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Links between sex change and fish densities in marine protected areas

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ABSTRACT

Sex change is widespread among marine fishes, including many species that are fished heavily, and is thought to be of conservation concern under some circumstances. As such, an important question in conservation is whether the implementation of marine protected areas (MPAs), which is a commonly used marine conservation tool, works as effectively for sex-changers as for non-sex-changers. To address this issue, we used meta-analyses of the ratio of fish abundances inside vs. outside MPAs to determine whether sex change affects the extent to which fish densities respond to protection. When all data were considered, there were similar responses to protection irrespective of reproductive mode. However, when analyses were restricted to older reserves (at least 10 years' protection), female-first sex-changers consistently benefited from protection. Non-sex-changers and male-first sex-changers showed more variable responses to protection and, as a result, there were no significant differences between fish with different reproductive modes in their overall response to protection. The same results were observed when the effects of fisheries status (targeted vs. not targeted) were controlled. Our results support the use of MPAs as important components of conservation and demonstrate that old reserves are most consistently beneficial to female-first sex-changing species. Finally, our results highlight the fact that some effects of protection are only detectable after several generations.

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1. Introduction

There is evidence that the behaviour, ecology and life histories of species can affect the extent to which they benefit from protection from exploitation (DeMartini, 1993; Mosqueira et al., 2000; Gerber et al., 2002; Micheli and Halpern, 2005; Mumby et al., 2006; Barrett et al., 2007). A particularly interesting feature of many marine species, unlike terrestrial vertebrates, is that many change sex naturally over the course of their lives (Warner, 1984; Devlin and Nagahama, 2002). Among fish, sex change in either direction (female-first or male-first) has been documented, although female-first is more common, with examples from groupers, wrasses, parrotfish and seabreams (Teleostei: Serranidae, Labridae, Scaridae and Sparidae) (Robertson and Warner, 1978; Warner, 1984; Buxton, 1990; Heemstra and Randall, 1993). Examples of male-first sex

change include anemonefishes, shads and snooks (Teleostei: Pomacentridae, Clupeidae and Centropomidae) (Godwin, 1994; Blaber et al., 1999; Taylor et al., 2000).

It is of interest to know whether reproductive mode affects species' response to conservation measures because there is a debate surrounding whether or not sex change increases the vulnerability of species to recruitment failures due to overfishing (Bannerot et al., 1987; Huntsman and Schaaf, 1994; Jennings and Lock, 1996; Vincent and Sadovy, 1998; Côté, 2003; Hawkins and Roberts, 2003; Alonzo and Mangel, 2004, 2005; Molloy et al., 2007a). It has been hypothesised that size-selective fishing may disproportionately kill members of the second and larger sex, thereby skewing sex ratios leading to egg or sperm limitation. However, if fish are able to adjust their size-at-sex-change in response to fishing-induced changes in social structures, sex ratios may be buffered, thereby reducing susceptibility to recruitment failure (Buxton, 1993; Hawkins and Roberts, 2003; Alonzo and Mangel, 2004; Molloy et al., 2007a). The extent to which sex change affects vulnerability to recruitment overfishing in reality remains unknown, but it is notable that many endangered marine fish species are sex-changers (Anon., 2002; IUCN, 2004; CITES, 2005).

The aim of this study was to investigate whether marine protected areas (MPAs) are equally effective at protecting sex-changing and non-sex-changing species. MPAs are one of the most widespread tools used to protect marine resources from human exploitation, and their generally positive effects on fish populations have been well documented (e.g. Mosqueira et al., 2000; Halpern and Warner, 2002; Gell and Roberts, 2003; Micheli et al., 2004; Williamson et al., 2004; Goñi et al., 2006; Shears et al., 2006). We used meta-analyses of 1043 marine fish abundance estimates from paired protected and fished areas. Meta-analyses enable the amalgamation of related empirical studies, providing a quantitative estimate of the overall effect (Gurevitch et al., 2001; Gurevitch and Hedges, 2001). Since it is known that species that are the target of local fisheries show greater responses to protection (Mosqueira et al., 2000; Micheli et al., 2004), we carried out our analysis of reproductive mode separately on targeted and non-targeted fish. Our results show that female-first sex-changers benefit most consistently from protection.

