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RESEARCH ARTICLE

Influence of marine reserve size and boundary length on the initial response of exploited reef fishes in the Florida Keys National Marine Sanctuary, USA

Aaron Bartholomew · James A. Bohnsack · Steven G. Smith · Jerald S. Ault · Douglas E. Harper · David B. McClellan

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Abstract We examine the influence of reserve size and boundary length on the relative rate of fish density change in reserves versus fished reference reefs for three exploitable-sized reef fish categories: (1) combined fish (34 species of Haemulidae, Lutjanidae, Serranidae, and hogfish *Lachnolaimus maximus*); (2) Haemulidae (13 species); and (3) Lutjanidae (9 species). If reef habitat boundaries are highly permeable to fish movements then fish recovery within a reserve would be inversely proportional to: reserve perimeter (RP)/total reserve area (RA) (RP/RA). If, however, reef habitat boundaries are relatively impermeable barriers to fish movements, recovery within the reserve would be inversely proportional to: reserve boundary that intersects reef habitat (HI)/reef habitat area within the reserve (HA) (HI/HA). From 1994 to 2001 we monitored reef fishes within and outside of no-take marine reserves established in 1997 in the Florida Keys, USA. A significant majority of reserves had greater rates of density change than reference reefs for Lutjanidae and combined fish (22 of 24 reserves for both categories). Significantly higher rates of density change were found in ten reserves for Lutjanidae, two reserves for combined fish, and one reserve for Haemulidae. Reserves appeared to promote an increased density of exploitable fishes. A significant, negative, but weakly correlated relationship was found between the relative rate of density change (RDC) for combined fish and the HI/HA ratio. Reserve size and placement appeared to have a minimal effect upon RDC.

Keywords Landscape ecology · Fish density · Reserve boundary · Habitat · Perimeter to area ratio · Marine reserve · Conservation

A. Bartholomew · J. A. Bohnsack · D. E. Harper · D. B. McClellan
National Marine Fisheries Service, 75 Virginia Beach Drive, Miami, FL 33149, USA

Present Address:
A. Bartholomew (✉)
American University of Sharjah, P. O. Box 26666, Sharjah, United Arab Emirates
e-mail: abartholomew@aus.edu

S. G. Smith · J. S. Ault
University of Miami, Rosenstiel School of Marine and Atmospheric Science, 4600 Rickenbacker Causeway, Miami, FL 33149, USA

Introduction

A growing number of theoretical and empirical studies have demonstrated increased density and sizes of exploited species within reserve boundaries (Bohnsack 1998a, b; Murray et al. 1999; National Research Council 1999; Fogarty et al. 2000; Horwood 2000; Lindeboom 2000; Roberts and Hawkings 2000; Halpern 2003; Williamson et al. 2004; Ault et al. 2006). Fisheries outside reserves may also benefit from resulting increased reproductive output

and juvenile dispersal from reserves to fishing grounds (Carr and Reed 1993; DeMartini 1993; Murawski et al. 2000; Gell and Roberts 2003), and from spillover of adult fish moving from reserves into adjacent fishing grounds (Bohnsack 1992; Russ and Alcala 1996a; McClanahan and Mangi 2000; Roberts et al. 2001; Russ et al. 2003). Definitive empirical evidence supporting the idea that reserves enhance fisheries through reproductive output and studies demonstrating a spillover benefit for fisheries are both rare, however (Sale et al. 2005).

