Effects of marine reserve protection on the mud crab *Scylla serrata* in a sex-biased fishery in subtropical Australia

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ABSTRACT: The impact of sex-biased fishing and marine reserve protection on the mud crab *Scylla serrata* was examined by comparing the catch rates (catch-per-unit-effort, CPUE), mean size, sex ratios and movement of crabs in 2 coastal marine reserves (1.9 and 5.7 km^2) and 4 fished non-reserve sites in subtropical Australia. Five years after closure, both marine reserves supported higher catch rates and a larger mean size of *S. serrata* than non-reserve sites. Males dominated catches of *S. serrata* in both marine reserves, where CPUE was at least twice as high within the reserves compared to non-reserve sites. Male crabs were also 10% larger in the reserves compared to adjacent fished areas, and of the total male catch, over 70% were equal to or greater than legal size compared to less than 50% outside the reserves. The sex ratio of *S. serrata* was skewed towards females in all non-reserve sites, which was most likely a result of the ban on taking female *S. serrata* in Moreton Bay. As only male crabs of ≥15 cm CW made up the *S. serrata* fishery in Moreton Bay, sex ratios of mature male and female crabs were examined, revealing a strong skew (2:1) towards mature males in both marine reserves. Of the 472 *S. serrata* captured in this study, 338 were tagged in the reserves in order to document movement of the crabs between the reserve and non-reserve sites. Of the 37 recaptured crabs, 73% were recorded inside the reserves, with some spillover (i.e. cross-boundary movement) of crabs recorded in fished areas. This study demonstrates the effectiveness of small (<6 km^2) marine reserves for sex-biased exploited fisheries species.

KEY WORDS: Marine reserves · *Scylla serrata* · Sex-biased fishery · CPUE · Sex ratio · Reserve size · Subtropical · Australia

INTRODUCTION

Due to the ongoing direct depletion of the world's marine resources as well as the indirect effects of fishing, no-take marine reserves are being promoted as an ecosystem-level management tool. No-take marine reserves (referred to as 'marine reserves' in this paper) prohibit extractive activities such as fishing, offering a

way to conserve marine biodiversity whilst at the same time sustaining fisheries (Roberts & Hawkins 2000, Ward et al. 2001, Halpern 2003, Lubchenco et al. 2003). Marine reserves provide an additional fisheries management tool that has the potential to dramatically reverse the detrimental effects of fishing (Dugan & Davis 1993, Roberts & Hawkins 2000). There is unequivocal evidence that fishing reduces the abun-

dance and size of the most reproductively valuable members of a population (Chapman & Kramer 1999, Edgar & Barrett 1999, Johnson et al. 1999, McClanahan et al. 1999, Chiappone et al. 2000, Willis et al. 2003, Williamson et al. 2004). Recent empirical evidence suggests that establishing well-designed and managed marine reserves can result in rapid increases in the size and abundance of once exploited species (see empirical studies within the following reviews: Gell & Roberts 2003, Halpern 2003, Lubchenco et al. 2003).

The species most likely to show dramatic responses to reserve protection will have limited movements, and age and size distributions that have been lowered by fishing pressure (Rowley 1994). The mud crab *Scylla serrata* (Forksal) is a large aggressive portunid crab largely fished throughout the Indo-Pacific region, and within Australia it occurs in tropical and warm water mangrove-lined estuaries from southern New South Wales north to Exmouth Gulf in Western Australia (Heasman 1980, Kailola et al. 1993, Williams 2002). Juvenile crabs inhabit intertidal regions associated with mangroves (Fielder & Heasman 1978) whilst adult crabs spend most of their lives restricted to sheltered inshore and estuarine areas, associated with deeper subtidal regions (Hill 1975, 1978, Hill et al. 1982, Hyland et al. 1984). *S. serrata* live in burrows which provide protection to crabs during their moulting and mating periods, when they are most vulnerable (Fielder & Heasman 1978). *S. serrata* is a fast-growing species which can, depending on water temperature, recruit to the fishery and reach sexual maturity within 18 to 36 mo (Fielder & Heasman 1978, Heasman 1980). As *S. serrata* reach maturity, noticeable differences between the sexes become obvious. Male *S. serrata* are larger than females (at maturity) and large male claws (17 cm CW) make up 45% of total male weight whereas claws contribute only 22% of the weight for equivalent-width females (Hill 1976). The major threats to *S. serrata* populations in Moreton Bay are damage to burrows, loss of mangrove habitat and increasing fishing pressure (Williams 2002).