2. Methods

2.1. Data collection and manipulation

Analyses were based on the database used by Mosqueira et al. (2000), updated with data from 11 additional studies (Bell, 1983; Buxton and Smale, 1989; La Mesa and Vacchi, 1999; Paddack and Estes, 2000; Macpherson et al., 2002; Denny et al., 2003; García-Charton et al., 2004; Ashworth and Ormond, 2005; Parnell et al., 2005; Claudet et al., 2006; La Mesa et al., 2006). The studies used are summarised in Table 1. We used most of the study selection criteria described in Mosqueira et al. (2000); however, to increase sample sizes, we have also included studies conducted in areas with minimal, well-regulated fishing (e.g. García-Charton et al., 2004), and studies that recorded the densities of a subset of the fish community (Bell,

1983; Buxton and Smale, 1989; Paddack and Estes, 2000; Ashworth and Ormond, 2005; Parnell et al., 2005; La Mesa et al., 2006). Studies by Macpherson et al. (2002) and García-Rubies and Zabala (1988) were conducted in the same reserve, as were Bell (1983), Dufour et al. (1995), La Mesa and Vacchi (1999) and La Mesa et al. (2006). All six studies were included since the data reported in Macpherson et al. (2002) and Dufour et al. (1995) were obtained more than eight years after those of García-Rubies and Zabala (1988) and Bell (1983), respectively. Furthermore, Macpherson et al. (2002) included additional sites to those in García-Rubies and Zabala (1988). La Mesa and Vacchi (1999) and La Mesa et al. (2006) surveyed different fish species. Data from several other studies could not be included because densities inside and outside and/or species-level data were not available, transect or point-count surveys were not used, and/or because the marine protected areas were not enforced (Harmelin et al., 1995; Johnson et al., 1999; Evans and Russ, 2004; Kamukuru et al., 2004; Kaunda-Arara and Rose, 2004; Williamson et al., 2004; Bonaca and Lipej, 2005; Guidetti et al., 2005; McClanahan and Graham, 2005; Ault et al., 2006; Williams et al., 2006).

For most species, reproductive mode (non-sex-changer, male-first sex-changer, female-first sex changer or simultaneous hermaphrodite) was reported unequivocally and in accordance with the criteria described in Sadovy and Shapiro (1987). For the remaining species, we assumed non-sex-change if studies had been undertaken that were likely to have revealed hermaphroditic function and had performed gonadal histological analyses (Sadovy and Shapiro, 1987) but did not report reproductive mode. If no such studies were found, reproductive mode was assumed to be similar to that of congeners if the reproductive mode was known for more than one congener and was uniform. When the reproductive mode of congeners was not uniform or was unknown, the reproductive mode of the relative was not inferred and the species was excluded from analyses involving reproductive mode. Because they do not change sex, simultaneous hermaphrodites were excluded from comparisons of sex-changing and non-hermaphroditic fishes. Analyses restricted to species whose reproductive mode was known unequivocally yielded identical results to those including species with inferred reproductive modes; we therefore only report results from the latter analyses.

Abundance was recorded as the mean number of individuals per unit area inside and outside marine reserves. Some studies reported more than one abundance estimate for a single species in different parts of a reserve or non-reserve site. These data were aggregated to give a single overall weighted mean abundance measure for inside and outside reserve areas, using the method described in Mosqueira et al. (2000). Paddack and Estes (2000) reported paired inside–outside fish densities from three different reserves; each pair was included separately in our database. García-Charton et al. (2004) reported data from four reserves but they were not paired with data from neighbouring non-reserve sites. In this case, densities within each reserve were included separately and compared to the same averaged non-reserve density. Since the resulting density ratios for the four reserves are not independent, we repeated all analyses without these data

Table 1 – A summary of studies included in the analysis					
Reserve name and country	Protection year	Area protected (ha)	Location	Fishing status	Source
South El Ghargana, Nabq Managed Resource Protected Area, Egypt	1995/7	120	Indo-Pacific	Prohibited	Ashworth and Ormond (2005)
Banyulus-Cerbère, France	1979/1	150	Mediterranean	Limited to designated areas	Bell (1983)
Tsitsikamma Coastal National Park, South Africa	1964/20	30,000	Atlantic	Prohibited	Buxton and Smale (1989)
Côte Bleue Marine Park, France	1983/18	295	Mediterranean	Prohibited	Claudet et al., 2006
Goat Island, New Zealand	1975/13	500	Indo-Pacific	Prohibited	Cole et al. (1990)
Poor Knights, New Zealand	1998/4	24,100	Indo-Pacific	Prohibited	Denny et al., 2003
Banyulus-Cerbère, France	1979/12	150	Mediterranean	Limited to designated areas	Dufour et al. (1995)
Maria Island and others, Tasmania	1991/6	1655	Indo-Pacific	Limited to designated area	Edgar and Barrett, 1999
Scandola, Corsica	1975/13	509	Mediterranean	Limited to designated area	Francour (1991)
Cabo de Gata, Spain	1987/9	12,200	Mediterranean	Prohibited	García-Charton et al. (2004)
Cabo de Palos, Spain	1995/1	1898			
Cabrera Island, Spain	1991/5	8703			
Mallorca, Spain	1990/6	4000			
Medes Islands, Spain	1983/5	93.2	Mediterranean	Prohibited	García-Rubies and Zabala (1988)
Cousin Island, Seychelles	1968/26	124	Indo-Pacific	Prohibited	Jennings et al. (1995)
Ustica Island Marine Reserve, Italy	1986/10	60	Mediterranean	Zoned: prohibited to artisanal fishing	La Mesa and Vacchi (1999)
Ustica Island Marine Reserve, Italy	1986/16	60	Mediterranean	Zoned: prohibited to artisanal fishing	La Mesa et al. (2006)
Passe de Longogori, Île de Mayot	1992/3	400	Indo-Pacific	Prohibited	Letourneur (1996)
Medes Island, Spain	1983/16	93	Mediterranean	Prohibited	Macpherson et al. (2002)
Malindi NP, Kenya	1968/23	630	Indo-Pacific	Prohibited	McClanahan (1994)
Watamu NP, Kenya	1972/19	1000			
Kisite NP, Kenya	1973/18	2800			
Kisite NP, Kenya	1974/22	1000	Indo-Pacific	Prohibited	McClanahan et al. (1999)
Chumbe Island, Tanzania	1991/5	50			
Hopkins Marine Life Ridge, USA	1984/11	140	Pacific	Prohibited	Paddack and Estes (2000)
Point Lobos State & Ecological Reserve, USA	1973/22	780		Prohibited	
Big Creek Marine Ecological Reserve, USA	1994/1	518		Prohibited	
San Diego-La Jolla Ecological Reserve, USA	1971/21	216	Pacific	Prohibited	Parnell et al. (2005)
Barbados, Caribbean	1981/11	66	Caribbean	Cast netting for Clupeids only	Rakitin and Kramer (1996)
Ras Mohamed, Egypt	1975/15	17,100	Indo-Pacific	Prohibited	Roberts and Polunin (1992)
Saba Island, NL Antilles	1987/6	120	Caribbean	Zoned: prohibited to unlimited	Roberts (1995)

