau 1999; *E. coruscans* <700 mm, Everson et al. 1989; *P. filamentosus* <450 mm, Ralston & Miyamoto 1983), smaller mature (*E. carbunculus* 279–450 mm; *E. coruscans* 700–850 mm; *P. filamentosus* 450–600 mm), and larger mature (*E. carbunculus* >450 mm; *E. coruscans* >850 mm; *P. filamentosus* >600 mm) fish inside and outside each BRFA over time to provide additional insight into length trends seen over time.

To address our second null hypothesis, that economically important Deep 7 fish abundance, fish length, and species richness did not change with distance from the boundary of the BRFAs, we examined whether fish length, relative abundance (MaxN), and species richness data collected by our camera system declined with distance away from each BRFA using simple linear regression (length data), a generalized linear model with a negative binomial distribution (MaxN data; Martinez et al. 2011, Smith et al. 2012), and a generalized linear model with a Poisson distribution (species richness data). All sampled habitat types being equal, a decline in these metrics with distance from the BRFAs would indicate that the protected areas were a source of more and larger fish to fished areas (i.e. spillover; McClanahan & Mangi 2000, Russ & Alcala 2004, Forcada et al. 2009, Russ & Alcala 2011). Distances were measured as the shortest straight line distance within the 100–400 m depth range, as this is the depth at which these species reside (Kelley et al. 2006, Parke 2007, Kelley & Moriwake 2012, Weng 2013). To reduce error, we measured the shortest distance from the BRFA to the sample site within the 100–400 m depth range 3 times in ESRI ArcMap 10 and took a mean from those measurements. In addition, those sites greater than 50 km away from Penguin Bank BRFA were excluded from these analyses because of their close proximity to Makapu'u BRFA (~14–20 km; see Fig. 1). Sample sites inside the BRFAs were given a distance of 0 m from the BRFA. Also, to ensure that our results were not an artifact of differences in habitat type among sample sites and because hard habitat types are often preferred (as measured by presence and relative abundance) by Deep 7 species (Kelley et al. 2006, Parke 2007, Misa et al. 2013, Sackett et al.

2014), relative abundance and species richness analyses used only those data collected from hard bottom habitat types. Further, for those species that have shown evidence of a size-related shift in preference for soft or hard habitats types, specifically *P. filamentosus* and *P. sieboldii* (Misa et al. 2013), length analyses were limited to only those data collected from hard bottom habitat types. While the way these fishes use their deepwater habitats is much more complex than a 'soft' or 'hard' category can describe (Sackett et al. 2014), limiting these data to only include 1 of these 2 'types' was a conservative approach that allowed for comparisons and analyses to focus on the effects of protection and not on the distribution of sampled habitat types. However, to further demonstrate that the distribution of hard habitat types did not influence our results, we examined whether sampled hard habitat types varied with distance from each protected area.

To address our third null hypothesis, that spatial trends in fish abundance, fish length, and species richness did not change over time, we examined the spatial trends described above using 4 separate datasets: sampling Years 1 and 2, Years 3 and 4, Years 5 and 6, and Year 8 separately. We then compared the results from each of these datasets to determine whether trends were consistent over time or had changed.

We addressed our fourth null hypothesis, that commercial fishery CPUE in neighboring fished zones would not vary over time after the expansion of the BRFA boundaries in 2007, using reported commercial fisheries catch data collected by the State of Hawai'i Division of Aquatic Resources from 2007 to 2015 (Zellar et al. 2008). This analysis also served to determine whether any relative spillover effects seen with camera data were evident in CPUE data. Further, reported commercial CPUE were used instead of total yields because of the strong influence weather can have on annual total yields in the MHI and because recreational harvest is not recorded for this fishery (Zellar et al. 2008), and is therefore unknown. Effort data were measured as the number of trips (representing a day of fishing) anglers took in a single fishing area (Fig. 1) around the MHI. A trip is represented by approximately 11 h of fishing (Hospital & Beavers 2012). In addition, the fishery is commercial hook-and-line, using primarily electric reels (Zellar et al. 2008, Hospital & Beavers 2012). The total reported commercial annual weight (kg) and number of fish caught for each Deep 7 species from 2007 to 2015 were recorded in each fishing area (Fig. 1). To determine whether spillover from Pen-

guin Bank and Makapu'u BRFAs were having an impact on CPUE, we summed data collected from those fishing areas that intersected each BRFA, thus creating a database of catch data that surrounded each BRFA. Catch data (total weight and number of fish caught) were then divided by the total number of trips in these areas from each year to standardize catch by effort and create 2 CPUE metrics (kg of fish caught per trip and number of fish caught per trip). The CPUE metrics were \log_{10} transformed to meet assumptions of normality and equal variance and then analyzed over time using linear and non-linear (degree 2 polynomial fit) regression to determine which fit the data best (based on the regression coefficient and a lack of fit test $p > 0.05$). These analyses were run for pooled data from both BRFAs, because BRFAs shared a fishing area (see Fig. 1), and for each BRFA separately.

All analyses were conducted using JMP 9.0.2 (2010, SAS Institute) and SPSS 22 (2013, IBM). Statistical results with $p \leq 0.05$ were deemed significant, while results with $0.10 > p > 0.05$ were considered marginally significant, as these results still hold 90 % confidence.

RESULTS

Changes over time

Non-linear regression analyses of Deep 7 species inside Penguin Bank BRFA over the first 6 yr of monitoring showed an increase in *Etelis carbunculus*, *E. coruscans*, and *Pristipomoides filamentosus* lengths over time that began to reach an asymptote in Years 5 and 6 ($p < 0.01$, $r^2 = 0.11$, 0.06, and 0.47, respectively; Fig. 2a,c,e). This was also true for 2 other Deep 7 species, *P. sieboldii* and *Aphareus rutilans* ($p < 0.01$, $r^2 = 0.03$; $p = 0.02$, $r^2 = 0.20$; Table S1A in the Supplement at www.int-res.com/articles/suppl/m568p175_supp.pdf). Outside of Penguin Bank BRFA, *P. filamentosus* lengths increased ($r^2 = 0.15$) while *E. coruscans* lengths initially declined over time and then began to increase ($r^2 = 0.19$) at approximately the same time the asymptote in fish length was reached inside

the BRFA ($p < 0.01$; Fig. 2d,f). *E. carbunculus* showed no trend over time ($p = 0.82$; Fig. 2b), whereas *P. sieboldii* and *A. rutilans* showed the same trend outside as was seen inside Penguin Bank BRFA, an increase that seemed to reach an asymptote over time ($p < 0.01$, $r^2 = 0.10$; $p < 0.01$, $r^2 = 0.41$; Table S1A).

