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Impacts of a Hawaiian marine protected area network on the abundance and fishery sustainability of the yellow tang, *Zebrasoma flavescens*

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ABSTRACT

Marine protected areas can enhance fish stocks within their boundaries, but the circumstances in which they might also supplement stocks or enhance fisheries outside their boundaries are less clear. Using visual survey and fishery data, we assess the impacts of increasing fishing effort, and of the establishment in Hawaii of a network of areas closed to aquarium fishing, on the prime-target species, yellow tang (*Zebrasoma flavescens*), and draw conclusions about MPA impacts on long-term fishery sustainability. Between 1999, when 27.8% of the coastline was closed to collecting, and 2007, the number of active fishers and total catch of yellow tang doubled. Prior to MPA establishment, yellow tang densities were similar at sites open to fishing and those slated for closure. By 2007, closed areas had five times the density of prime targeted sized fish (5–10 cm), and 48% higher density of adults than open areas. Densities of adults in 'boundary' areas (open areas <1 km from nearest MPA boundary) were significantly higher than in open areas far from MPA boundaries, which was indicative of spillover at that scale. Given the long life-span of yellow tang (>40 years) relative to the duration of protection and the increasing intensity of fishing, the likelihood is that protected areas will become increasingly important sources for the adult fishes which will sustain stocks and the fishery over the longer term.

1. Introduction

In response to concerns about the status of coral reef ecosystems, there has been growing interest in the use of marine protected areas (MPAs) as tools to restore or conserve fish stocks and, sometimes also, associated fisheries. There is now abundant evidence that effectively managed MPAs can generally be expected to have positive effects on fish assemblages within their boundaries, particularly in terms of increased biomass and greater number of large individuals of target species (Russ and Alcala, 2003; McClanahan and Graham, 2005; Friedlander et al., 2007), but the extent to which MPAs might also benefit fish stocks or fisheries outside their boundaries is less clear (Palumbi, 2004).

MPAs could benefit areas beyond their boundaries by two mechanisms: (1) 'spillover', i.e. net export of post-settlement fishes; and (2) 'replenishment effects', i.e. increase reproductive output from protected areas that ultimately increased population size or landings in connected unprotected areas. A number of studies have demonstrated some degree of spillover of coral reef fishes across MPA boundaries (McClanahan and Mangi, 2000; Russ et al., 2003; Abesamis and Russ, 2005; Abesamis et al., 2006; Tupper, 2007), but quantifying spillover is generally complicated by varying fishing intensity outside MPA boundaries (Abesamis et al., 2006), and by practical difficulties associated with identifying the occasional large-scale home-range relocations which may be particularly important in adult spillover (Kramer and Chapman, 1999). Similarly, because populations with more and larger fishes will tend to produce more eggs per unit area, the build-up of fish stocks within effectively managed MPAs might be expected to lead to some replenishment effects (Paddack and Estes, 2000; Evans et al., 2008). Quantifying replenishment in real situations is complicated by the high degree of natural spatio-temporal variability in recruitment strength which is typical of coral reef fishes (Sale et al., 1984; Walsh, 1987), and by practical difficulties in determining the source of settlers arriving on a reef. Therefore, although some spillover and enhanced replenishment could be expected from an effective MPA system, the absolute extent to which they are likely to supplement stocks outside protected areas remains difficult to predict in any particular situation.

For MPAs to produce a net fishery benefit, spillover or replenishment effects need to be of sufficient magnitude to ultimately compensate fishers for the costs associated with lost access to closed areas. A particular case of that would be if the establishment

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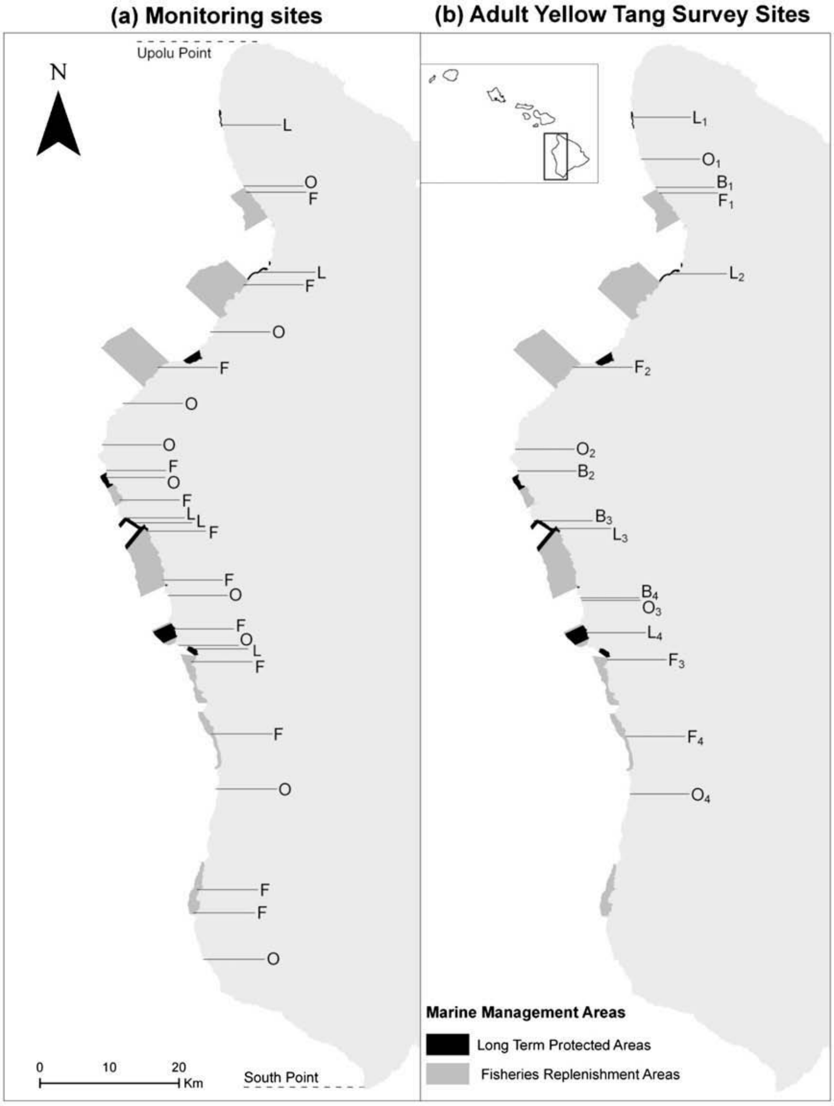