Protection year: the year when protection was effectively enforced, where applicable/the number of years of protection at time of study.

and report the results only when they differ from analyses including them.

Maximum length refers to total length (TL) reported for a species in FishBase (Froese and Pauly, 2007) and was checked against additional sources where possible (Humann and Deloach, 2002; Allen et al., 2003). Where necessary, other length measurements (e.g. standard length) were converted to total length using the equations reported in FishBase. In the rare cases where length relationships were not available for a species, maximum length was inferred using relationships from a similarly-sized congener.

Fisheries status (i.e. targeted or non-targeted) was assigned to each species using information from source studies, which ensured that the categorisation was appropriate for the population studied. Species that were caught as by-catch, of minor importance to fisheries or whose importance to fisheries was not reported or known were excluded from all analyses where data were grouped by fisheries status since the fishing levels on these species were unclear.

The effectiveness of marine reserves is known to increase with age (Russ and Alcala, 1996; Micheli et al., 2004; McClanahan and Graham, 2005; Barrett et al., 2007); a similar effect is observed in our dataset (Molloy et al., unpublished data). Therefore, we repeated all analyses using only data from reserves that had been protected for at least 10 years. Micheli et al. (2004), found that the magnitude of response to

protection by piscivorous fish was six times greater in reserves that were at least 10 years old, compared to those in younger reserves. This cut-off point also provided a good trade-off between the magnitude of response to protection and sample size, which became too small for analyses restricted to even older reserves. McClanahan et al. (1999) and McClanahan (1994) reported fish densities averaged across several reserves that had been protected for different durations. Variation in reserve age was negligible in McClanahan (1994) (19–23 years), so data from this study were included in all analyses. Reserve age varied greatly in McClanahan et al. (1999) (5 and 22 years), so data from this study were not included in analyses using only data from older reserves.

2.2. Effect size metric and data transformation

Meta-analyses require that data be standardized along a common scale of effect. For this study, the effect size was taken as the natural logarithm of response ratio (ln R), i.e. the relative difference between fish abundance inside and outside a reserve (see also Mosqueira et al., 2000; Côté et al., 2001). With this scale, values greater than 0 indicate greater abundances inside than outside reserves. ln R was used instead of R because it linearises the metric so that changes in the denominator and numerator are treated equally, and yields better sampling distributions (Hedges et al., 1999).

Data transformation were necessary in order to use the natural logarithm of effect sizes involving abundance estimates of zero (i.e. where a species was absent either inside or outside a marine reserve). Preliminary trials in which constant values (1, 0.1, 0.001 and 0.0001), and percent values (1%, 0.1%, 0.01% and 0.001%) of total abundance estimates for each species were added to all abundance estimates revealed that adding 0.0001 to all estimates had the smallest impact on overall ln R.

In meta-analyses, effect sizes are often weighted by the inverse of the sample variance to incorporate a measure of the robustness of each effect size (Rosenberg et al., 2000). However, the use of variance in this study resulted in weightings that differed by an order of magnitude, which we felt was an unrealistic reflection of variation in effect size robustness. Instead, we weighted each response ratio by the natural logarithm of the area that had been surveyed to generate the response ratio (see also Mosqueira et al., 2000; Côté et al., 2001). In addition to being more biologically realistic, this method allowed the inclusion of studies that did not report error measures.