The addition of Year 8 data inside Penguin Bank BRFA generally followed the expected trajectory for all except *E. carbunculus*, which demonstrated a significant drop in mean fish sizes inside of the BRFA (Fig. 2a). This decline was likely related to the decrease in the number of large individuals observed in Year 8 (Fig. 3). For instance, a significant increase ($p = 0.01$, $r^2 = 0.85$) in the percent of large *E. carbunculus* (> 450 mm) was seen over time, increasing from 14 to 50 % by Year 6 inside Penguin Bank BRFA

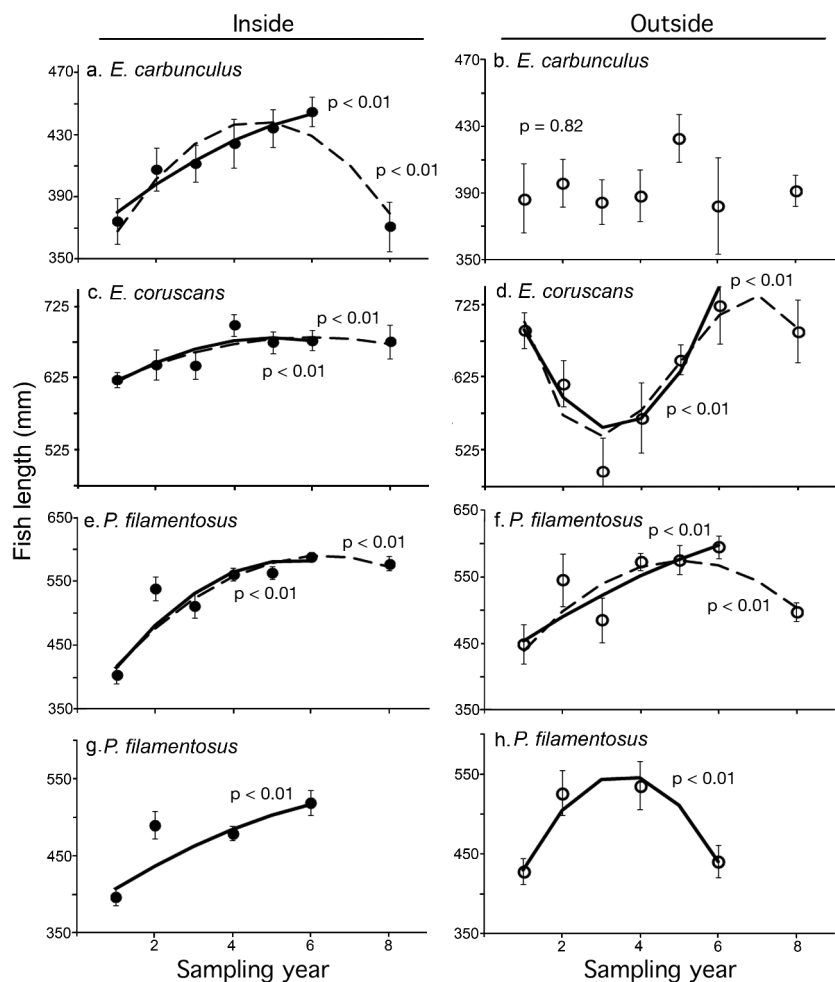


Fig. 2. Mean (\pm SE) fish length collected with a baited camera system inside (black filled circles) and outside (black open circles) (a–f) Penguin Bank and (g, h) Makapu'u bottomfish restricted fishing areas (BRFAs) over time. Polynomial regressions for Years 1 through 6 are solid black, while polynomial regressions for Years 1 through 8 are dashed black. Genera in the figure are *Etelis* and *Pristipomoides*. For significant polynomial regression equations see Table S1A in the Supplement

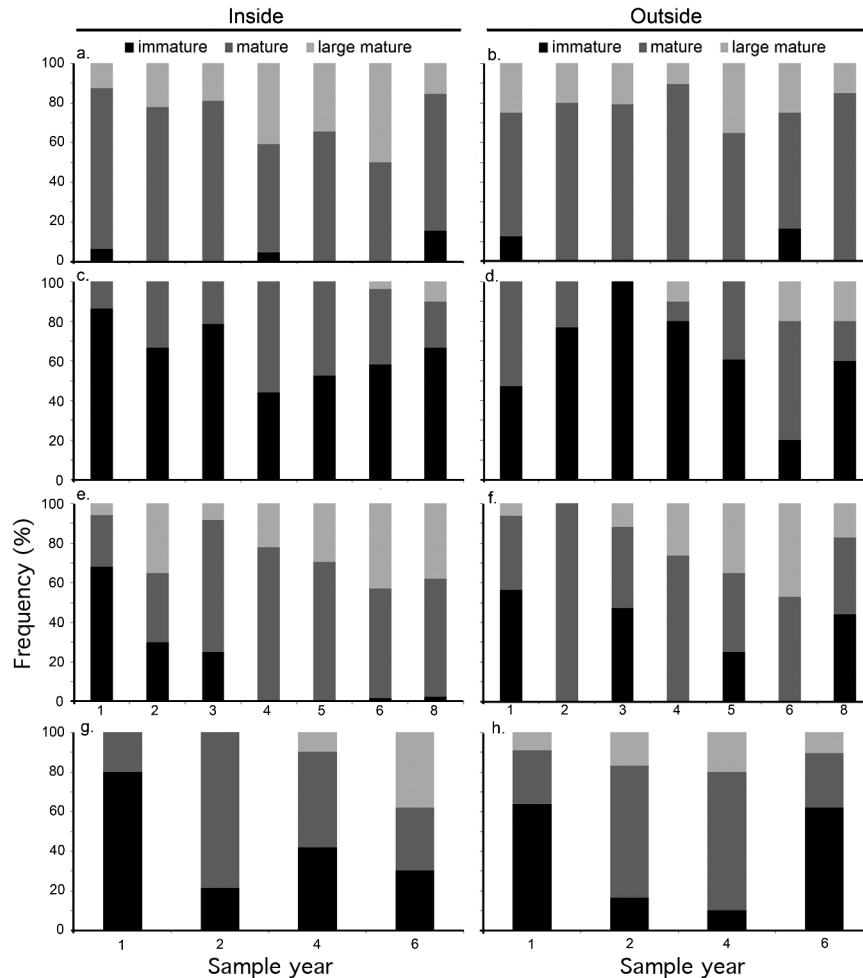


Fig. 3. Percentage of immature, mature, and large mature (a,b) *Etelis carbunculus*, (c,d) *E. coruscans*, and (e-h) *Pristipomoides filamentosus*, inside and outside Penguin Bank (a-f) and Makapu'u (g,h) bottomfish restricted fishing areas (BRFAs) over time. Sizes at maturity were 279 mm for *E. carbunculus* (DeMartini & Lau 1999), 700 mm for *E. coruscans* (Everson et al. 1989), and 450 mm for *P. filamentosus* (Ralston & Miyamoto 1983). Large mature fish were defined as *E. carbunculus* ≥ 450 mm, *E. coruscans* ≥ 850 mm, and *P. filamentosus* ≥ 600 mm

(Fig. 3). However, in Year 8, this percent dropped to approximately the level seen in the first year of sampling (15%). An addition of small fish could have also contributed to this decline as there was an increase in the percent of immature fish (<279 mm, DeMartini & Lau 1999) from sampling Year 6 to 8 (Fig. 3). For *E. coruscans* ($p < 0.01$, $r^2 = 0.05$, Fig. 2c), *P. filamentosus* ($p < 0.01$, $r^2 = 0.45$, Fig. 2e), *P. sieboldii* ($p < 0.01$, $r^2 = 0.03$), and *A. rutilans* ($p = 0.01$, $r^2 = 0.21$) (Table S1A) the addition of Year 8 data either did not change or improved the fit of the relationship. Examining the proportion of immature *E. coruscans* (<700 mm; Everson et al. 1989), mature *E. coruscans* <850 mm, and mature *E. coruscans* >850 mm inside Penguin Bank over time demonstrated that the proportion of mature fish increased over the first several years of monitoring, followed by an increase in the proportion of im-

mature fish and larger mature fish (Fig. 3). For *P. filamentosus* inside Penguin Bank BRFA, the proportion of smaller immature fish (<450 mm; Ralston & Miyamoto 1983) declined, while the proportion of large mature fish (>600 mm) increased over time. Outside of Penguin Bank BRFA, the addition of Year 8 data indicated a lower than projected mean length for *P. filamentosus* and *A. rutilans* ($p < 0.01$, $r^2 = 0.38$; Table S1A) and that an asymptote may have been reached for *E. coruscans* and *P. sieboldii* (Fig. 2d,f; $p = 0.01$, $r^2 = 0.11$; Table S1A). The lower than expected mean *P. filamentosus* size outside Penguin Bank in Year 8 seemed to be related to the increase in the relative proportion of immature fish and simultaneous decrease in the proportion of large *P. filamentosus* from Years 6 to 8 (Fig. 3). Indeed, the proportions of smaller immature *P. filamentosus* had been declining