Fig. 1. Survey locations. (a) Long-term monitoring stations (mid-depth reef zones which are yellow tang settlement and juvenile habitat), surveyed 4–6 times per year since 1999. (b) Adult yellow tang survey sites (shallow pavement zones) surveyed five times each in 2006. Lightly shaded areas are Fish Replenishment Areas (FRAs), established December 31st 1999. Black areas are long-term protected areas, closed to aquarium collecting since at least 1991. Key to labels: 'B' = boundary site, open to fishing and mid-point <1 km from closed area boundary 'F' = FRA'; 'L' = long-term protected area; 'O' = open to fishing and mid-point >2 km from closed area boundary. 'West Hawaii', as used in this study, refers to the coastline from Upolu Point to South Point, which area constitutes the 'West Hawaii Regional Fisheries Management Area'.

of an MPA system, by acting as a bulwark against extreme overexploitation, helped to ensure the long-term sustainability of the fishery (Hart, 2006).

In this study we consider the impacts of fishing, and protection within a network of MPAs on the west coast of the Big Island of Hawaii (hereafter 'West Hawaii', Fig. 1) on populations of the yellow tang, *Zebrasoma flavescens* and the sustainability of the yellow tang fishery. West Hawaii is the most important region for the aquarium fishery in the Hawaiian Islands, and yellow tang is the most heavily exploited species (Walsh et al., 2003; Friedlander et al., 2005), constituting around 80% by number and 70% by value of aquarium landings from West Hawaii in recent years (HDAR unpublished data). The yellow tang fishery largely targets young juvenile fish in the size range of 5–10 cm (T.C. Stevenson, pers., comm.), but there is some indication that larger-sized juveniles are beginning to be taken to some extent. Smaller and younger fish, i.e. very recent settlers, have low survivorship in holding tanks, and older and larger fish are less desired by the trade. Adults (>13 cm as females, >15 cm as males), as well as being larger than the preferred size for aquarium collecting, are hardly taken by other fishers because yellow tang is not a desired food fish. Therefore, as yellow tang reach sexual maturity at 4–6 years old and can live for at least 41 years (J.T. Claisse, unpublished data), individuals which reach adulthood have the potential to be reproductively active for decades.

The life cycle of yellow tang and nature of the fishery make it particularly suitable for a study of replenishment and spillover effects. First, it is relatively easy to distinguish, and therefore quantify, recruit, juvenile and adult stages. Second, since yellow tang recruit into mid-depth high coral habitat, but relocate into shallow pavement zones on reaching adult sizes (Walsh, 1984), adult and sub-adult populations are spatially distinct. Third, as is typical for surgeonfish (Choat and Axe, 1996), yellow tang grow rapidly as juveniles but growth slows once they become reproductive adults, and hence there is a limited size range of adult yellow tang. For those reasons, the size of yellow tang populations in adult habitats is likely a meaningful measure of total breeding stock size. Finally, because yellow tang are primarily targeted as juveniles, at which stage they are very site-attached (Walsh, 1984), the greatest scope for spillover to occur is at life stages which are relatively unfished, and so spillover effects are not prone to being confounded by fishing outside of MPAs.

On December 31st 1999 the State of Hawaii established nine Fish Replenishment Areas (FRAs) that prohibited aquarium collecting along 27.8% of the West Hawaii coastline (Fig. 1). The creation of the FRAs brought the total coastline closed to aquarium collecting to 35.2%, as existing MPAs comprising 7.4% of the coastline were already closed to aquarium fishing. In a study of the FRA network conducted three years after its establishment, Tissot et al (2004) reported 78% higher yellow tang density in FRAs than in open areas. Their monitoring stations were located in mid-depth high-complexity reef areas which are the most intensively collected reef zones, but which have few adults. Thus, the reported rise in yellow tang density within FRAs was largely of juvenile fish. Crucial fishery questions remain concerning whether the protected area network has already, or will eventually, act to sustain or enhance the yellow tang breeding stock that ultimately supports the fishery.

Here, we extend the earlier study on the impacts of the FRA network, to include yellow tang catch and recruitment data, together with what is now nine years of monitoring data on abundance and size distribution in and out of protected areas. Those data, together with survey data on densities of yellow tang in adult habitats at sites: (i) within MPAs; (ii) outside MPAs, but close to protected area boundaries; and (iii) in open areas distant from any MPA boundary, are used to assess spillover and the role of the MPA network in ensuring the long-term sustainability of the yellow tang fishery.