It is possible that closely related species might respond similarly to protection due to shared ancestral traits. To reduce this problem of phylogenetic non-independence, we calculated mean ln R for each genus within each study. For those genera that contained species exhibiting different reproductive modes (e.g. *Symphodus*), genus ln R were recalculated within each mode. Likewise, separate ln R were recalculated for congeners with different fisheries statuses for analyses involving only targeted or non-targeted genera.

2.3. Meta-analysis

An overall effect size for all genera (including those species whose reproductive modes was unknown), $\overline{\overline{\ln R}}$, was calculated as

$$\overline{\overline{\ln R}} = \frac{\sum_{i=1}^{n} w_i \ln R_i}{\sum_{i=1}^{n} w_i}$$

where w_i is the ln area surveyed and R_i the abundance ratio inside:outside reserves for genus i. A 95% bias-corrected bootstrapped confidence interval (CI) was calculated around $\overline{\overline{\ln R}}$ generated from 5000 iterations. For ease of interpretation, both $\overline{\overline{\ln R}}$ and CIs are presented back-transformed. The back-transformed response ratio ($\overline{\overline{R}}$) therefore represents the ratio of fish densities inside to outside the reserve. Following meta-anlaysis convention, the lower and upper limits of the CIs are presented. A significant benefit to protection was indicated when the lower limit of a (back-transformed) CI was greater than one. We used the statistic Q_r to test whether there was significant heterogeneity in effect sizes among genera (Rosenberg et al., 2000).

To compare how fish with different reproductive modes respond to protection, random-effects models were applied to data grouped by reproductive mode (i.e. mixed-effect models, Rosenberg et al., 2000). In each analysis, we sought to answer two questions: firstly, which of the groups, if any, show a significant response to protection? Secondly, do fish with different reproductive modes differ from one another in their response to protection? To answer the first question, for each reproductive mode an overall, group-specific, response ratio ($\overline{\ln R}$) was calculated with 95% bias-corrected bootstrapped CI. A significant benefit from protection was shown when a (back-transformed) CI was greater than one. To answer the second question, we used the statistic Q_M (Rosenberg et al., 2000) to test for overall and pair-wise differences in response ratios among groups. The significance of Q_M was determined using a randomisation procedure (Adams et al., 1997). Since targeted genera benefited significantly more than non-targeted genera ($Q_{M,1} = 9.54$, $p = 0.004$), all analyses involving reproductive modes were repeated within fisheries status.

All meta-analyses were conducted in MetaWin Version 2.0 (Rosenberg et al., 2000).

2.4. Additional analyses

We sought to determine whether any variables, in addition to fisheries status, explained significant amounts of variation in response to protection and, if so, whether they could have confounded our analyses of reproductive mode. The variables considered were: reserve study (grouped into 28 classes: one for each study of each reserve), survey method (two classes: line transects vs. point counts), and species-specific maximum body length (continuous). We used the Q_M statistic to test whether reserve study or survey method explained a significant amount of variation in response to protection. When this was the case, the distribution of reproductive mode across classes was investigated using log-likelihood G tests. G tests were used in preference to chi-square analyses due to the prevalence of low count data (Zar, 1999); all frequencies were $x + 1$ transformed to remove zero counts. When reproductive modes were not equally distributed across classes, the overall effect size of each class was correlated with the frequencies deviations (i.e. observed frequency minus expected frequency) within reproductive mode. A significant correlation for any reproductive mode would indicate that

the factor in question could have biased our analyses of reproductive mode.

We used a continuous-method meta-analysis to investigate the effect of species-specific maximum length (averaged for each genus within studies) on the response to protection. Specifically, we used weighted least-squares regressions (Rosenberg et al., 2000), which generated estimates of slope and intercept. The significance of the slope parameter was determined using randomisation tests. Maximum length data were log_{10}-transformed prior to analyses. To determine whether maximum length confounded analyses of reproductive mode, we tested for differences among reproductive modes in maximum length using Kruskal–Wallis χ^2 tests, the significance of which was assessed using Monte-Carlo simulations. Kruskal–Wallis tests were performed in SPSS (2006). Although few individuals will reach the species' maximum length, this metric provides a simple and widely-used means of comparing size-related differences among species.

2.5. Publication bias

Meta-analyses may be biased by a tendency for significant results to be published disproportionately often. As recommended by Begg (1994), we sought evidence for publication bias prior to analysis using a normal quartile plot (Wang and Bushman, 1998; Rosenberg et al., 2000). Although most data fell within the 95% confidence lines, there was a slight bias on each side of zero. However, this was due to a clustering of data points into three groups: small, intermediate and large lnR, which was the result of the data transformation necessary to include genera that were absent inside and outside marine reserves (see above).