Table 2. Summary of regression relationships between fish length, relative abundance (MaxN), and species richness with distance from 2 protected areas (Makapu'u and Penguin Bank) in the main Hawaiian Islands. Spatial trends were temporally delineated by sampling Years 1 and 2, 3 and 4, 5 and 6, and Year 8 of monitoring. Arrows represent the direction of the relationship between the independent variable and distance from the protected area. The intercept and slope of each relationship are in parentheses. Marginally significant relationships ($0.10 > p > 0.05$) are in *italics*. BRFA: bottomfish restricted fishing area. Genera in the table are *Etelis* and *Pristipomoides*; Deep 7 refers to a complex of 7 deepwater bottomfish species (see Table 1). '–': not significantly different; blank cells: insufficient data

Data	BRFA	Species	Sampling years			
			1 and 2	3 and 4	5 and 6	8
Length	Makapu'u	<i>E. carbunculus</i>	↑(324.3, 12.8)	↑(308.7, 6.7)	–	
		<i>E. coruscans</i>			–	
		<i>P. filamentosus</i>	↑(419.9, 4.3)	↑(480.1, 4.2)	↓(516.1, –11.4)	
	Penguin Bank	<i>E. carbunculus</i>	–	↓(416.4, –1.9)	–	–
		<i>E. coruscans</i>	↑(630.3, 1.7)	↓(673.7, –7.7)	↓(684.1, –4.9)	–
		<i>P. filamentosus</i>	↑(436.6, 2.0)	–	↓(590.6, –3.0)	↓(577.2, –3.1)
MaxN	Makapu'u	<i>E. carbunculus</i>	–	↓(1.2, –0.10)	↓(–0.03, –0.06)	
		<i>E. coruscans</i>	–	–	↓(1.0, –0.20)	
		<i>P. filamentosus</i>	↓(1.5, –0.10)	↓(2.0, –0.09)	↓(1.8, –0.17)	
	Penguin Bank	<i>E. carbunculus</i>	–	–	↓(1.0, –0.07)	–
		<i>E. coruscans</i>	–	↓(1.7, –0.06)	↓(1.6, –0.07)	–
		<i>P. filamentosus</i>	↓(1.9, –0.05)	↓(1.5, –0.05)	↓(1.5, –0.04)	–
Species richness	Makapu'u	Deep 7	–	–	↓(–0.1, –0.05)	
	Penguin Bank	Deep 7	–	↓(0.07, –0.02)	↓(0.6, –0.04)	–

and larger mature *P. filamentosus* increasing over time prior to Year 8 (Fig. 3). Further, despite declining proportions of smaller immature and increasing proportions of larger mature *P. filamentosus* over time inside Makapu'u BRFA, *P. filamentosus* lengths began to reach an asymptote (Figs. 2g & 3; $p < 0.01$, $r^2 = 0.13$). Similar to Penguin Bank, outside of Makapu'u BRFA, *P. filamentosus* showed a decline in the proportion of smaller immature fish over time until the last year of monitoring when a drastic increase in the proportion of immature fish was seen. This large addition of smaller immature fish in Year 6 contributed to the drop in mean fish size seen in Year 6 (Fig. 2h; $p < 0.01$, $r^2 = 0.15$).

Distance from BRFA

Spatial trends in sampling Years 1 through 4

Our spatial analyses of sampling Years 1 and 2, 3 and 4, 5 and 6, and Year 8 demonstrated largely consistent significant declines in fish length, MaxN, and species richness with distance from both BRFAs developed in Years 5 and 6 (Table 2). Prior to Years 5 and 6, the relationships between these independent factors and distance from BRFAs were inconsistent, often showing no significant trends or an increase with distance from the BRFAs (Table 2). For instance, in the first 2 yr of monitoring around Penguin Bank BRFA, *E.*

carbunculus ($p = 0.17$), *E. coruscans* ($p < 0.06$, $r^2 = 0.04$), and *P. filamentosus* ($p = 0.07$, $r^2 = 0.04$) lengths increased or remained the same with distance from the BRFA. However, in Years 3 and 4, *E. coruscans* lengths began to decline with distance from this BRFA ($p < 0.01$, $r^2 = 0.24$), while *P. filamentosus* lengths showed no spatial trends ($p = 0.41$). For Makapu'u BRFA, sample sizes were limited for all species except *P. filamentosus* (see Table 1). However, length results for the first 2 yr of sampling in Makapu'u BRFA were similar to Penguin Bank BRFA (*E. carbunculus*: $p = 0.02$, $r^2 = 0.42$; *E. coruscans*: $p = 0.86$; *P. filamentosus*: $p = 0.07$, $r^2 = 0.04$; Table 2). In sampling Years 3 and 4, *E. carbunculus* still showed an increase in length with distance from Makapu'u BRFA ($p = 0.03$, $r^2 = 0.19$), while *P. filamentosus* showed a slight increase ($p = 0.06$, $r^2 = 0.03$) in length with distance.

MaxN and species richness data showed the same general trends in the first 4 yr of sampling. In Makapu'u and Penguin Bank BRFAs, relative abundance of *E. carbunculus* and *E. coruscans* collected in the first 2 yr of monitoring did not vary with distance from these BRFAs (Makapu'u: *E. carbunculus* $p = 0.12$, *E. coruscans* $p = 0.20$; Penguin Bank: *E. carbunculus* $p = 0.22$, *E. coruscans* $p = 0.48$). In the second 2 yr of monitoring, *E. carbunculus* began to demonstrate a marginally significant decrease in MaxN with distance from Makapu'u BRFA ($p < 0.10$), though not yet from Penguin Bank BRFA ($p = 0.12$). *E. coruscans* also began to demonstrate a decline in MaxN with

distance from Penguin Bank BRFA in monitoring Years 3 and 4 ($p < 0.01$). In contrast, the relative abundance of *P. filamentosus* showed a significant or marginally significant decline with distance from both Penguin Bank and Makapu'u BRFAs since sampling began (Makapu'u_{yr1,2}: $p < 0.01$; Makapu'u_{yr3,4}: $p = 0.01$; Penguin Bank_{yr1,2}: $p = 0.08$; Penguin Bank_{yr3,4}: $p = 0.03$; Table 2). Species richness of the Deep 7 did not show any spatial trends over the first 4 yr of monitoring in Makapu'u BRFA (Makapu'u_{yr1,2}: $p = 0.99$; Makapu'u_{yr3,4}: $p = 0.43$). Similarly in Penguin Bank BRFA, there were no spatial trends in the first 2 yr of monitoring (Penguin Bank_{yr1,2}: $p = 0.56$), while in the second 2 yr, there was a marginally significant decline in species richness with distance from the BRFA (Penguin Bank_{yr3,4}: $p = 0.06$).