One concern of landscape ecology is the effect of spatial patterning on the movement, distribution and conservation of fauna (Turner 1989; Wu and Hobbs 2002). An important research topic in landscape ecology is optimal landscape design to accomplish management goals (Wu and Hobbs 2002). Important questions when designating marine reserves are whether the size, shape and placement of reserves will influence their effectiveness, and whether it is better to have a single large or several smaller (SLOSS) reserves of equivalent total area (Simberloff and Abele 1982; Meester et al. 2004). Polacheck (1990) and DeMartini (1993) modeled marine reserves and predicted that a single large reserve performed better at increasing spawning stock biomass than several smaller reserves. Because small reserves have larger perimeter to area ratios than large reserves, fish are more likely to disperse across boundaries and are less likely to accumulate biomass within smaller reserves (Buechner 1987). Exploited species with large home ranges relative to reserve size may not realize any protection because of their extended exposure to fishing while outside of the reserve (Rowley 1994; Sale et al. 2005). For these species, costs would be imposed by the formation of the reserve, but with no benefit to the stock, possibly resulting in disincentives to create further reserves in a region (Hilborn et al. 2004). Highly mobile reef species such as jacks (*Carangidae*), for example, may migrate long distances, even over non-reef habitats (Hixon and Carr 1997; Chapman and Kramer 2000). Evidence exists, however, that even small reserves can accumulate highly mobile fish (Holland et al. 1996; Russ and Alcala 1996b; Roberts and Hawkins 1997). This may occur for some populations of "mobile" fish species as there appears to be intra-specific differences in mobility, with a portion of the population remaining relatively sedentary (Gell and Roberts 2003).

Another question concerns how to maintain biological connectivity between marine reserves (Murray et al. 1999). Several small reserves in a network that are spaced at wider intervals would ensure that species with long-distance dispersal that are produced in one reserve will recruit to another reserve (Carr and Reed 1993; Roberts et al. 2003). Multiple reserves within a network may be particularly important if there is strong advective transport of larvae by ocean currents (Gaines et al. 2003). A single large reserve would be better for species with short dispersal, however, as the larvae would be retained within the reserve itself (Roberts et al. 2003; Shanks et al. 2003). This would increase the likelihood that the reserve would be self-sustainable (Grantham et al. 2003; Sale et al. 2005).

Few studies have empirically addressed the influence of marine reserve size on effectiveness. Edgar and Barrett (1999) compared four marine reserves in Tasmania with unprotected reference regions. They found that the largest reserve had higher fish species richness, higher density of large fish, and larger sized exploitable fishes when compared with non-reserve reference sites. The smaller reserves were not different from the reference sites, except that one smaller reserve had a higher density of large fish. These results suggest that a single large reserve may be more effective at protecting fishes than several small reserves of equal area.

Halpern (2003) compared fish density, biomass, size and species richness between marine reserves and fished reference areas from 89 studies conducted worldwide. He concluded that there was no effect of reserve size on a per unit area basis and that several small reserves may be comparable to a single large reserve in promoting recovery. He stressed the need, however, for more studies of different sized reserves within the same biogeographical region.

Another question is whether reserve placement relative to the underlying habitat influences fish recovery within reserves. Emigration from habitat patches depends upon individuals crossing habitat boundaries (Stamps et al. 1987; Kramer and Chapman 1999). Landscape ecology studies have found that the extent of similar habitat types surrounding reserves influences dispersal of fauna from the reserves, and that "porous" or "permeable" boundaries result in increased boundary crossings (Collinge 1996). Species that are habitat specific may not cross over into

different habitat types (Plan Development Team 1990). Reef fish, for example, may not cross sand, seagrass or deep water, especially during the day (Hobson 1973; Sale et al. 1984; Chapman and Kramer 2000). Some studies have concluded that the "edge permeability" of coral habitat is low for some reef fish species (Russ and Alcala 1996a; Chapman and Kramer 2000). In these cases, marine reserves that have boundaries conforming to natural habitat edges may be more likely to retain fish and show higher density and larger average sizes (Chapman and Kramer 2000). In contrast, a reserve boundary that intersects reef habitats should have high permeability and facilitate movement of fish into surrounding fished areas at that boundary, possibly at the expense of greater fish density, average size, and larval output within the reserve (Ratkin and Kramer 1996; Roberts 2000).

In this paper, we predict that if reef habitat boundaries are highly permeable to a reef fish species, or if a species does not discriminate between habitat types, then fish retention, and therefore recovery, within a reserve will be inversely proportional to the ratio of reserve perimeter to total reserve area (RP/RA) (Buechner 1987). However, if reef habitat boundaries are relatively impermeable barriers to fish movement, then fish retention would be adversely impacted only at the portion of the reserve perimeter that intersects reef habitat. Fish retention, and therefore recovery, within the reserve would then be inversely proportional to the ratio of length of the reserve boundary that intersects reef habitat to reef habitat area within the reserve (HI/HA). In both scenarios, fish retention and recovery within a reserve should increase with larger reserve size, all else being equal. Under the impermeable habitat boundary scenario, however, fish retention and recovery in small reserves is predicted to be greater than that of much larger reserves if the small reserve has little or no overlap between the reserve boundary and reef habitat. So, in Fig. 1, for example, recovery within reserve (b) may be higher than recovery within reserve (a) even though reserve (a) is larger, because the reserve boundary in reserve (b) does not intersect any reef habitat.