3. Results

3.1. Distribution of reproductive modes

Data were collected from 23 studies yielding 1043 estimates of abundances inside and outside marine reserves for 438 species. Of these species, 25% were sex-changers, 18% were non-sex-changers, 1% was simultaneous hermaphrodites and the remaining 56% were species whose reproductive mode was not known. Of the sex-changers, 92% were female-first sex-changers, and 8% were male-first sex-changers.

3.2. Effect of reproductive mode on response to protection

Overall, fish showed no significant response to protection as indicated by the fact the confidence interval (CI) around the back-transformed overall response ratio ($\overline{R}$) overlaps one ($\overline{R} = 1.34$, CI = 0.97 to 1.84, $n = 592$). However, when only data from reserves that had been established for at least 10 years were considered, fish were nearly three times more abundant inside than outside reserves – a difference which was significant ($\overline{R} = 2.84$, CI = 1.76–4.66, $n = 231$). Significant heterogeneity existed among genera in their lnR ($Q_{T,591} = 86,099.18$, $p < 0.0001$), suggesting that all genera do not respond to marine reserves in either the same direction or to the same degree.

When taxa from all reserves were grouped by reproductive mode, all groups showed non-significant responses to protection (non-sex-changers: $\overline{R} = 2.01$, CI = 0.95–4.15, $n = 134$; female-first sex-changers: $\overline{R} = 1.16$, CI = 0.65–2.01, $n = 152$; male-first sex-changers: $\overline{R} = 1.03$, CI = 0.24–4.83, $n = 36$; Fig. 1a). However, when data from García-Charton et al. (2004) were excluded (see Section 2), female-first sex-changers showed a significant benefit from protection (non-sex-changers: $\overline{R} = 1.83$, CI = 0.73–4.91, $n = 91$; female-first sex-changers: $\overline{R} = 2.21$, CI = 1.21–4.20, $n = 112$; male-first sex-changers: $\overline{R} = 3.08$, CI = 0.56–15.93, $n = 20$). There was no difference among fish with different reproductive modes in their overall response to protection when all modes were considered together ($Q_{M,2} = 0.60$, $p = 0.74$), or in pair-wise comparisons (all $Q_{M,1} < 1.33$, all $p > 0.25$). In older reserves, only female-first sex-changers showed significant and consistent benefits from protection (non-sex-changers: $\overline{R} = 1.11$, CI = 0.33–3.69, $n = 50$; female-first sex-changers: $\overline{R} = 4.59$, CI = 1.94–12.14, $n = 58$; male-first sex-changers: $\overline{R} = 4.43$, CI = 0.37–47.59, $n = 13$; Fig. 1b), although there were no significant differences between reproductive modes in responses to protection ($Q_{M,2} = 3.55$, $p = 0.18$; pair-wise contrasts: all $Q_{M,1} < 3.36$, all $p > 0.07$).

When only targeted genera were considered across all reserves, non-sex-changers and female-first sex-changers were significantly more abundant inside reserves than outside (Fig. 2a). However, there were no significant differences in overall response to protection among reproductive modes ($Q_{M,2} = 4.32$, $p = 0.12$; pair-wise comparisons: all $Q_{M,1} < 4.02$, all $p > 0.05$). When only targeted taxa in older reserves were considered, female-first sex-changers again showed a significant and consistent benefit from protection (non-sex-changers: $\overline{R} = 2.25$, CI = 0.45–11.98, $n = 27$; female-first sex-changers: $\overline{R} = 5.67$, CI = 1.29–23.79, $n = 28$; male-first sex-changers: $\overline{R} = 0.62$, CI = 0.03–3.39, $n = 9$; Fig. 2b). However, there were no significant differences in overall responses to protection between reproductive modes ($Q_{M,2} = 2.17$, $p = 0.35$; pair-wise comparisons: all $Q_{M,1} < 2.32$, all $p > 0.15$). Among non-targeted genera, no reproductive modes responded significantly to protection (Fig. 2c and d), and there were no significant differences in effect sizes between fish with different reproductive modes ($Q_{M,1} = 0.30$, $p = 0.61$; our dataset contained no non-targeted male-first sex-changers). This result held when only data from older reserves were used.

3.3. Other potential correlates of response to protection

Reproductive modes were not equally distributed across reserve studies ($G_{2,7} = 146.24$, $p < 0.001$) or survey methods ($G_{2,1} = 22.46$, $p < 0.001$); however, neither of these variables confounded our analyses of reproductive mode. Genus response ratios varied significantly among reserve studies ($Q_{M,27} = 63.36$, $p = 0.0002$, $n = 592$). However, there was no correlation between the skew in frequencies of any reproductive mode within reserves and the overall effect sizes of reserves (all Pearson's $r < 0.262$ and > -0.268, all $p > 0.16$, all $n = 28$). This suggests that, for example, the positive effect of protection on female-first sex-changers was not observed simply because these genera happened to be more abundant in particularly effective reserves. Survey method did not explain a significant