Although the sample sizes for the other Deep 7 species were limited (Table 1), some did show similar inconsistent trends in the first 4 yr of sampling. For example, *P. sieboldii* length data declined with distance from Penguin Bank BRFA in the first 2 and second 2 sampling years ($p_{1,2} < 0.01$, $r^2 = 0.23$, intercept = 325.1, slope = -7.3 ; $p_{3,4} < 0.05$, $r^2 = 0.03$, intercept = 346.7, slope = -1.6), while *Hyporthodus quernus* MaxN data showed no significant spatial trend in the first 4 yr of sampling ($p_{1,2} = 0.38$, $p_{3,4} = 0.48$). *A. rutilans* also showed no spatial trends with distance from Penguin Bank BRFA in the first 2 yr of monitoring, while in the second 2 yr, it showed a significant ($p < 0.01$) decline in MaxN with distance from this BRFA ($p_{3,4} < 0.01$, intercept = -0.7 , slope = -0.43). Simply put, these results signify that the spatial distribution of Deep 7 species in the first 4 yr of monitoring were relatively inconsistent.

Spatial trends in sampling Years 5, 6, and 8

In the fifth and sixth sampling years, declines in MaxN, fish length, and species richness with distance from both BRFAs were evident for nearly every species with sufficient data to test (Tables 1 & 2, Fig. 4). All 3 of our target species (*E. carbunculus*, *E. coruscans*, and *P. filamentosus*) showed declines in relative abundance (MaxN) with distance from Penguin Bank and Makapu'u BRFAs in the fifth and sixth years of sampling (Figs. 2d & 4c). *P. filamentosus* also showed significant ($p < 0.01$) declines in fish length with distance from both the Penguin Bank ($r^2 = 0.18$) and Makapu'u ($r^2 = 0.09$)

BRFAs, while *E. coruscans* lengths significantly ($p < 0.01$) declined with distance from Penguin Bank BRFA ($r^2 = 0.07$) in sampling Years 5 and 6 (Table 2, Figs. 2b & 4a). Sample distribution may have contributed to the lack of a significant result for *E. carbunculus* length data in Years 5 and 6. For example, in Years 3 and 4, when a significant decline in *E. carbunculus* length with distance from Penguin Bank BRFA was seen, there were 29 sample sites >10 km away from the BRFA. In Years 5 and 6, there were only 5 *E. carbunculus* length sample sites >10 km away from the BRFA. *H. quernus* ($p = 0.04$), *A. rutilans* ($p = 0.09$), and *P. sieboldii* ($p < 0.01$) also showed significant or marginally significant declines in MaxN data with distance from Penguin Bank BRFA in the fifth and sixth years of sampling. This was also seen for *P. sieboldii* length data ($p < 0.01$, $r^2 = 0.19$, intercept = 360.8, slope = -6.6). Species richness also significantly

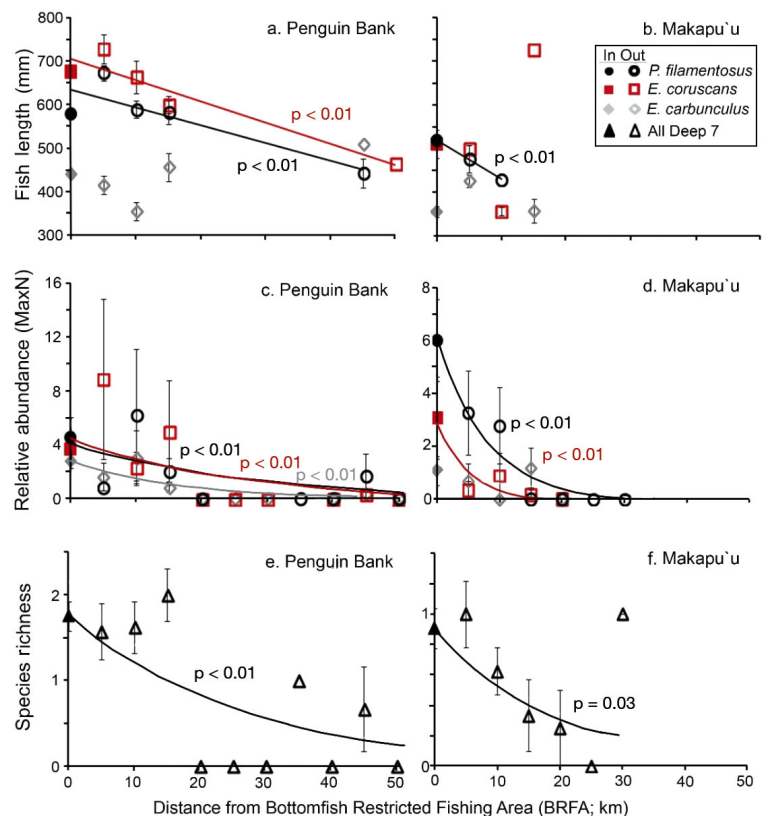


Fig. 4. Relationships for (a,b) fish length, (c,d) relative abundance, and (e,f) species richness (all Deep 7 species in a single sample) with distance from each bottomfish restricted fishing area (BRFA; Penguin Bank and Makapu'u) from the fifth and sixth years of monitoring. While regressions were conducted using individual data points, data displayed here were averaged in 5 km distance bins (10 km = 6–10 km ... 50 km = 46–50 km) with standard error bars because the range in data, the overlap of individual data points, and excess zeros in the MaxN database made these relationships difficult to discern.

Genera in the figure are *Etelis* and *Pristipomoides*

declined with distance from Penguin Bank ($p < 0.01$) and Makapu'u ($p = 0.03$) BRFA in Years 5 and 6 (Table 2, Figs. 2f & 4e).

However, in Year 8, many of these relationships were no longer significant or even marginally significant ($p > 0.10$; Table 2). Indeed, the only significant spatial relationship was for *P. filamentosus* lengths from Penguin Bank BRFA ($p < 0.01$, $r^2 = 0.36$). Further, while the declines in relative abundance with distance from the BRFA were no longer significant for the most economically important species of the Deep 7, significant declining spatial trends away from Penguin Bank BRFA were still evident for a species considered less economically important than other Deep 7 species, viz. *P. sieboldii* ($p = 0.03$, intercept = 2.5, slope = -0.06 ; Haight et al. 1993, Kelley et al. 2006).

Lastly, to ensure that sampled habitat types in our analyses did not influence spatial results, we examined tested habitat types with distance from each protected area. There were no differences in the types of habitat sampled with distance from Penguin Bank BRFA for each set of years tested in our analyses ($p_{yr1,2} = 0.69$; $p_{yr3,4} = 0.35$; $p_{yr5,6} = 0.56$; $p_{yr8} = 0.95$). Further, for Makapu'u BRFA, more hard-low habitat was sampled closer to the BRFA than hard-high habitat in Years 1 and 2 ($p < 0.01$) and Years 5 and 6 ($p < 0.01$). Being that more hard-low habitat was sampled closer to this BRFA in both of these datasets, and yet results with distance from this BRFA for these 2 datasets were very different (1 increasing and 1 decreasing with distance for *P. filamentosus*), suggests that sampled habitat was not a factor in these results. Additionally, as noted by others (Kelley et al. 2006, Parke 2007, Misa et al. 2013, Sackett et al. 2014), hard-low habitat would generally suggest the presence of smaller and less abundant bottomfish, including *P. filamentosus*. However, the higher proportion of this habitat sampled near Makapu'u BRFA in Years 5 and 6 did not result in smaller fish size but instead the opposite was seen; *P. filamentosus* were larger near the BRFA.