In this study we examine changes in fish density for exploited reef fishes following the establishment of marine reserves in the Florida Keys National Marine Sanctuary (FKNMS) USA, to evaluate whether reserve size, and placement relative to the underlying reef habitat, influence fish recovery.

Methods

Divers have monitored coral reef fishes annually since 1979 in the Florida Keys by visual census (Bohnsack et al. 1999). In July 1997 the FKNMS established 22 small sanctuary protected areas (SPAs) and one larger ecological reserve (ER) (U.S. Department of Commerce 1996). The reserves were established because fishing pressure and mortality in the Keys are "very intense," and many fish stocks were over fished according to US federal spawning potential ratio guidelines (Ault et al. 1998). A map of the SPA's and the ER is available at:

http://www.fknms.nos.noaa.gov/research_monitoring/map.html.

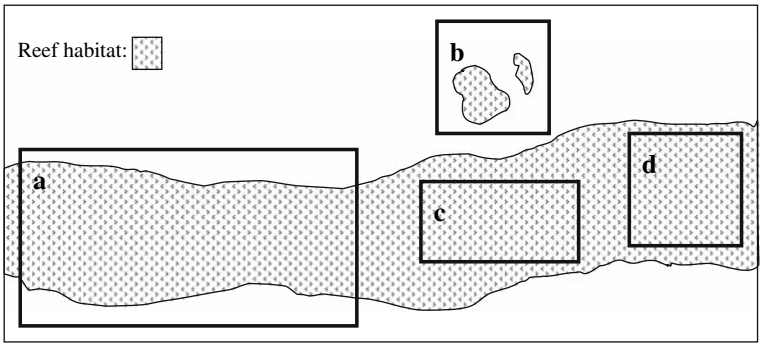

Fig. 1 Hypothetical reserves: **b**, **c** and **d** all have the same area. If fish do not cross reef habitat boundaries (impermeable habitat boundaries), exploitable fish retention (recovery) would be highest in **b** (HI/HA = 0) followed by **a** > **d** > **c** (increasing HI/HA). If fish use all habitats within a reserve equally (permeable habitat boundaries) retention would be highest in **a** (lowest RP/RA) followed by **b** = **d** > **c** (based on RP/RA)

Four SPAs are "research only" and closed to all fishing, snorkeling, and SCUBA diving without a research permit. The ER and 14 SPAs allow snorkeling and SCUBA diving, but prohibit all fishing. The remaining four SPAs allow snorkeling, SCUBA diving, and catch-and-release fishing by trolling. Because all SPAs and the ER are technically "no-take," they are treated as replicates in this paper. Regulations are enforced by the sanctuary enforcement team consisting of 17 enforcement personnel in 2004–2005. They rely heavily on voluntary compliance with regulations combined with education of fishermen. In 2004–2005 they issued 201 fisheries resources violations for fishing within reserves (U.S. Department of Commerce 2005).

Divers conducted visual censuses using the stationary diver method (Bohnsack and Bannerot 1986) on reef habitats within and outside of reserves, before and after reserves were implemented. In each sample, divers identified each fish species, counted individuals, and estimated the mean, minimum and maximum sizes for each species seen in a 15 m diameter cylinder. We estimated the size-frequency distribution for each species according to Meester et al. (1999) and used this to determine the density of legally exploitable individuals for each fish species.

Prior to 1999, sampling consisted of randomly selected sites on non-randomly chosen reefs. Some reefs became reserves in 1997 while other reefs, considered "reference" reefs for comparison purposes, remained open to all fishing, snorkeling, and SCUBA diving. In 1999 we adopted a two-stage stratified random sampling approach which expanded sampling to all reef habitat in the Florida Keys. We selected individual sample sites randomly within 200×200 m^2 sampling blocks stratified by region (upper, middle, and lower Keys) and by reef type as described in Ault et al. (2002) and Franklin et al. (2003). Sanctuary reserves included four reef types: fore reef, mid channel reef, inshore patch reef, and offshore patch reef.