2. Materials and methods

2.1. Fish monitoring in recruit and juvenile habitats

Between 1999 and 2007, fish populations were surveyed four to six times per year for a total of 47 survey rounds. For each survey round, fish surveys were conducted on four fixed transects at each of 23 monitoring sites distributed along the West Hawaii coastline (Fig. 1). Therefore, we have nine years of data from those sites: one year from prior to the establishment of the FRA network, and eight years post-closure. Nine of the 23 monitoring sites were established in areas which were to become FRAs, nine in areas that remained open to fishing after creation of the FRA network, and five in long-term protected areas, all of which had been closed to aquarium fishing since at least 1991.

Details of the survey sites and methodology are given elsewhere (Tissot et al., 2004), but, in brief, monitoring stations were located on medium-depth reefs (site means of 8.0–13.6 m) with moderate to high coral cover, particularly of the finger coral, *Porites compressa*. Such reefs are typical of much of the West Hawaii coast at that depth. Fish surveyors recorded the number and species of all fishes on transects. Between 1999 and 2002 yellow tang were classified as 'recruits', 'young juveniles' or 'others'. 'Recruits' are recently settled yellow tang (~3–5 cm), which are pale and vertically-elongated compared to older fish. 'Young-juveniles' are slightly larger (~5–6 cm), but notably smaller than other juvenile yellow tang in the habitat and therefore readily identifiable as having settled during the most recent recruitment season. Starting in 2003, surveyors continued to identify 'recruits', but otherwise classified fishes by total length in 5 cm bins (0–5 cm, 5–10 cm, 10–15 cm, 15–20 cm).

2.2. Fish surveys in adult habitats

To supplement data from the long-term monitoring program, we surveyed adult yellow tang populations in their prime daytime habitat, i.e. the deep edge of the shallow pavement zone around 3–6 m deep. Along the West Hawaii coast, shallow pavement areas generally have a distinct deep boundary where the main reef slope begins and where coral cover increases rapidly, and therefore the target habitat zone for our surveys was mostly well defined. Recognizing that adult yellow tang have highly clumped distributions, we developed a survey approach which allowed divers to count yellow tang over long transects running approximately parallel to shore through the prime adult habitat. Survey divers utilized leg-mounted propulsive units and a tank mounted battery pack named 'Jetboots' (http://www.jetboots.com), which enabled them to cover large areas while having both hands free. Survey divers remained as much as possible over the prime adult habitat while counting all yellow tang within a visually-estimated 5-m wide belt. Surveys were run at relatively constant speed for 18 min each which allowed two surveys per battery charge. Each transect covered approximately one kilometer beginning from a fixed starting point, but actual distance covered per survey was determined by recording the end point on a GPS unit in a support boat, and using a GIS to calculate the distance along the 5 m depth contour between start and end points.

To reduce environmentally-driven variability among counts, we established adult yellow tang (AYT) survey sites as much as possible in areas which had 1 km or more of largely continuous high quality habitat: i.e. areas of 3–6 m deep pavement with little sediment or sand. Most sites were established on narrow shelves adjacent to low shoreline cliffs, which is a common shoreline structure along the West Hawaii coastline. We established four AYT sites within FRAs, four within long-term protected areas (LTP); and eight in open, i.e. fished, areas (Fig. 1b). As adults have daily movements between diel and night time areas of up to at least 800 m (J.T. Claisse, unpublished data; Walsh, 1984), we assumed that there could be spillover across protected area boundaries over at least that scale. We therefore established four open sites as 'boundary' sites, centered <1 km from the nearest protected area boundary, and four as 'open' sites with mid-points >2 km from the nearest boundary (Fig. 1b). The 16 AYT survey sites were each surveyed five times between March 6th 2006 and December 6th 2006.

Preliminary trials of the AYT survey methodology indicated that although adult yellow tang were present across nearly all shallow reef areas, they were much more abundant in hard bottom areas with substantial vertical relief, particularly underwater gullies and valleys. To account for the potential impact of structural differences among sites, a survey diver used a dive computer to record their depth to nearest 30 cm at 2 s intervals on one survey dive at each site. As they maintained a constant height of around 1 m above the bottom, their depth corresponded with reef profile.

2.3. Fisheries data

Since 1976, all aquarium fishers in Hawaii have been required to be licensed and to submit monthly catch reports listing the species and number of all fishes caught and sold in that period (N.B. 'caught' includes fishes which are captured but are not sold for any reason). Most catch reports are filed by individual collectors, but teams of up to seven collectors can report their monthly catch on a single report. For this study we summarized data from West Hawaii reporting zones to generate total reported catch per fiscal year from 1976 to 2007. Hawaii fiscal years run from July through June (i.e. fiscal year 2007 data covers 07/2006–06/2007). Because yellow tang recruitment is highly concentrated in summer months (Walsh, 1987), and because young juveniles are targeted, the start of each fiscal year approximately coincides with the arrival of a new cohort of catchable fish.