(a) All reserves
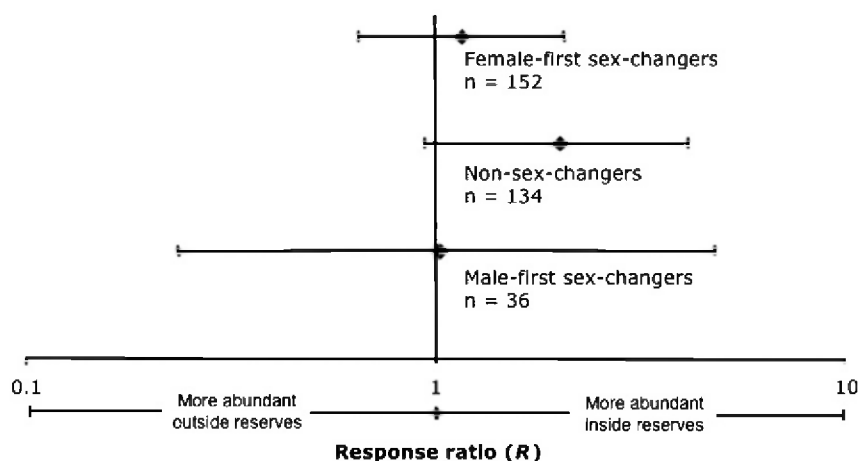
(b) Reserves with at least 10 years of protection
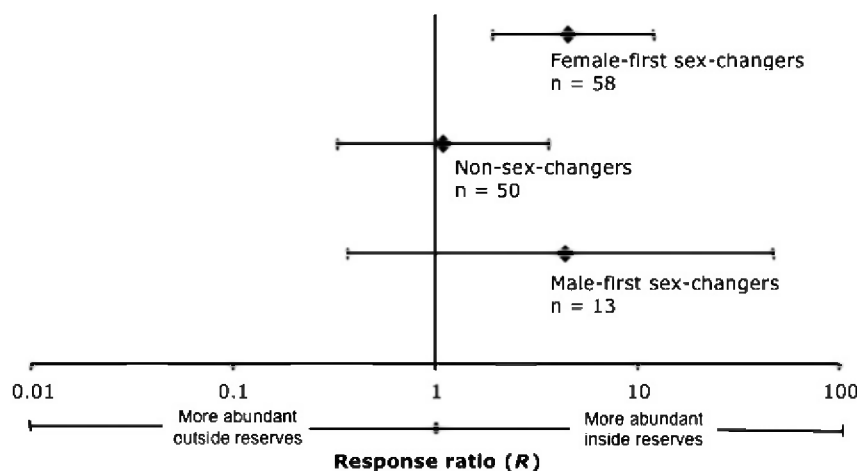
Fig. 1 – Ratios of abundance (response ratio, R) of non-sex-changing, female-first and male-first sex-changing genera in and out of all marine reserves (a), and marine reserves with at least 10 years of protection (b). Overall response ratios are shown ±95% bias-corrected bootstrapped confidence intervals, with sample sizes. Note that the log scale on the x-axis makes the CIs appear more symmetric than they really are (see Section 3).

amount of variation in genus response to protection ($Q_{M,1} = 0.77$, $p = 0.38$, $n = 409$).

Although species maximum length explained a significant amount of variation in genus response to protection ($Q_{M,1} = 4.82$, $p = 0.03$, $n = 570$), it did not confound our analyses of reproductive mode since there was no significant difference among reproductive modes in maximum length (Kruskal–Wallis $\chi_2^2 = 2.56$, Monte Carlo $p = 0.28$).

4.   Discussion and conclusions

The aim of this study was to test whether sex change influences the degree to which fish densities are affected by one of the most popular marine conservation measures – marine protected areas (MPAs). This question is important, given the ongoing debate surrounding the role of sex change in species' vulnerability to overfishing (Bannerot et al., 1987; Buxton, 1993; Huntsman and Schaaf, 1994; Vincent and Sadovy, 1998; Armsworth, 2001; Côté, 2003; Hawkins and Roberts,

2003; Alonzo and Mangel, 2004, 2005; Molloy et al., 2007a). Populations of female-first sex-changers were consistently more abundant within reserves, particularly in older (10+ years) reserves. Non-sex-changers and male-first sex-changers showed slightly weaker and, in the case of male-first sex-changers, more varied responses to protection. We also found particularly strong benefits for taxa that are targeted by local fisheries. Our results highlight the importance of testing for effects of protection using data from older reserves, which have had sufficient time for fish populations to recover from exploitation.