We compared exploitable sized reef fishes in marine reserves to nearby reference reefs located outside of reserves. We did not observe any exploitable sized individuals in samples for some species and years, thus we pooled the data for some species and analyzed the data for three fish categories: (1) total combined exploitable-sized reef fishes in the families Haemulidae (13 grunt species), Lutjanidae (9 snapper species), Serranidae (11 grouper species), and Labridae (1 wrasse species *Lachnolaimus maximus*); (2) exploitable-sized grunts and (3) exploitable-sized snappers (Table 1). We did not observe exploitable-sized grouper frequently enough analyze them as a separate category, due to intensive fishing for groupers in the Florida Keys (Ault et al. 2005a, b).

Using a non-parametric Sign test, we tested the null hypothesis that that there was no difference in the number of reserves that exhibited greater density changes over time than their corresponding reference reefs. We also performed ANCOVA analyses to determine if rates of density change were significantly different in each reserve compared to its corresponding reference reefs. The main factor was status (reserve or reference), the covariate was year, and the dependent variable was exploitable fish density. A significant interaction between year and status indicated that density in the reserve was changing at a significantly different rate than in the corresponding reference reefs.

Fish densities were block means within a reserve or reference site. Data were log $(x + 1)$ transformed to meet the statistical assumptions of normally distributed residuals and homoscedascity of variance for the ANCOVA tests. Reference fish densities were the block means in the same region with the same reef type as the reserve. Many of the reserves were in the same region and had the same reef types, so a specific set of reference reefs was usually compared to multiple separate reserves. We combined the 1994–1996 data and statistically treated them as a single pre-implementation baseline, by using all of the block means for reserves or reference sites within those years.

We estimated the relative rate of density change (RDC) for each reserve, where the RDC equals the rate of density change in the reserve minus the rate of density change in reference reefs following reserve establishment. We then performed least square regressions of RDC for the reserves versus the RP/RA ratio (permeable reef habitat boundary scenario) and the HI/HA ratio (impermeable reef habitat boundary scenario) for all three fish categories. RP/RA and HI/HA are influenced by reserve size and shape, and HI/HA is also influenced by reserve boundary placement relative to the underlying reef habitat, and these analyses assessed whether these

Table 1 Species of reef fish included in the three fish categories for this study

Grunts Haemulidae	
Black Margate	*Anisotremus surinamensis*
Porkfish	*A. virginicus*
Margate	*Haemulon album***
Tomtate	*H. aurolineatum**
Caesar grunt	*H. carbonaroum*
Smallmouth grunt	*H. chrysargyreum*
French grunt	*H. flavolineatum*
Spanish grunt	*H. macrostomum*
Cottonwick	*H. melanurum*
Sailor's choice	*H. parra**
White grunt	*H. plumieri***
Bluestriped grunt	*H. sciurus**
Striped grunt	*H. striatum*
Snapper Lutjanidae	
Mutton snapper	*Lutjanus analis**
Schoolmaster	*L. apodus***
Blackfin snapper	*L. buccanella**
Cubera snapper	*L. cyanopterus***
Gray snapper	*L. griseus***
Dog snapper	*L. jocu***
Mahogany snapper	*L. mahogoni*
Lane snapper	*L. synagris**
Yellowtail snapper	*Ocyurus chrysurus**
Combined fish	
All Haemulidae and Lutjanidae (above)	
Rock hind	*Epinephelus adscensionis**
Red hind	*E. guttatus***
Goliath grouper	*E. itajara***
Red grouper	*E. morio***
Nassau grouper	*E. striatus***
Black grouper	*Mycteroperca bonaci***
Yellowmouth grouper	*M. interstitialis***
Gag	*M. microlepis***
Scamp	*M. phenax***
Tiger grouper	*M. tigrinus*
Yellowfin grouper	*M. venenosa***
Hogfish	*Lachnolaimus maximus**