Collectors vary widely in terms of their effort and catch. Several collectors report little or no catch, many are occasional or part time collectors, and a smaller number devote large amounts of time to aquarium collecting. Catch reports include information on total effort, but it is not partitioned among species or among the collectors included in the report. Therefore, we did not believe it was possible to generate meaningful measure of fishing effort for yellow tang. Instead, we calculated the number of collectors actively fishing for yellow tang per year by counting the number of fishers reporting catch of more than 1000 yellow tang in that year, either individually or as part of a larger group reporting catch on a single form. 1000 yellow tang was chosen somewhat arbitrarily as the cut-off point, but does not represent a high bar to being considered an 'active collector' as it is not uncommon for some collectors to report catch of that level in a single month. Prior to 1999, only the first mentioned collector on any report was entered into the catch database, and therefore we could only derive a consistent measure of 'active fishers' for 1999 onwards. Reports or instances of illegal fishing, either poaching within closed areas or collection by unlicensed fishers, are rare (W.J. Walsh, pers., comm.). Fishers targeting yellow tang are highly conspicuous because target habitats are close to shore and because fishers must work from boats to land large numbers of fish. We therefore believe that illegal fishing for yellow tang is negligible in West Hawaii.

2.4. Data handling and analysis

We evaluated changes in mean yellow tang density between 1999 and 2007 at FRA sites, at sites open to fishing throughout, and at LTP sites, by first generating an annual mean density per site excluding young-of-year (defined below), and then conducting paired *t*-tests on annual mean densities per survey site (before FRA creation = 1999; after = 2007). Differences between FRAs and other management categories by year are assessed using 95% confidence intervals of difference in means derived from *t*-tests. Young-of-year were excluded because of non-trivial variability in recruitment strength at the site level, and because high early mortality of yellow tang recruits meant that estimates of settlement at any site were highly dependent on whether surveys happened to coincide with recruitment peaks. Between 1999 and 2002, fish considered to be young-of-year were those identified as 'recruits' or 'young-juveniles,' and from 2003 onwards they were all fish identified as 'recruits' or which were <5 cm. Because of the change in methodology, data from 2003 onwards slightly underestimate young-of-year relative to earlier years as fish up to ∼6 cm can still have young-juvenile characteristics.

Using data from 2003 onwards, we examined yellow tang density in two size-classes, 5–10 cm and 10–15 cm. The 5–10 cm size class comprised of approximately two-month to two-year old fish (J.T. Claisse, unpublished data), which are the prime targets of the fishery. The density of 10–15 cm size class yellow tang in the habitats where we conducted long-term monitoring, mostly comprise large juveniles/sub-adults plus a much smaller number of mature fish which either remained in mid-depth habitats, or were making temporary migrations from their normal shallow daytime ranges (J.T. Claisse, unpublished data). We calculated annual density ratios of FRA:open for each size class, and determined 95% confidence intervals for those ratios by first doing *t*-tests of differences of means between FRA and open sites, and then standardizing confidence limits by dividing by mean densities at open sites. We assessed temporal trends in density within size classes, and in FRA:open ratios, by means of linear regressions.

The shallowest LTP site was located very close to the shoreline and had over three times the density of 10 cm and larger yellow tang than other LTP sites. Because densities of 10–15 cm yellow tang at that site are not likely representative of sub-adult fish, we excluded that site when determining size class densities at LTP sites. Excluding that site did not affect statistical analyses, since we did not conduct tests involving size class data from LTP sites.

Mean adult yellow tang densities per site were calculated based on five surveys per site. Differences in densities among sites in different management categories (FRA, LTP, Boundary, Open; four sites per group) were tested using ANCOVA, with management group as main effect, and structural complexity (defined below) as covariate. Fisher's tests were used to identify significant pairwise differences among management groups ($\alpha = 0.05$). The structural complexity metric for each site was calculated using the depth data recorded at that site. First we calculated the maximum change of depth within each 30 s interval (∼30 m distance), and then averaged those values for the entire survey. Conformity with requirements of homogeneity of variance was tested using Levene's test ($p > 0.1$), and of homogeneity of slopes (management $*$ structural complexity, $p = 0.73$) prior to application of ANCOVA. All analyses were performed using JMP-IN 5.1 (SAS, 2003).

3. Results

3.1. Fisheries data

Reported yellow tang catch increased 30-fold between 1976 and 2007. Reported catches were ∼10,000 year^{-1} between 1976 and 1985, but over the next decade increased to nearly 200,000 year^{-1}. Annual catch stabilized at around that level until 2003, before again increasing rapidly and peaking at 382,921 in 2006. In 2007, reported catch declined to 291,013; although substantially less than fiscal year 2006, that was still the third highest on record (Fig. 2). The number of active collectors increased from 16 in 1999, to 37 in 2007 (Fig. 2).

3.2. Yellow tang density at monitoring sites (juvenile and recruit habitat)

Prior to establishment of the FRAs, yellow tang densities were similar at ∼10–15 per 100 m^2 at FRA and open sites, whereas densities at LTP sites were ∼20–25 per 100 m^2 (Table 1, Fig. 3). By 2003, and in all subsequent years, mean yellow tang densities in

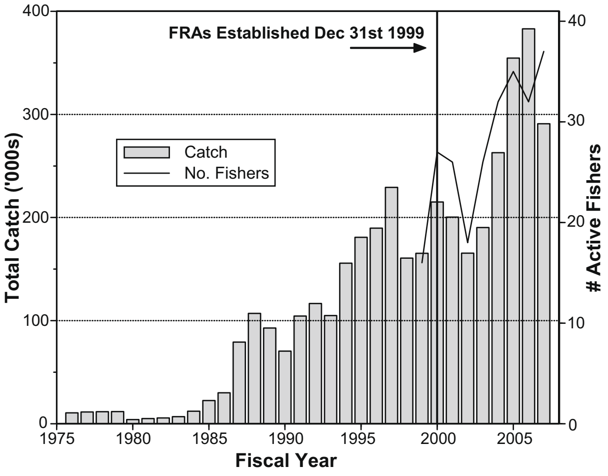

Fig. 2. Number of active fishers and annual reported catch of yellow tang from West Hawaii reporting zones, derived from monthly catch reports. In total 35.2% of the West Hawaii coastline was closed to fishing once the Fish Replenishment Area network (FRA) was established. Fiscal years cover July to June. Active fishers are collectors who reported catch of >1000 yellow tang in a year, either as individually or as members of a team reporting on common reports. Data on active fishers was only available from 1999.