At first glance our results appear to be paradoxical since we show that female-first sex-changers respond more clearly to protection than other fishes, and yet there was no difference in the overall response to protection between taxa with different reproductive modes. The first observation comes from a comparison of the ratio of fish density in and out of reserves to a baseline of unity (1:1), which showed that female-first sex-changing species are consistently more abundant

(a) All reserves; targeted taxa
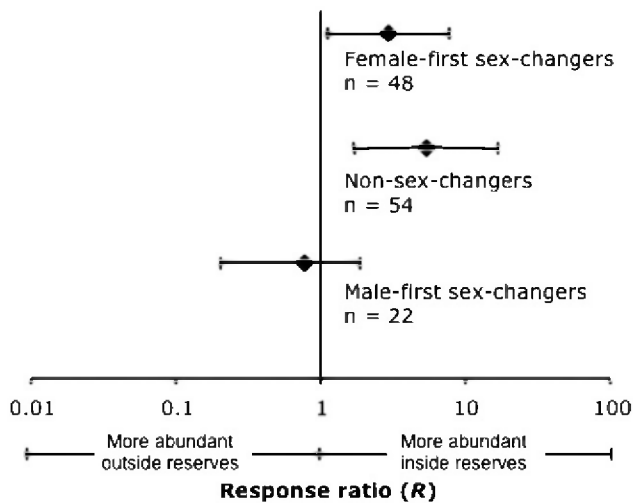
(b) Old reserves; targeted taxa
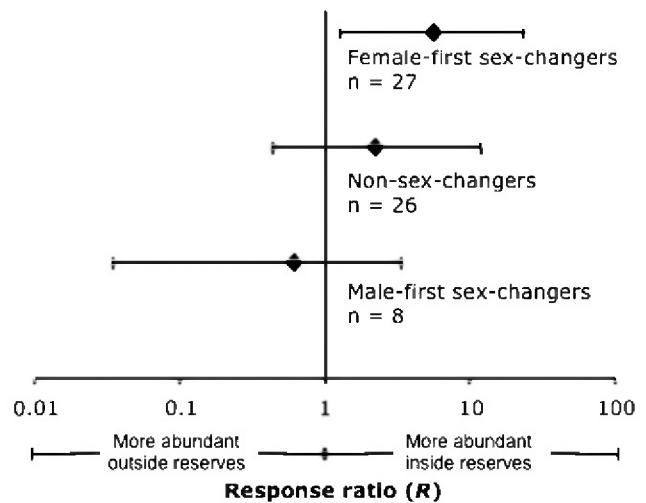
(c) All reserves; non-targeted taxa
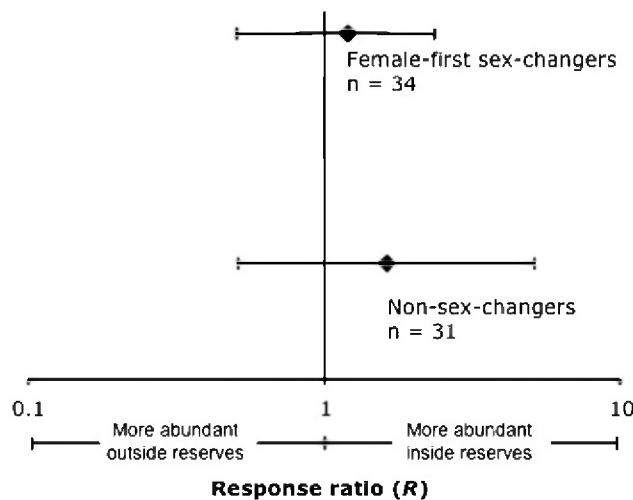
(d) Old reserves; non-targeted taxa
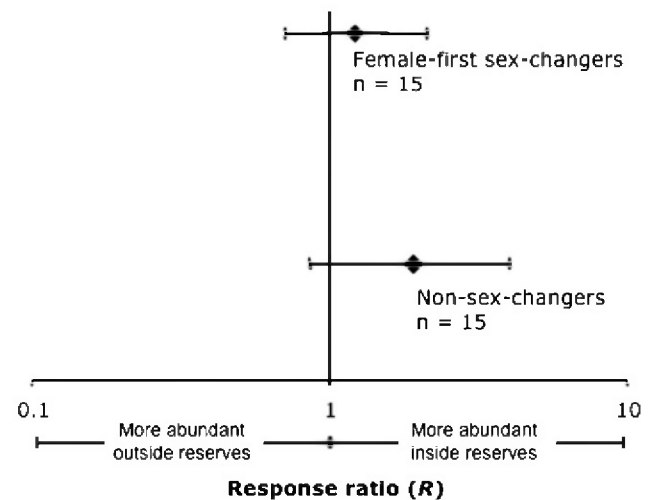
Fig. 2 – Ratios of abundance (response ratio, R) of targeted (a and b) and non-targeted (c and d) non-sex-changing, female-first and male-first sex-changing genera in and out of all marine reserves (a and c), and marine reserves with at least 10 years of protection (b and d). Overall response ratios are shown ±95% bias-corrected bootstrapped confidence intervals, with sample sizes.

within reserve boundaries. Non-sex-changers and male-first sex-changers showed weaker responses to protection, but these were not weak enough to differ significantly from those of female-first sex-changers. Taken together, these results mean that a marine park manager can expect that, given enough time, female-first sex-changers will benefit from protection. They cannot be as confident for non-sex-changers and male-first sex-changers, nor can they predict whether these two groups will benefit more or less than female-first sex-changers.