Note that we only included fish of legally exploitable size for each species. Fish with a single asterisk did not meet the U.S. Federal standard of being overfished in 1996, whereas fish with two asterisks did meet this standard (Ault et al. 1998)

factors were important to fish density change in reserves relative to reference reefs. The RP/RA and HI/HA ratios were determined from habitat maps in ArcView GIS Version 3.1 compiled by NOAA and the Florida Marine Research Institute. The Conch Reef "research only" SPA and the Conch Reef SPA were combined and treated as one reserve in our analyses because they shared a common boundary. Also, because the larger Western Sambo ER encompassed three reef types (fore reef, offshore patch reef, and inshore patch reef), we treated each reef type as a separate reserve in the analyses. Data for each reserve are shown in Table 2. All statistical tests were performed using Minitab Version 13.31.

Results

For total combined exploitable-sized reef fish, a significant majority of reserves (22 of 24, Table 3) exhibited greater rates of density change than their corresponding reference reefs ($p < 0.00005$, Sign test). In the ANCOVA analysis, two reserves exhibited significantly greater rates of fish density change than their reference reefs and no reserve had significantly lower rates of fish density change than reference reefs (Table 3).

For exploitable-sized grunt, 16 of 24 reserves exhibited greater rates of density change than their corresponding reference reefs (Table 3), which was not statistically significant ($p = 0.15$, Sign test). In the ANCOVA analysis, 1 reserve exhibited a significantly greater rate of fish density change than its reference reefs and no reserve had significantly lower rates of fish density change than reference reefs (Table 3).

For exploitable-sized snapper, a significant majority of reserves (22 of 24, Table 3) exhibited greater rates of density change than their corresponding reference reefs ($p < 0.00005$, Sign test). In the ANCOVA analysis, ten reserves exhibited significantly greater rates of fish density change than their reference reefs and no reserve had significantly lower rates of fish density change than reference reefs (Table 3). Note that both of the inshore patch reef reserves and six of eight reserves located in the middle Florida Keys exhibited significantly higher rates of change in snapper density than their corresponding reference reefs (Table 3).

There were no statistically significant relationships between RDC for snapper and grunt versus either the RP/RA ratio or the HI/HA ratio. For the combined exploitable-sized reef fish there was no significant

Table 2 Information on the sanctuary protection areas (*SPAs*) used in this study

SPA	Latitude/longitude (N/W)	Florida Keys region	Reef type	RP/RA (km^{-1})	HI/HA (km^{-1})	Years data not available
Carysfort reef	25.22/−80.21	Upper	Fore	1.70	1.24	′99
The Elbow	25.14/−80.26	Upper	Fore	3.85	4.05	′99
Dry rocks	25.12/−80.30	Upper	Off. Patch	7.96	2.29	′94–′96, ′99
Grecian rocks	25.11/−80.31	Upper	Off. Patch	5.48	1.17	
French Reef	25.04/−80.35	Upper	Fore	5.98	4.91	
Molasses Reef	25.01/−80.37	Upper	Fore	3.90	3.53	
Conch Reef	24.95/−80.46	Middle	Fore	4.43	3.97	
Davis Reef	24.92/−80.51	Middle	Fore	6.13	5.20	
Hen and Chickens	24.94/−80.55	Middle	Mid. Chan.	5.72	0.00	
Cheeca Rocks	24.90/−80.62	Middle	Mid. Chan.	8.43	7.86	′94–′96
Alligator Reef	24.85/−80.62	Middle	Fore	4.03	1.23	
Tennessee Reef	24.77/−80.75	Middle	Fore	5.68	2.00	
Coffins Patch	24.69/−80.97	Middle	Fore	4.00	1.36	′94–′96
Sombrero Key	24.63/−81.11	Middle	Fore	5.04	4.00	
New Found Harbor	24.62/−81.39	Lower	Insh. Patch	6.86	0.00	′94–′96
Looe Key (Res)	24.57/−81.39	Lower	Off. Patch	5.06	1.25	′94–′96
Looe Key (SPA)	24.55/−81.41	Lower	Fore	3.25	1.19	
Eastern Sambo	24.49/−81.66	Lower	Fore	4.88	3.91	
Western Sambo	24.48/−81.71	Lower	Fore	0.65	1.62	
Western Sambo	24.50/−81.71	Lower	Off. Patch	0.65	0.00	′94–′96
Western Sambo	24.55/−81.70	Lower	Insh. Patch	0.65	0.00	′99
Eastern Dry Rocks	24.46/−81.84	Lower	Fore	6.35	5.55	
Rock Key	24.46/−81.86	Lower	Fore	7.37	6.70	
Sand Key	24.46/−81.88	Lower	Fore	3.36	2.91	′00