Fishery data

The overall number ($p = 0.04$, $r^2 = 0.66$) and weight ($p = 0.02$, $r^2 = 0.73$) of *E. coruscans* caught per fishing trip reflected trends in length data collected with BotCam outside Penguin Bank (compare Fig. 2d to Fig. 5a), demonstrating an initial decline in CPUE after the BRFA was enlarged in 2007 followed by an increase in CPUE in the last several years. *E. carbunculus* CPUE data from Makapu'u followed a similar

trend to *E. coruscans* ($p_{weight} = 0.01$, $r^2 = 0.77$; $p_{number} < 0.01$, $r^2 = 0.79$; Fig. 5b). The number ($p = 0.04$, $r^2 = 0.24$) and weight ($p = 0.03$, $r^2 = 0.27$) of *P. filamentosus* caught per fishing trip around both Penguin Bank and Makapu'u BRFAs together also increased linearly (results were pooled because BRFAs shared a fishing grid and *P. filamentosus* have been noted to move between these 2 BRFAs (PIFG 2013; see Fig. 1; Fig. 5c). Separately, Makapu'u showed a significant linear increase in CPUE data over time ($p_{number} = 0.01$, $r^2 = 0.66$; $p_{weight} < 0.01$, $r^2 = 0.70$); however, Penguin Bank did not ($p > 0.05$). For *P. sieboldii*, number ($p < 0.01$, $r^2 = 0.55$) and weight ($p = 0.02$, $r^2 = 0.43$; Table S1B) CPUE around both BRFAs together increased at an increasing rate over time. Results for the number and weight of *P. sieboldii* caught per trip over time were significant ($p < 0.01$) and linear when analyzed for Penguin Bank ($r^2 = 0.92$; $r^2 = 0.92$) alone.

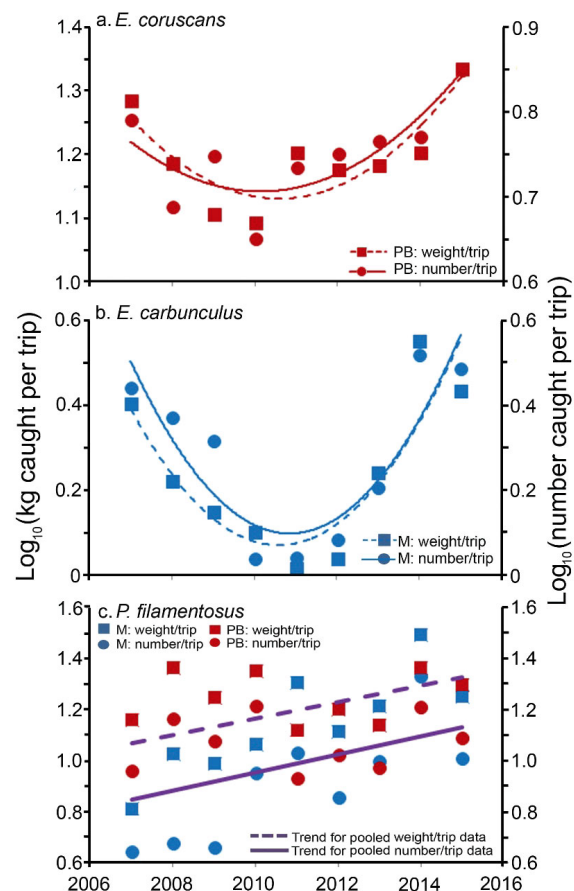


Fig. 5. Catch per unit effort metrics associated with protected areas, i.e. fishing areas that intersected with bottomfish restricted fishing areas (BRFAs, where PB: Penguin Bank; M: Makapu'u; see Fig. 1) over time, beginning when protected areas were revised in 2007 and monitoring began. Genera in the figure are *Etelis* and *Pristipomoides*. Model equations are given in Table S1B in the Supplement

P. sieboldii number and weight CPUE initially declined following the enlargement of Makapu'u BRFA in 2007 with an increase in CPUE in the last several years, similar to *E. coruscans* and *E. carbunculus* above ($p = 0.02$, $r^2 = 0.72$; $p < 0.01$, $r^2 = 0.92$; $p = 0.06$, $r^2 = 0.62$; Table S1B). Lastly, *H. quernus* CPUE measures declined over time near Penguin Bank ($p_{\text{number}} = 0.01$, $r^2 = 0.83$; $p_{\text{weight}} < 0.01$, $r^2 = 0.74$; Table S1B). Examining trends in effort alone around each BRFA demonstrated no significant ($p = 0.34$) changes over time around Penguin Bank BRFA. However, there was a significant decrease in effort seen around Makapu'u BRFA over time ($p = 0.03$, $r^2 = 0.59$, $\log(\text{effort}) = 64.1 - 0.03 \times \text{calendar year}$).

DISCUSSION

The primary evidence often provided for spillover is a decline in relative abundance, fish size, or biodiversity with distance from an MPA at a single point in time (Russ & Alcala 2004, Abesamis et al. 2006, Harmelin-Vivien et al. 2008, Forcada et al. 2009, Stamoulis & Friedlander 2013). These results suggest that the protected area is a source of more and larger fish to fished areas and that the increasing community complexity inside the protected areas is spilling over the boundary of the MPA (Kellner et al. 2007, Russ & Alcala 2011). For instance, McClanahan & Mangi (2000) measured biodiversity, fish sizes, and CPUE data with distance from the Mombasa Marine Park in Kenya to identify spillover and noted that all 3 metrics declined with distance from the reserve within 5 km. Here we temporally examined the spatial relationship between relative abundance, fish size, and species richness with distance from 2 deepwater MPAs (Makapu'u and Penguin Bank BRFAs) that were first established in 1998 and later expanded in 2007, and demonstrated that declines with distance from these protected areas developed in the fifth and sixth year of sampling for nearly all species with enough data to test these relationships. Further, we demonstrated that asymptotes in fish length inside and increases in fish length outside these protected areas temporally coincided with the development of these spatial trends.

There were 2 exceptions to these results, namely the declining trend in *Pristipomoides filamentosus* relative abundance with distance from both Makapu'u and Penguin Bank protected areas, which did not change over time. However, the spatial distribution in *P. filamentosus* lengths did change over time, suggesting that larger fish were spatially distributed

closer to the protected areas in recent years. In addition, the fit of some of the significant spatial relationships in this study was relatively low, signifying that there were likely numerous other factors in the open ocean that contributed to the spatial distribution of these species (e.g. prey movements, currents) besides distance from the protected area (Curran-Everett 2011). Also, as we were only able to broadly classify habitat, it is likely that more specific habitat classifications would better explain some of this variability (Misa et al. 2013, Sackett et al. 2014, Moore et al. 2016). Regardless, the early inconsistencies in these spatial relationships followed by consistent declining relationships across species, independent factors (species richness, relative abundance, fish length), and areas did explain, at least in part, the spatial distribution of these species (Curran-Everett 2011). These results also suggested that the recovering Deep 7 community inside these reserves had begun to spill over the boundary of the BRFAs and that BRFAs were a source of more and larger fish to fished areas in the fifth and sixth years of sampling.