Table 1
Yellow tang densities by management strata. Data are from long-term monitoring of mid-depth high coral cover habitats, so largely comprise sub-adults and juveniles, which are the targets of the aquarium fishery. 95% confidence intervals of difference in means between FRA-CTRL and FRA-open that do not overlap zero (i.e. significantly different at α of 0.05) are indicated by an asterisk.

	Long-term protected	Fish replenishment	Open	95% Confidence interval of difference in means	
	(LTP)	Area (FRA)		FRA–LTP	FRA-open
Number of stations					
	5	9	9		
Density/100 m^2 (Mean ± SE)					
1999	23.6 ± 6.5	13.4 ± 1.2	11.6 ± 1.9	(1.1, 19.2)*	(−5.8, 9.5)
2000	22.6 ± 6.1	12.0 ± 1.5	8.9 ± 1.7	(1.9, 19.3)*	(−4.2, 10.5)
2001	21.6 ± 4.8	12.4 ± 1.9	7.1 ± 5.0	(1.2, 17.0)*	(−1.4, 12.0)
2002	22.2 ± 4.2	14.0 ± 2.1	8.9 ± 1.6	(0.6, 15.7)*	(−1.3, 11.5)
2003	26.0 ± 4.9	22.8 ± 2.0	13.4 ± 2.8	(−6.2, 12.7)	(1.4, 17.3)*
2004	28.7 ± 6.1	26.2 ± 2.8	11.4 ± 2.4	(−8.1, 13.1)	(5.8, 23.7)*
2005	26.8 ± 6.7	24.7 ± 2.3	11.3 ± 2.0	(−8.2, 12.4)	(4.7, 22.1)*
2006	25.8 ± 6.7	25.6 ± 2.8	11.6 ± 1.9	(−10.7, 11.1)	(6.8, 25.3)*
2007	24.4 ± 6.3	23.0 ± 3.3	6.3 ± 1.3	(−9.4, 12.1)	(7.6, 25.8)*
% Change 1999–2007					
Mean	+4%	+72%	−45%		
95% CI	(−9%, 16%)	(14%, 130%)	(−4%, −87%)		
Paired *t*-test	d.f. = 4	d.f. = 8	d.f. = 8		
	t-ratio = 0.78	*t*-ratio = 2.85	*t*-ratio = −2.54		
	p = 0.48	*p* = 0.02	*p* = 0.03		

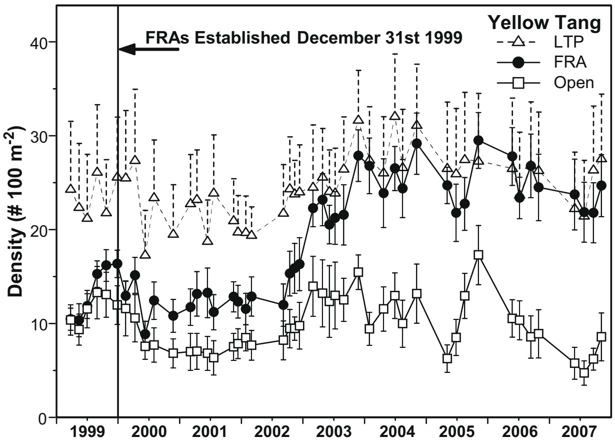

Fig. 3. Mean yellow tang density trends (±1 SE) at West Hawaii monitoring sites. Data exclude young-of-year. LTP sites ($n = 5$) were closed to aquarium collecting since at least 1991. FRA sites ($n = 9$) are Fish Replenishment Areas, i.e. were open to fishers prior to establishment of the FRA network. Open sites ($n = 9$) were open to fishers throughout the study. Monitoring stations were located in yellow tang juvenile habitat, thus densities reflect sub-adult fish. Only upper SE bars shown for LTP sites.

FRA sites had risen to values similar to those at LTP sites and were higher than at sites which remained open to fishing throughout (Table 1, Fig. 3). Between 1999 and 2007, mean density increased by 72% at FRA sites, remained approximately stable at LTP sites, and declined by 45% at sites which were open to fishing (Table 1).

Recruitment strength, measured by the number of recent settlers observed during surveys, varied considerably among years: peak densities of recent settlers ranging from ~2 per 100 m^2 in low-recruitment years (1999, 2000, 2006, Fig. 4a) to around 10–17 per 100 m^2 in good recruitment years (2002, 2003, 2005, Fig. 4a). Little recruitment occurred in the first three of the nine years we have data from, but recruitment was moderate to high in five of the six most recent years (Fig. 4a).