Duration of protection is an important determinant of the extent to which some fish populations recover from exploitation (Russ and Alcala, 1996; Micheli et al., 2004; McClanahan and Graham, 2005; Barrett et al., 2007). In our study, an overall significant benefit from protection was observed only when analyses were restricted to reserves established for at least

a decade. In these MPAs, fish were nearly three times more abundant inside reserve boundaries. Most notably, the abundance of female-first sex-changers was more than 4.5 times greater within old reserves, which was more than double the response observed when reserves of all ages were considered. The fact that the benefit of protection to female-first sex changers is particularly apparent in old reserves hints at a link between sex-change and life-history traits such as longevity, which have been shown to affect the time taken for reserve benefits to be observed (Roberts et al., 2001). More importantly, our results demonstrate the value of including reserve age in any assessment of MPA effectiveness.

A key variable known to affect both population declines and recovery from fishing is body size, either directly or through its correlation with age at maturity and other life history traits (Denney et al., 2002; Reynolds et al., 2005). We

found no difference between non-sex-changers and female-first sex-changers in mean body size, nor any difference in variation in maximum body size (Levene's $F = 2.41$, $p = 0.12$). If size and its correlates are the most important determinants of population response to protection, the similarity we observed in sizes across reproductive modes could explain the similarity in responses to protection of fish with different reproductive modes. There was a non-significant trend for female-first sex-changers to benefit more from protection than non-sex-changers. If future research shows that this trend is real, this would hint that specific features associated with this reproductive mode could lead to stronger population responses to protection. For example, female-first sex change is associated with female-biased sex ratios and haremic mating systems (Robertson and Warner, 1978; Warner and Robertson, 1978; Charnov, 1982; Warner, 1984; Buxton, 1990; Allsop and West, 2004; Molloy et al., 2007b). It would be interesting to examine the links between such traits and population dynamics.

A full understanding of how marine reserves affect sex-changing populations, and how such effects compare to non-sex-changers, requires information on how sex-specific sizes and sex ratios change after protection. Concerns regarding the impact of sex change on a species' vulnerability to overfishing are based on the fact that size-selective fishing disproportionately removes the larger sex and could skew sex ratios to the extent of sperm- or egg-limited recruitment (depending on the direction of sex change) (e.g. Bannerot et al., 1987; Huntsman and Schaaf, 1994; Milton et al., 1998; Alonzo and Mangel, 2004; Molloy et al., 2007a). Studies that report sizes and abundances inside and outside reserves rarely report sex-specific data. This scarcity of data prevented us from including sex ratios in our meta-analyses. When sufficient data are available, future studies could test the predictions that sex-changers should show greater sex-ratio differences across reserve boundaries than non-sex-changers, and that these differences between reproductive modes will be most pronounced in old reserves. The studies that are currently available indicate that sex ratios are more skewed towards the smaller sex outside than inside reserves in sex-changing (Buxton, 1993; Beets and Friedlander, 1998; Hawkins and Roberts, 2003) and size-dimorphic non-sex-changing species (Kamukuru and Mgaya, 2004). Testing these predictions will be challenging with the large number of species that are neither sexually dimorphic nor dichromatic.

Numerous sociological, ecological and behavioural characteristics are known, or predicted, to affect protection effectiveness (DeMartini, 1993; Beets and Friedlander, 1998; Mosqueira et al., 2000; Jennings, 2001; Gerber et al., 2002; Gerber and Heppell, 2004; Parnell et al., 2006; Salomon et al., 2006; Barrett et al., 2007). Similarly, the efficacy of MPAs also depends on reserve characteristics (Côté et al., 2001; Jennings, 2001; Micheli et al., 2004; Mayfield et al., 2005; Barrett et al., 2007). Reserve-specific determinants of effectiveness, such as reserve size and levels of poaching, did not confound our analyses of reproductive mode because there were no correlations between overall reserve effectiveness and the relative abundance of fish with each reproductive mode within reserves.

In summary, female-first sex-changing fishes benefit more consistently, in terms of abundance, from protection afforded by marine reserves than fish with other reproductive modes. This effect is particularly strong in older reserves. It remains to be determined whether sex change influences other demographic parameters of protected populations, such sex ratio, as well as the effectiveness of other management methods, such as regulating minimum legal catch sizes or limiting fishing seasons. Increasing minimum legal sizes, for example, would ensure that more individuals reproduce before capture, but it would also increase the size selectivity of a fishery. In the case of sex-changing species, this would mean more precise targeting of individuals of a single sex, and hence perhaps exacerbate problems associated with heavily biased sex ratios.

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