Spillover is often suggested to be a result of both density-independent and -dependent processes. Density-independent spillover occurs when fish movements unrelated to fish density inside the reserve cause fish to leave an MPA. A few types of density-independent movements that could cause spillover include adult migration, ontogenetic migrations, or when the lifetime home range of a fish extends beyond the boundaries of the reserve (Gruss et al. 2011). The few studies on the mobility of deepwater bottomfish in Hawaii have suggested that many move beyond the boundaries of protected areas over their lifetime, albeit to varying degrees (Williamson 2005, Weng 2013). For instance, *P. filamentosus* have been seen to move between Penguin Bank and Makapu'u BRFAs, and tracking studies have indicated that they move from inside to outside of the Kaho'olawe Island Reserve, a no-take protected area in Hawaii (Williamson 2005, PIFG 2013). *Etelis coruscans* and *E. carbunculus* have also been found to move from inside to outside of Ni'ihau BRFA in Hawaii (Weng 2013), where *E. coruscans* moved more frequently and over greater distances than *E. carbunculus*. Thus, the lifetime home range of these species likely extends beyond the boundary of the BRFAs, causing some degree of density-independent spillover into fished areas (Gruss et al. 2011). Many studies have examined fish home range in relation to MPA size and movement on the ability of MPAs to cause spillover and found that species with intermediate levels of mobility and home ranges that

extended beyond the boundaries of the MPA were predicted to provide the greatest spillover benefits to nearby fisheries (Holland & Brazee 1996, Kramer & Chapman 1999). Our results supported these findings, as *P. filamentosus* and *E. coruscans*, the 2 species that showed the strongest evidence of spillover, both have intermediate levels of movement (e.g. both spend enough time inside the reserve for protection to have an effect but also move outside of the boundaries of the BRFAs, providing benefits to the fishery). *E. carbunculus* also had higher relative abundance closer to Penguin Bank BRFA that developed in the fifth and sixth years of sampling and increasing sizes inside the BRFA over time that reached an asymptote, suggesting spillover, whereas *E. carbunculus* sizes showed no relationship over time outside this BRFA. As such, the cross-boundary movement of *E. carbunculus*, which is lower than other species (Weng 2013), may not export enough fish to show a significant increase in the mean size of fish in fished areas. In addition, *E. carbunculus* may be more vulnerable to anglers after they leave the BRFA because of their relatively low rate of movement (Berkeley et al. 2004, Tetreault & Ambrose 2007). While CPUE increased with time in the nearby Makapu'u BRFA, number and weight CPUE in the fishing areas surrounding Penguin Bank did not change over time, which suggests that vulnerability to fishers probably has not played a large role in explaining a lack of increasing *E. carbunculus* size outside Penguin Bank BRFA.

The asymptote in *E. carbunculus*, *E. coruscans*, *P. filamentosus*, *P. sieboldii*, and *Aphareus rutilans* lengths over time inside the BRFAs in the fifth and sixth years of monitoring may also indicate some degree of density-dependent spillover. Density-dependent spillover occurs when resources such as food or space are in short supply inside the reserve, causing fish to move outside of the protected area in search of these resources (Sánchez-Lizaso et al. 2000). With the increase in larger individuals inside these BRFAs, competition between larger fish could cause a net emigration from the BRFAs, resulting in the increase in fish sizes seen outside the BRFAs over time, and that higher relative abundance and larger fish outside the BRFAs were found closer to the boundary of the reserve. Further evidence of density-dependent spillover occurred for *E. carbunculus* in Penguin Bank BRFA and *P. filamentosus*, in both Penguin Bank and Makapu'u BRFAs, where asymptotes in mean fish sizes developed despite a declining percent of juveniles and an increasing percent of larger individuals. Also, because Deep 7 species

often prefer specific depth ranges (Misa et al. 2013, Sackett et al. 2014) and are relatively site attached to high-relief structures such as pinnacles (many of which the BRFA system were designed to protect; Ralston et al. 1986, Kelley et al. 2006, Parke 2007), it is easy to conceive that space on these preferred habitat structures may be limited, particularly for a higher number of larger individuals inside these BRFAs. Another possible contributing factor to the asymptotes in mean *E. coruscans* sizes and declines in mean *P. filamentosus* sizes outside both BRFAs seen in later sampling years was recruitment of juveniles to our sampling gear. For instance, the decline in mean *P. filamentosus* size in Year 6 outside Makapu'u BRFA and in Year 8 outside Penguin Bank BRFA was at least partly driven by a large increase in the percent of sampled juveniles. Although difficult to distinguish empirically, recruitment is among the most important benefits to using MPAs as fishery management tools (Roberts & Polunin 1991, Bohnsack 2011). Evidence of recruitment from MPAs are often based on theoretical concepts, models, and increases in adult fish sizes (Sackett et al. 2014, A. C. Vaz et al. unpubl.). Here we provided some empirical evidence of recruitment and demonstrated the influence it has on mean fish size over time, a result often used to prove the effectiveness of protection. Thus, empirically demonstrating that recruitment can cause a decline in mean fish sizes over time is a necessity in understanding, interpreting, and managing MPAs.

The drastic decline in mean *E. carbunculus* size seen inside Penguin Bank BRFA in sampling Year 8 was largely driven by the loss of larger adults. Indeed, prior to Year 8, the percent of larger *E. carbunculus* increased inside Penguin Bank BRFA with each sampling year. Two possible explanations for a loss of large adults is increased fishing pressure or emigration from the sampling area. As *E. carbunculus* do not seem to have high rates of movement (Weng 2013), it is unlikely that the fish emigrated from the BRFA but instead were removed through harvesting. Although not quantitative, we did observe many more anglers bottom-fishing within the BRFAs while sampling in Year 8 than in previous years. This may have been due to several public announcements suggesting that some of the BRFAs would be opened to fishing. In March 2014, after many years of contentious debate over the BRFAs (e.g. Hospital & Beavers 2012, FisheryNation 2013, WESTPAC 2013) the State of Hawai'i Department of Land and Natural Resources announced that it would open 6 of the 12 BRFAs in the MHI at some point in the near future.

However, before this plan was finalized or carried out, public announcements were made to the fishery. Announcements often did not distinguish that the BRFA were not open yet, would not be opening for at least another year (e.g. Moore 2014, WESTPAC 2014), and the fact that Penguin Bank and Makapu'u BRFA would not be opened were far down in the text of these articles. As such, these announcements may have led to increased fishing pressure in and around the protected areas just prior to sampling Year 8. However, as spatial analyses combined 2 yr of data up until Year 8 (because sampling was suspended in Year 7), sample sizes were smaller for Year 8 data than for previous years. Thus, we suspect that both a loss of statistical power and increased fishing pressure could have contributed to the lack of significant spatial trends seen in Year 8.

Despite the crude format of the fishing areas, fishery data also supported spillover results for *P. filamentosus*, *E. coruscans*, *E. carbunculus*, and *P. sieboldii*, with CPUE showing an increasing trend over time around Makapu'u and Penguin Bank BRFA in the most recent years. For instance, the CPUE in weight and CPUE in number for these species began increasing approximately 1 yr after fish lengths, relative abundance, and species richness began to decline with distance from the BRFA, and after asymptotes in fish lengths developed inside these BRFA. Therefore, the increase in CPUE for *P. filamentosus* in 2011 to 2015, for *E. coruscans* in 2012 to 2015, for *E. carbunculus* in 2013 to 2015, and for *P. sieboldii* in 2012 to 2015 suggested that, not only did our camera system record more and larger fish in and around the BRFA, but approximately 1 yr or less later, catch rates by local fishers were increasing around the BRFA. The size-selective nature of fishing pressure may have also caused initial declines in *E. coruscans* lengths outside of Penguin Bank BRFA (camera data; Fig. 2) after the BRFA was revised in 2007 (Bianchi et al. 2000, Berkeley et al. 2004). Thus, displaced fishing pressure may have caused these early declines in mean *E. coruscans* lengths (Halpern et al. 2004). However, it appears that the net export of large adults in later years was enough to reverse this decline in mean fish sizes adjacent to the BRFA in the fifth and sixth sampling years. Fishery data further supported this interpretation of camera data, demonstrating a parallel trend; an initial decline over time followed by an increase over time in *E. coruscans* CPUE. This BRFA, therefore, seemed to be able to offset the initial decline in CPUE 6 yr after expansion. Additionally, at the beginning of sampling Year 5, the total allowable catch for the Deep 7 fish-