The highest densities of prime-target size (5–10 cm) yellow tang at FRA and LTP sites were recorded in 2004, following two years with good recruitment (Fig. 4). However, over the 2003–2007 period as a whole, densities at FRA and LTP were stable (linear regression, $r^2 < 0.15$, $p > 0.5$ in both cases). In contrast, their density declined in open areas throughout the entire period we have size data from (2003–2007: linear regression, $r^2 = 0.91$, $p = 0.01$, Fig. 4b). Just between 2006 and 2007, i.e. following the

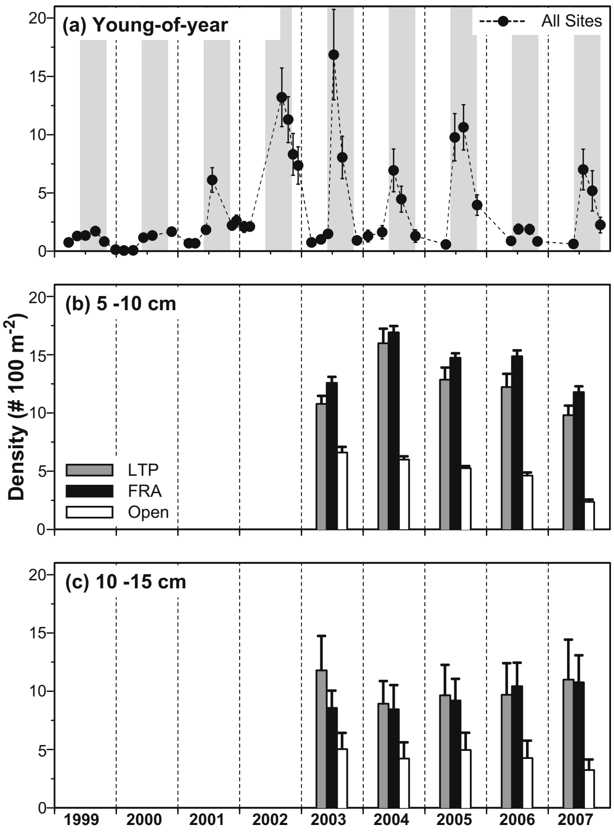

Fig. 4. Yellow tang density trends at West Hawaii monitoring sites. (a) Young-of-year. Identification was based on the distinct morphology and color of recently settled fish from 1999 to 2002, but from 2003 on, young-of-year were all recent recruits or those <5 cm. Recruitment data were pooled for all 23 as an index of coast-wide recruitment strength. Shaded areas in figure (a) show the May–August prime yellow tang settlement period (Walsh 1987). Size data, which is only available from 2003 is shown for (b) 5–10 cm, i.e. prime-target size yellow tang; and (c) 10–15 cm, which are largely older-juveniles. Columns in (b) and (c) show mean densities (±1 SE) by management strata: LTP, FRA, and open (as for Fig. 3).

one poor recruitment year in that period, densities dropped nearly in half, from 4.6 (±0.3 SE) to 2.4 (±0.2) per 100 m^2. The net effect was that the FRA:open ratio of density of 5–10 cm yellow tang significantly increased over that period (linear regression, $r^2 = 0.84$, $p = 0.03$), from 1.9:1 in 2003 (95% CI: 1.0, 2.8) to 4.9:1 in 2007 (CI: 3.0, 6.9).

Between 2003 and 2007, the density of large juvenile yellow tang (10–15 cm) was stable in LTP areas (linear regression, $r^2 = 0.01$, $p = 0.86$), rose marginally in FRAs (linear regression, $r^2 = 0.90$, $p = 0.01$), and tended to decline at sites open to fishing, although that decline was not significant (linear regression, $r^2 = 0.60$, $p = 0.12$, Fig. 4c). FRA:open ratios significantly increased between 2003 and 2007 (linear regression, $r^2 = 0.80$, $p = 0.04$), from 1.7:1 (CI: 0.8, 2.6) in 2003, to 3.3:1 (CI: 1.6, 5.0) in 2007.

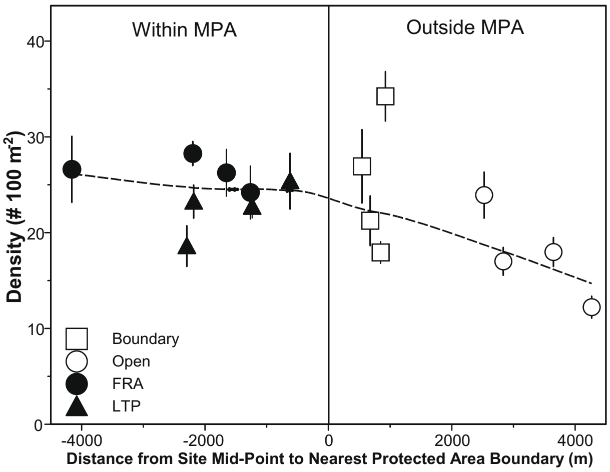

Fig. 5. Mean yellow tang densities (±1 SE) in adult habitats against distance of survey site mid-point from nearest protected area boundary ($n = 5$ surveys per site). FRA, LTP, boundary, and open management groups are described in Table 2. The trend line was generated using a LOESS smoothing function.

Table 2
Yellow tang densities and site characteristics and at adult survey sites in 2006. Site locations are shown in Fig. 1b. $n = 5$ surveys per site. Aquarium fishing was closed at LTP sites by 1991, and at FRA sites on December 31st 1999. Boundary sites were open to fishing and had mid-points <1 km from the nearest closed area boundary. 'Open' sites had survey mid-points >2 km from nearest closed area boundary. Structural complexity is the mean vertical range in meters derived from diver depth gauges over 30 s intervals (∼30 m).