"Years data not available" refers to years in which there was no data for that SPA and/or corresponding reference reefs

relationship between RDC and the RP/RA ratio. A weak linear relationship was found for the RDC and HI/HA ratio ($p = 0.05$, $T = -2.08$, $R^2 = 0.126$, Fig. 2) expressed by:

$$\mathrm{RDC} = 0.119 - 0.0134\mathrm{HI/HA}.$$

Discussion

This study tested whether no-take marine reserves had greater changes in exploitable fish density than reference reefs for commonly exploited fish species in the Florida Keys. This study also determined whether reserve size, and placement relative to the underlying reef habitat, influenced the rate at which fish density changed in reserves relative to reference reefs. This paper addresses several key landscape ecology issues and research priorities identified by Wu and Hobbs (2002) including integrating basic research and applications, understanding how spatial patterns influence ecological processes, optimizing landscape design for conservation management purposes and including studies from aquatic environments.

Our results indicate that most reserves exhibited higher rates of fish density change than their corresponding reference reefs for exploitable sized snapper and total combined exploitable reef fish. Ten of 24 reserves exhibited significantly greater rates of change in exploitable snapper density compared with reference reefs. These results support the prediction that exploitable fish densities would increase within marine reserves in the Florida Keys relative to reference reefs, and is consistent with results showing increased abundance of yellowtail snapper *Ocyurus chrysurus* (a numerically dominant snapper species)

Table 3 Rates of density change of exploitable sized fishes in reserves and corresponding reference reefs for grunt, snapper, and total combined fish (grunt, snapper, grouper, and hogfish)

SPA	Density change rate grunts SPAs	Density change rate grunts reference	Significance	Density change rate snapper SPAs	Density change rate snapper reference	Significance	Density change rate Total fish SPAs	Density change rate Total fish reference	Significance
Carysfort reef	0.0103	−0.0013	ns	0.044	0.0167	ns	0.0364	0.0112	ns
The Elbow	−0.0123	−0.0013	ns	0.149	0.0167	$p = 0.015$	0.0676	0.0112	ns
Dry rocks	0.0603	0.0419	ns	0.0032	0.0021	ns	0.0553	0.0397	ns
Grecian rocks	0.2058	0.0419	ns	0.0088	0.0021	ns	0.2208	0.0397	ns
French reef	0.0504	−0.0013	ns	0.0078	0.0167	ns	0.1004	0.0112	ns
Molasses reef	0.0821	−0.0013	ns	0.0696	0.0167	ns	0.0848	0.0112	ns
Conch reef	−0.1557	−0.0016	ns	0.1484	−0.0137	$p = 0.028$	−0.0304	0.0156	ns
Davis reef	0.0155	−0.0016	ns	0.2091	−0.0137	$p = 0.010$	0.051	0.0156	ns
Hen and chickens	0.1217	0.1026	ns	0.2267	0.0164	$p = 0.001$	0.1693	0.0968	ns
Cheeca rocks	0.0604	0.1026	ns	0.2771	0.0164	$p = 0.005$	0.1151	0.0968	ns
Alligator reef	0.2058	−0.0016	$p = 0.047$	0.2259	−0.0137	$p = 0.001$	0.2411	0.0156	$p = 0.034$
Tennessee reef	−0.0107	−0.0016	ns	0.0586	−0.0137	ns	0.0515	0.0156	ns
Coffins patch	0.2418	−0.0016	ns	0.0109	−0.0137	ns	0.2204	0.0156	ns
Sombrero key	0.0671	−0.0016	ns	0.2411	−0.0137	$p = 0.001$	0.1413	0.0156	ns
New found harbor	0.1322	−0.0495	ns	0.174	−0.0306	$p = 0.001$	0.1612	−0.0578	ns
Looe key (research only)	0.1147	0.0151	ns	0.0725	−0.0195	ns	0.1382	−0.0078	ns
Looe key (SPA)	−0.0248	−0.043	ns	0.144	−0.0003	$p = 0.001$	0.0934	−0.0391	$p = 0.048$
Eastern sambo	0.0309	−0.043	ns	0.0349	−0.0003	ns	0.0637	−0.0391	ns
W. sambo (fore reef)	−0.0655	−0.043	ns	0.0595	−0.0003	ns	−0.0105	−0.0391	ns
W.sambo (offshore patch)	−0.0511	0.0151	ns	0.1345	−0.0195	ns	0.0536	−0.0078	ns
W. sambo (inshore patch)	−0.1075	−0.0495	ns	0.1427	−0.0306	$p < 0.0005$	−0.0378	−0.0578	ns
Eastern dry rocks	0.0352	−0.043	ns	0.0612	−0.0003	ns	0.0574	−0.0391	ns
Rock key	−0.1176	−0.043	ns	−0.012	−0.0003	ns	−0.0518	−0.0391	ns
Sand key	−0.0370	−0.043	ns	0.1011	−0.0003	ns	0.0318	−0.0391	ns