ery increased, resulting in increased total catch (Brodziak et al. 2014). Thus, higher mean CPUE occurred around the BRFA during this time, suggesting that despite the higher fishing pressure, which was likely targeted near the boundaries of the BRFA, the BRFA became a source of more and larger fish to fished areas in these same years. Identifying the ability, time span, and circumstances for an MPA to offset the cost of removing fishing grounds and begin to benefit a fishery is crucial to resolving debates regarding the use of MPAs in fisheries management (Hilborn et al. 2004, 2006). Buxton et al. (2014) suggested that increased yield from spillover only occurs when a fishery is already depleted. The Deep 7 fishery complex was, at this time, managed with a near 50% probability of overfishing and a 45% probability that the stock was overfished in 2013 (Brodziak et al. 2014). Thus, it is possible that the Deep 7 stock was depleted at the time of this study, and as a result, could have driven spillover and the increases seen in CPUE in recent years. However, the fisheries and reserves modeled by Buxton et al. (2014) were non-structured and non-specific (e.g. did not consider structured environments or protected areas to be any more important than surrounding areas), which is not necessarily the case here where Deep 7 species are site attached to particular habitat structures, some of which were targeted for protection (Ralston et al. 1986, Haight et al. 1993, Kelley et al. 2006, Parke 2007, Merritt et al. 2011). Therefore, these model results may not apply to the circumstance in the MHI. Regardless, a comprehensive analysis of catch data throughout the MHI, particularly with reporting grids tailored to protected areas, would make any changes in CPUE surrounding BRFA more evident.

Overfishing and the worldwide depletion of predatory fishes have caused global declines in marine biodiversity, population abundance, and size structure, altered genetic diversity, and caused landscape level impacts on entire ecosystems (Friedlander & DeMartini 2002, Harmelin-Vivien et al. 2008, Estes et al. 2011, Mora & Sale 2011). In addition, mean fishing depth has been increasing each year since the 1950s across the globe with a higher rate of increase occurring in more recent years (Morato et al. 2006). These results represent a problematic trend, as deepwater species are often long-lived with slow growth rates and late maturity, making them acutely vulnerable to overfishing (Morato et al. 2006, Drazen & Haedrich 2012, Williams et al. 2013). Protecting areas from fishing has been one proposed solution to reverse declining marine biodiversity and other negative

consequences of overharvesting (Lester et al. 2009, Molloy et al. 2009, Russ & Alcala 2011, White & Costello 2014). Besides conservation, well designed and managed MPAs can export adults (spillover) into fished areas as well as stabilize spawning stock and subsidize recruitment, ultimately improving fishery yield over time (McClanahan & Mangi 2000, Russ & Alcala 2004, Abesamis et al. 2006, Kerwath et al. 2013). Here temporal changes in spatial distributions showed more, larger, and a more diverse array of fish in fished areas closer to protected areas that did not always exist but developed in the fifth and sixth years of monitoring; along with temporal increases in fish lengths that reached an asymptote inside protected areas, while fish lengths began to increase outside, together suggested that these protected areas had become source populations of adults to fished areas. Consequently, our results suggest that deepwater MPAs are a potential solution to protect vulnerable deepwater species with site attachment and intermediate levels of movement in the Pacific and elsewhere, but also suggest that enforcement and public approval are needed to maintain these benefits (Haedrich et al. 2001, Williams et al. 2013).

Acknowledgements. We thank Virginia Moriwake for advice and help with data compilation and analysis. We also thank the BotCam crew, Chris Demarke, Bo Alexander, William Misa, John Yeh, Jason Friedman, Matt Waterhouse, Aharon Fleury, and Clif Nunnally for their tireless field efforts, video analysis, and advice. Thanks also to Reginald M. Kokubun of the Division of Aquatic Resources for access to catch data and the Sea Engineering crew for ship support on RV 'Huki Pono.' We thank the State of Hawai'i Division of Aquatic Resources for providing funding directly and via the Federal Aid in Sport Fish Restoration program (F17R38-study IX). We also thank 4 anonymous reviewers for their contributions to this paper.

LITERATURE CITED

- ✦ Abesamis RA, Russ GR (2005) Density-dependent spillover from a marine reserve: long-term evidence. *Ecol Appl* 15: 1798–1812
- Abesamis RA, Alcala AC, Russ GR (2006) How much does the fishery at Apo Island benefit from spillover of adult fish from the adjacent marine reserve? *Fish Bull* 104: 360–375
- ✦ Agardy T, Bridgewater P, Crosby MP, Day J and others (2003) Dangerous targets? Unresolved issues and ideological clashes around marine protected areas. *Aquat Conserv* 13:353–367
- ✦ Berkeley SA, Hixon MA, Larson RJ, Love MS (2004) Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries* 29: 23–32
- ✦ Bianchi G, Gislason H, Graham K, Hill L and others (2000) Impact of fishing on size compositions and diversity of demersal fish communities. *ICES J Mar Sci* 57:558–571
- ✦ 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
- ✦ Brodziak J, Yau A, O'Malley J, Andrews A and others (2014) Stock assessment update for the Main Hawaiian Islands Deep 7 bottomfish complex through 2013 with projected annual catch limits through 2016. NOAA-TM-NMFS-PIFSC-42, US Dept of Commerce, Honolulu, HI
- ✦ Buxton CD, Hartmann K, Kearney R, Gardner C (2014) When is spillover from marine reserves likely to benefit fisheries? *PLOS ONE* 9:e107032
- ✦ Curran-Everett D (2011) Explorations in statistics: regression. *Adv Physiol Educ* 35:347–352
- DeMartini EE, Lau BB (1999) Morphometric criteria for estimating sexual maturity in two snappers, *Etelis carbunculus* and *Pristipomoides sieboldii*. *Fish Bull* 97:449–458
- ✦ Drazen JC, Haedrich RL (2012) A continuum of life histories in deep-sea demersal fishes. *Deep Sea Res I* 61:34–42
- ✦ Estes JA, Terborgh J, Brashares JS, Power ME and others (2011) Trophic downgrading of planet earth. *Science* 333:301–306
- Everson AR, Williams HA, Ito BM (1989) Maturation and reproduction in two Hawaiian eteline snappers, uku, *Aprion virens*, and onaga, *Etelis coruscans*. *Fish Bull* 87:877–888
- Executive Order 13158 (2000) Marine Protected Areas. Federal Register 65:34909–34911
- ✦ FisheryNation (2013) Eliminate bottomfish restricted fishing areas in Hawaii, Western Pacific Regional Fishery Council Recommends. Available at <http://fisherynation.com/archives/16344> (accessed on 1 July 2015)
- ✦ Forcada A, Valle C, Bonhomme P, Criquet G, Cadiou G, Lenfant P, Sánchez-Lizaso JL (2009) Effects of habitat on spillover from marine protected areas to artisanal fisheries. *Mar Ecol Prog Ser* 379:197–211
- ✦ Friedlander AM, DeMartini EE (2002) Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: the effects of fishing down apex predators. *Mar Ecol Prog Ser* 230: 253–264
- ✦ Gruss A, Kaplan DM, Guenette S, Roberts CM, Botsford LW (2011) Consequences of adult and juvenile movement for marine protected areas. *Biol Conserv* 144:692–702
- ✦ 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. *Trans Am Fish Soc* 122:328–347
- ✦ Halpern BS (2014) Making marine protected areas work. *Nature* 506:167–168
- ✦ 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 and others (2008) Gradients of abundance and biomass across reserve boundaries in six Mediterranean marine protected areas: evidence of fish spillover? *Biol Conserv* 141:1829–1839
- ✦ Hilborn R, Stokes K, Maguire JJ, Smith T and others (2004)