Site	Yellow tang density/100 m^2 (mean ± SE)	Distance to nearest MPA boundary (m)	Structural complexity
FRA sites			
F_1	24.2 ± 2.8	1264	1.1
F_2	26.2 ± 2.4	1653	1.4
F_3	28.3 ± 1.3	2199	1.6
F_4	26.6 ± 3.5	4158	1.5
LTP sites			
L_1	22.7 ± 1.2	1236	1.6
L_2	23.2 ± 1.7	2185	2.3
L_3	18.6 ± 2.1	2296	1.2
L_4	25.4 ± 2.9	621	1.8
Boundary sites			
B_1	21.2 ± 2.6	679	1.5
B_2	17.9 ± 1.1	847	1.3
B_3	26.9 ± 3.8	546	1.4
B_4	34.2 ± 2.6	926	1.3
Open sites			
O_1	12.2 ± 1.2	4270	1.6
O_2	18.0 ± 1.5	3651	1.2
O_3	23.9 ± 2.4	2527	2.4
O_4	17.0 ± 1.5	2838	1.3

Table 3
ANCOVA of yellow tang densities from surveys in adult habitats, with management group as main effect, and structural complexity as covariate. Management groups are as for Table 2. Differences among management groups were tested using a Fisher's test. Groups with the same letter were not significantly different at alpha = 0.05.

Source	DF	*F* ratio	*p*
Management group	3	3.60	0.049
Structural complexity	1	2.17	0.169

Management group			Density/100 m^2 (mean ± SE)
FRA	A		26.3 ± 0.8
Boundary	A		25.1 ± 3.6
LTP	A	B	22.5 ± 1.4
Open		B	17.8 ± 2.4

3.3. Adult yellow tang densities

Yellow tang densities in adult habitats varied from 12.2 ± 1.2 ($\bar{x}$ ± SE) to 34.2 ± 2.6 per 100 m^2 (Fig. 5). Density was similar at seven of eight MPA sites (the four FRA sites and three of four LTP sites), ranging between 22.7 ± 1.2 and 28.3 ± 1.3 per 100 m^2. The protected site with notably lower adult densities (L_3: 18.6 ± 1.5 per 100 m^2) had the second lowest structural complexity value of the 16 sites surveyed (Table 2). Adult yellow tang densities at three of four boundary sites varied between 17.9 ± 1.1 and 26.9 ± 3.8 per 100 m^2. The other boundary site (B_4) had the highest density of any survey site, 34.2 ± 2.6 per 100 m^2. Open sites tended to have lowest adult densities. Densities at three of four open sites ranged from 12.2 ± 1.2 to 18.0 ± 1.5 per 100 m^2. Adult density was higher at site O_3 (23.9 ± 2.4 per 100 m^2), which also had the highest structural complexity of the 16 adult survey sites (Table 2).

After controlling for the effect of reef structural complexity, adult densities differed among management groups (Table 3, ANCOVA $F_{[1,3]} = 3.6$, $p < 0.05$). Mean adult yellow tang densities were 48% higher at FRA sites and 41% higher at 'boundary' sites than at open sites (Fisher's test $p < 0.05$, Table 3). Mean adult density at LTP sites was 26% higher than at open sites, but there were no significant pair-wise differences between LTP and other management groups (Table 3). Reef structural complexity did not differ among management groups (ANOVA $F_{[1,3]} = 1.0$, $p = 0.45$).

4. Discussion and conclusions

Yellow tang are the prime targets of the aquarium fishery in West Hawaii, with reported annual catch of 300–400 thousand since 2005. Assuming a third of the catch is not reported (Dierking, 2007), the total annual take from West Hawaii areas open to collectors is approximately three thousand fish per km of coastline. Given that scale of harvest, it is perhaps not surprising that in common with other marine protected area studies (Polunin and Roberts, 1993; Russ and Alcala, 2003; McClanahan and Graham, 2005; Friedlander et al., 2007) we found clear evidence of within-MPA effects, including that density of prime targeted size yellow tang (5–10 cm) within FRAs was five times that of fished areas. Since there was no difference in yellow tang densities between FRA and open sites prior to the creation of the FRAs, recent differences represent real effects of protection, rather than being indicative of underlying habitat or other environmental differences among sites. While the difference in density of small yellow tang between FRA and open sites was striking, of more significance to the role the FRAs may have in enhancing or sustaining West Hawaii yellow tang stocks and ultimately also the fishery, was the effect of protection on adult yellow tang densities, which were 48% higher in FRAs than in non-boundary open sites in 2006.

The significantly higher density of adult yellow tang in boundary sites than in open areas distant from MPAs is indicative of spillover. Furthermore, as all boundary sites included reef areas which were more than a kilometer from the nearest protected area boundary, the fact that mean adult yellow tang density in boundary sites was nearly as high as within protected areas suggests that considerable spillover can occur at that spatial scale. As is common for benthic-associated reef fishes (Kramer and Chapman, 1999), juvenile and adult yellow tang tend to have small daytime ranges. In contrast, adult yellow tang make daily migrations between daytime and nighttime ranges which can be at least 800 m apart (J.T. Claisse, unpublished). It does not seem implausible that spillover could operate over comparable spatial scales. In the absence of tagging or other movement studies we cannot distinguish among possible spillover mechanisms including occasional relocation as adults or ontogenic habitat shifts. However, the highest adult density we found was at B_4, a boundary site adjacent to a large FRA. That FRA has abundant high quality juvenile habitat, i.e. mid-depth high-complexity coral habitats (DeMartini and Anderson, 2007), but largely lacks the unsedimented pavement habitat preferred by adults, inshore areas there being predominantly sandy. High adult density at site B_4 is therefore consistent with their being scope for considerable ontogenic spillover.