Significance refers to a significant interaction between year and status (reserve and reference) in the ANCOVA analysis, indicating that density increased at a significantly faster rate within reserves relative to reference reefs

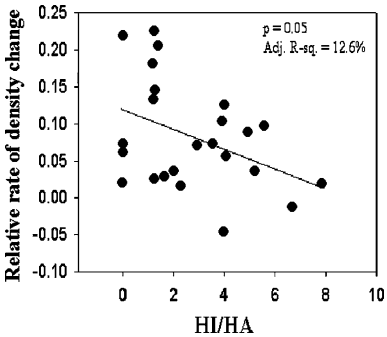

Fig. 2 Relative rate of density change versus HI/HA for combined exploitable reef fish. Relative rate of density change is the rate of density change in reserves minus the rate of density change in reference areas. HI/HA is the perimeter of the reserve that intersects reef habitat divided by the area of reef habitat within the reserve

and "combined grouper species" within reserves relative to reference areas (Ault et al. 2006; J.A. Bohnsack, unpublished data).

While correlation was relatively low, we found a significant negative relationship between RDC and HI/HA ratio for total combined exploitable sized reef fishes. This relationship may offer some support for the idea that reserves which have boundaries that correspond to natural reef habitat boundaries may have higher recovery rates than reserves in which the boundaries intersect reef habitat. Reef fish may be more likely to cross from reserves into fishing grounds where a reserve boundary crosses reef habitat. The relatively low adjusted R-squared value observed indicates that the HI/HA ratio did not explain much of the variation in RDC for combined exploitable fish. Therefore, overall reserve size and placement did not affect fish recovery that much, suggesting that other factors were more important for fish recovery within reserves.

Relative rate of density change for combined exploitable fish decreased in response to increasing the HI/HA ratio, but did not respond to the RP/RA ratio. This suggests that reef habitat boundaries may have been relatively impermeable to fish movement for combined exploitable fish, and does not support the permeable habitat boundary scenario. Our study did not address fish movement directly, however, and information regarding adult fish movement, and whether reserve shape influences movement, are important landscape ecology concerns for designing effective reserves (Kupfer 1995; Griffiths and Wilke 2002). Information regarding species movement could be key to successfully integrating a reserve into an existing ecosystem (Kupfer 1995). Determining whether reef habitat boundaries are permeable or impermeable to fish movement may also be very useful in determining where to place reserves.

Studies examining fish movement patterns directly have shown mixed results. For example, some snapper and grunt species may school over reefs and be relatively inactive during the day, but may forage away from the reef nocturnally (Hobson 1973). Samoilys (1997) demonstrated that coral trout *Plectropomus leopardus* showed strong site attachment to relatively small home ranges, but were not restricted to these home sites and could range over several kilometers. Fish and Savitz (1983) tracked four species of freshwater fish and demonstrated that each species had different home range sizes and habitat preferences. Zeller (1997) tracked coral trout, *P. leopardus*, and demonstrated that the shape and size of their home range is affected by the seascape characteristics of the reefs they inhabit. Zeller and Russ (1998) demonstrated low flux across a reserve boundary for coral trout, *P. leopardus.* Lowe et al. (2003) demonstrated that kelp bass, *Paralabrax clathratus*, preferred certain habitats within a marine reserve and concluded that reserve boundaries that corresponded with natural habitat boundaries may help limit kelp bass movement out of the reserve.