- When can marine reserves improve fisheries management? *Ocean Coast Manag* 47:197–205
- ✦ Hilborn R, Micheli F, De Leo GA (2006) Integrating marine protected areas with catch regulation. *Can J Fish Aquat Sci* 63:642–649
- ✦ Holland DS, Brazee RJ (1996) Marine reserves for fisheries management. *Mar Resour Econ* 11:157–172
- Hospital J, Beavers C (2012) Economic and social characteristics of bottomfish fishing in the Main Hawaiian Islands. Pacific Islands Fish Sci Cent Admin Rep H-12-01. Pacific Islands Fisheries Science Center, NMFS, NOAA, Honolulu, HI
- ✦ Kaiser MJ (2005) Are marine protected areas a red herring or fisheries panacea? *Can J Fish Aquat Sci* 62:1194–1199
- Kelley CD, Moriwake VN (2012) Appendix 3: Essential fish habitat descriptions, Part 1: bottomfish. In: Western Pacific Regional Fisheries Management Council (ed) Final fishery management plan for coral reef ecosystems of the western 596 Pacific region, Volume III. Essential fish habitat for Management Unit Species, 597. WPRFMC, Honolulu, HI, p 1–109
- 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
- ✦ Kellner JB, Tetreault I, Gaines SD, Nisbet RM (2007) Fishing the line near marine reserves in single and multispecies fisheries. *Ecol Appl* 17:1039–1054
- ✦ Kerwath SE, Winker H, Gotz A, Attwood CG (2013) Marine protected area improves yield without disadvantaging fishers. *Nat Commun* 4:2347
- ✦ Kramer DL, Chapman MR (1999) Implications of fish home range size and relocation for marine reserve function. *Environ Biol Fishes* 55:65–79
- ✦ Lester SE, Halpern BS, Grorud-Colvert K, Lubchenco J and others (2009) Biological effects within no-take marine reserves: a global synthesis. *Mar Ecol Prog Ser* 384:33–46
- ✦ 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. *Hydrobiologia* 670:23–34
- ✦ McClanahan TR, Mangi S (2000) Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. *Ecol Appl* 10:1792–1805
- 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 FXE, Drazen JC, Kelley CD, Moriwake VN (2013) Establishing species-habitat associations for 4 eteline snappers using a baited stereo-video camera system. *Fish Bull* 111:293–308
- Moffitt R, Kobayashi D, Dinardo G (2006) Status of the Hawaiian bottomfish stocks, 2004, Admin Rep H-06-01. Pacific Islands Fisheries Science Center, NMFS, 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
- ✦ Moore CH, Drazen JC, Kelley CD, Misa WFXE (2013) Deep-water marine protected areas of the main Hawaiian Islands: establishing baselines for commercially valuable bottomfish populations. *Mar Ecol Prog Ser* 476:167–183
- ✦ Moore C, Drazen JC, Radford BT, Kelley C (2016) Improving essential fish habitat designation to support sustainable ecosystem-based fisheries management. *Mar Policy* 69: 32–41
- ✦ Moore M (2014) Half of Hawaii's bottomfishing restricted areas opening up. *Fishermen's News* 70. Available at www.fishermensnews.com/story/2014/05/01/features/half-of-hawaiis-bottomfishing-restricted-areas-opening-up/255.html (accessed on 1 July 2015)
- ✦ Mora C, Sale PF (2011) Ongoing global biodiversity loss and the need to move beyond protected areas: a review of the technical and practical shortcomings of protected areas on land and sea. *Mar Ecol Prog Ser* 434:251–266
- ✦ Morato T, Watson R, Pitcher TJ, Pauly D (2006) Fishing down the deep. *Fish Fish* 7:24–34
- ✦ 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. NOAA-TM-NMFS-PIFSC-11. US Dept of Commerce, Honolulu, HI
- Parrish FA (1989) Identification of habitat of juvenile snappers in Hawaii. *Fish Bull* 87:1001–1005
- ✦ PIFG (Pacific Islands Fisheries Group) (2013) Bottomfish tagging. Available at www.fishtoday.org/cooperative-research/bottomfish-tagging (accessed on 10 June 2014)
- ✦ 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
- ✦ Russ GR, Alcala AC (2004) Marine reserves: Long-term protection is required for full recovery of predatory fish populations. *Oecologia* 138:622–627
- ✦ Russ GR, Alcala AC (2010) Decadal-scale rebuilding of predator biomass in Philippine marine reserves. *Oecologia* 163:1103–1106
- ✦ Russ GR, Alcala AC (2011) Enhanced biodiversity beyond marine reserve boundaries: the cup spillth [sic] over. *Ecol Appl* 21:241–250
- ✦ Sackett DK, Drazen JC, Moriwake VN, Kelley CD, Schumacher BD, Misa WFXE (2014) Marine protected areas for deepwater fish populations: an evaluation of their effects in Hawai'i. *Mar Biol* 161:411–425
- ✦ Sánchez-Lizaso JL, Goni R, Renones O, Garcia Charton JA and others (2000) Density dependence in marine protected populations: a review. *Environ Conserv* 27: 144–158
- ✦ 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 ANH, Anderson MJ, Millar RB (2012) Incorporating the intraspecific occupancy-abundance relationship into zero-inflated models. *Ecology* 93:2526–2532
- ✦ Stamoulis KA, Friedlander AM (2013) A seascape approach to investigating fish spillover across a marine protected area boundary in Hawai'i. *Fish Res* 144:2–14
- ✦ 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, She-drawi G (2010) Assessing reef fish assemblage structure: How do different stereo-video techniques compare? *Mar Biol* 157:1237–1250
- ✦ Weng KC (2013) A pilot study of deepwater fish movement with respect to marine reserves. *Anim Biotelem* 1:17
- ✦ WESTPAC (Western Pacific Regional Management Council) (2013) Press release – eliminate bottomfish restricted fishing areas in Hawaii, Fishery Council Recommends. Available at www.wpcouncil.org/2013/10/22/press-release-eliminate-bottomfish-restricted-fishing-areas-in-hawaii-fishery-council-recommends/ (accessed on 1 July 2015)
- ✦ WESTPAC (2014) Press release – scientists reiterate recommendation to open Hawai'i bottomfish fishing areas, suggest revisions to coral reef fisheries annual quotas. Available at www.wpcouncil.org/2014/03/21/press-release-scientists-reiterate-recommendation-to-open-hawaii-bottomfish-fishing-areas-suggest-revisions-to-coral-reef-fisheries-annual-quotas/ (accessed on 1 July 2015)
- ✦ White C, Costello C (2014) Close the high seas to fishing? *PLOS Biol* 12:e1001826
- ✦ White C, Kendall BE (2007) A reassessment of equivalence in yield from marine reserves and traditional fisheries management. *Oikos* 116:2039–2043
- ✦ Williams AJ, Loeun K, Nicol SJ, Chavance P and others (2013) Population biology and vulnerability to fishing of deep-water eteline snappers. *J Appl Ichthyology* 29: 395–403
- Williamson J (2005) Bottomfish research demonstrates Kaho'olawe's ecological benefits: fishing community likely beneficiary of restricted usage of island reserve waters. Kaho'olawe Island Reserve Commission: news release. Available at www.denix.osd.mil/denix/crid/Coral_Reef_Initiative_Database/Kahoolawe_files/Kaho%27olawe%20Bottomfish%20Research.pdf (accessed on 10 June 2014)
- Zellar D, Darcy M, Booth S, Lowe MK, Martell S (2008) What about recreational catch? Potential impact on stock assessment for Hawaii's bottomfish fisheries. *Fish Res* 91:88–97

Editorial responsibility: Konstantinos Stergiou, Thessaloniki, Greece

*Submitted: April 7, 2016; Accepted: January 9, 2017
Proofs received from author(s): March 15, 2017*