There are a number of reasons for expecting that difference in adult densities between FRAs and open areas will increase in future. First, the duration of fishery closure in FRAs covered by our study is short relative to the life-span of yellow tang, which can live over 40 years (J.T. Claisse, unpublished). Specifically, as the prime-target size range for yellow tang corresponds with fish around two years or younger, (J.T. Claisse, unpublished), and our adult surveys were conducted in the seventh year of FRA closure, most adult fish $>\sim$9 years old at that time would likely have moved out of targeted size classes prior to FRA establishment. Second, catches and the impacts of fishing have increased in recent years. Average reported catch between 2004 and 2007 was 74% above the average of the previous 10 years. Recent high catches were made possible by relatively good recruitment in years 2002 through 2005, but also reflect a doubling of the number of active fishers between 1999 and 2007, and, perhaps also, increased application of more intensive fishing methods (Walsh, pers. obs.). The net result has been that even during a period of mostly good recruitment, the density of prime-target sized yellow tang (5–10 cm) declined in open areas between 2003 and 2007, and the FRA:open density ratio of that size class increased from 1.9:1 to 4.9:1. Over the same period, the FRA:open density ratio of large juvenile yellow tang increased from 1.7:1 to 3.3:1, indicating that a significantly smaller portion of juveniles in open areas were reaching large juvenile stages than previously. It seems likely that the supply of new adults from open areas will also be lower than in the past. Thus, assuming fishing pressure remains high, as older adults are lost and not replaced from open areas at the same rate as previously, continuing high levels of supply from protected areas will likely mean that those areas become even more important source areas for West Hawaii breeding stocks in coming years.

Information on dispersal of coral reef fish is limited (Mora and Sale, 2002), but there are a number of reasons to believe that most yellow tang settling onto West Hawaii reefs originated there. First, although fish larvae are capable of dispersing over very long distances, the scale of the West Hawaii coastline ($\sim$150 km from north to south) is large relative to several recent estimates of demographically meaningfully reef fish dispersal distances (Kinlan and Gaines, 2003; Shanks et al., 2003; Cowen et al., 2006). Second, the Hawaiian archipelago is isolated from other reef areas by >1000 km, and recent surveys across the Hawaiian Islands have demonstrated that there are no other yellow tang populations which are even remotely comparable in size to the West Hawaii population (HDAR unpublished). The absence of large populations elsewhere in the Hawaiian Islands is corroborated by the fact that >94% of all yellow tang collected come from West Hawaii (HDAR unpublished). Third, prevailing west-northwestward surface currents and the formation of eddies west of the Big Island of Hawaii (Calil et al., 2008) both suggest limited contribution to West Hawaii recruitment from elsewhere in the archipelago. Therefore, although West Hawaii yellow tang adult stocks may be supplementing populations elsewhere in the state, it seems likely that future levels of yellow tang recruitment onto West Hawaii reefs will ultimately depend on the status of breeding stocks within West Hawaii itself. Thus, any positive impacts of the protected area network on West Hawaii adult stocks and stock spawning potential would likely directly benefit the local yellow tang fishery.

It is important to recognize that there is a gap between identifying an MPA/fishing effect on adult densities, and being able to quantify the impact of that on future levels of yellow tang settlement or on recruitment into catchable size-classes. In addition, because we do not have pre-closure data on adult densities, we cannot conclusively distinguish between the benefits of increased survivorship within MPAs, and the detrimental consequences of concentrating fishing effort in the remaining open areas after the FRAs were established. There are therefore limits to what we can conclude about the net effect of West Hawaii MPAs on current or future fishery yields. However, increasing fishery participation and significantly increasing fishing impacts in recent years demonstrate the potential for fishery overexploitation to significantly reduce breeding stocks in the absence of regulation. By supplementing adult stocks within MPAs and in boundary areas, West Hawaii MPAs appear, at the very least, to be an effective means of preventing that kind of extreme overexploitation from occurring.

There are some relatively simple management actions which could improve long-term fishery sustainability, including limited-entry, and restricting the take of breeding-size yellow tang by aquarium collectors and other fishers. However, there are several reasons why the fishery would be difficult to effectively manage by approaches such as bag limits or total allowable catch limits. First, available catch in any year is highly dependent on recent recruitment strength, which for yellow tang is highly variable from year to year (Walsh, 1987). As a result, optimum catch limits will vary substantially and unpredictably from one year to another. Second, aquarium catch and landings are highly dispersed, which makes it difficult or unfeasible to enforce catch quotas or bag limits and to verify catches. In contrast, because large scale yellow tang collection requires fishers to be conspicuous, area based management is relatively straightforward to enforce.

The West Hawaii FRA system has been shown to have a number of benefits above and beyond any impacts on yellow tang. Those include greater numbers of other targeted species (Tissot et al., 2004), reduced conflict between collectors, commercial ocean recreation operations, and community members (Walsh et al., 2004), and greater numbers of attractive and conspicuous fishes in reef areas which are readily accessible to commercial and recreational divers and snorkelers. Our study provides strong evidence that in addition to the benefits mentioned above, the West Hawaii protected area network, by sustaining adult stocks over large areas of the coastline, acts as a bulwark against overexploitation, and thereby helps to ensure long-term sustainability of yellow tang stocks in West Hawaii and of the fishery which depends heavily on this species.

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