Further studies using acoustic fish tracking or mark-recapture studies could be used to compare fish movements in habitats with different landscape (seascape) characteristics and test ideas about potential retention within marine reserves (Griffiths and Wilke 2002). This would be an important way to test whether fish were spilling over from no-take reserves as well (Sale et al. 2005). For example, comparisons of fish tracked on continuous reefs versus patch reefs could be used to predict fish retention within different hypothetical reserves of the same area (compare Fig. 1b, d) or between different reef types. Tracking experiments could also be conducted on species with different migratory characteristics to determine how they respond to the different seascapes.

The size, shape and placement of a reserve may influence fish responses. Reserve size alone may not matter for some species, which may explain some of the conflicting results within the literature. All else

being equal, larger reserves would tend to have smaller perimeter to area ratios (RP/RA), which may explain results showing that large reserves were more effective in promoting fish recovery (Edgar and Barrett 1999) as predicted by Polacheck (1990) and DeMartini (1993), particularly for more mobile species. However, small reserves have also been shown to be effective in accumulating fish density and biomass, despite having small perimeter to area ratios (Russ and Alcala 1996a, b; Roberts and Hawkins 1997, 2000; Halpern 2003). Small reserves are more likely to benefit fish species with small home ranges and high habitat specificity (Friedlander 2001), and perhaps reserves with boundaries conforming to natural habitat edges can better protect these species than larger reserves where reserve boundaries cross reef habitat (compare Fig. 1a, b). Our results provide some evidence that reducing reserve boundary intersections with reef habitat may improve fish protection and conservation, but this may also reduce spillover of fish into adjacent fishing grounds, which may be a key reserve goal for supporting local fisheries (Halpern and Warner 2003; Neigel 2003; Sale et al. 2005). Intermediate-sized reserves that retain enough fish to be self-sustaining but provide some benefit to surrounding fisheries through export of larvae and spillover of adults may be ideal (Halpern and Warner 2003).

There are other issues to consider related to reserve placement and size. Protecting mass spawning sites is very important (Roberts et al. 2003). Larger reserves would tend to have larger populations which may be more resilient to local perturbations, and that are less likely to go extinct locally (Sale et al. 2005). However, many geographically dispersed reserves dilute the risk of complete loss in the event of catastrophic local events such as oil spills, harmful algal blooms, hurricanes and other large scale catastrophes (Simberloff and Abele 1982). For example, a river changed course in Washington State, completely eliminating the protected razor clams *Siliqua patula* in one of three regional reserves (Roberts and Hawkins 2000). If this had been a single reserve, all of the clams under protection may have been lost. Allison et al. (2003) advocate setting aside additional protected habitat as "insurance" during reserve planning in order to compensate for future catastrophic losses that occur over the long-term.

Law enforcement may be easier with a single large reserve than with multiple small and more widely spaced reserves (Roberts and Hawkins 2000; Halpern and Warner 2003). On the other hand, widely dispersed small reserves may be less disruptive to fishermen and more acceptable to the public, and therefore easier to establish (Roberts and Hawkins 2000; Halpern and Warner 2003).

A key component of preserving species diversity within a region is to include many or all habitat types (Simberloff and Abele 1982). This goal can be accomplished by establishing a network of small reserves that protect separate habitats or by a large reserve that encompasses multiple habitats in close proximity. Either approach can be used to protect habitats important to a species at different times during its life cycle (Rowley 1994) although their effectiveness can be influenced by spatial proximity and vulnerability of populations to exploitation during periods of transition between habitats.

Although marine reserve sites are often chosen opportunistically (Roberts 2000), most reserves seem to protect fish within their borders regardless of size or placement (Halpern 2003). Managers should weigh tradeoffs between reserve size and number, and may want to consider where reserve boundaries are placed in future reserve designs.

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