In the subtropical and tropical waters of Australia, *Scylla serrata* is a highly sought-after crustacean (Kailola et al. 1993, Williams 2002). In Queensland, a unique fishery exists for *S. serrata* where 2 types of catch restrictions apply, a sex limit and a size limit. The legal-size for male *S. serrata* is 15 cm CW and no female crabs can be taken in Moreton Bay. These regulations were designed to ensure the maintenance of the spawning stock by allowing crabs to reproduce before being exposed to the fishery (Brown 1993, Coates 1993). The commercial fishing effort for *S. serrata* in Moreton Bay has been categorized as high (Zeller 1998), producing approximately 11% of the State's harvest which in 2003 was worth an estimated \$1.2 million (Williams 2002, CHRIS 2003). In 2003, the commercial harvest for *S. serrata* in Moreton Bay recorded its highest annual catch in 15 yr (113.3 t), which is the result of an increased effort from both the number of boats used and the number of days fished (Williams 2002, CHRIS 2003). Interestingly, since 1997 the recreational harvest (approximately 260 t) has exceeded the commercial harvest in Moreton Bay (Williams 2002).

Simple identification of male and female *Scylla serrata* in the field, which in most fish species is almost impossible, enabled us to determine sex ratios in this study. The only records documenting sex ratios of *S. serrata* in the Moreton Bay fishery are population estimates carried out by fisheries agencies more than 10 yr ago. These revealed that, although there were seasonal variations in sex ratios, adult female mud crabs often outnumbered adult male crabs (Coates 1993); no doubt a result of the male-only fishery. Several studies have assessed the effects of fishing on sex ratios of protogynous hermaphroditic fish (Roberts & Polunin 1991, Buxton 1992, 1993, Hawkins & Roberts 2003), and have reported greater frequencies of exploited males within reserves for male-only fisheries. We are not aware of any studies that assess the impacts of a sex-biased (invertebrate) fishery together with the effects of marine reserve protection; however, a number of studies looking at sex ratios of the partially protected (i.e. protection of ovigerous females) spiny lobster *Jasus edwardsii* in New Zealand have revealed differences in sex ratios of *J. edwardsii* between marine reserves and adjacent fished sites (MacDiarmid & Breen 1992, Davidson et al. 2002, Kelly et al. 2002). Due to the intense fishing pressure, limited movement and relatively well-established populations within Moreton Bay, *S. serrata* was chosen as the species most likely to show dramatic responses to reserve protection.

The aim of this study was to assess the effects of sex-biased fishing on *Scylla serrata* populations in 2 established marine reserves in subtropical Australia. More specifically, we assessed the effects of marine reserve protection on mud crabs by comparing the catch rates, mean size, size distribution, sex ratio and movement of *S. serrata* between 2 marine reserves and 4 non-reserve sites. We tested the predictions that marine reserve protection would increase the catch rates, mean size and size distribution of *S. serrata* in the reserves compared to the non-reserve sites. We also predicted increases in the catch rates and mean size of male crabs in the reserves compared to areas exposed to sex-biased fishery and that sex ratios of mature *S. serrata* would be skewed towards females in non-reserve sites. In addition, we predicted that the major-

ity of *S. serrata* would remain within the reserves with some spillover (i.e. cross-boundary movement) into fished non-reserve sites expected.

MATERIALS AND METHODS

Study sites. This study was conducted in the Moreton Bay Marine Park (27° 25' S, 153° 20' E), which is a semi-enclosed subtropical bay covering an area of approximately 3400 km² (Environmental Protection Agency 1999). The 2 reserve sites surveyed were Tripcony Bight reserve (5.7 km² in area) in the northern tip of the Marine Park and Willes Island reserve (1.9 km² in area) located in southern Moreton Bay (Fig. 1). Tripcony Bight and Willes Island reserves are dominated by mud flats and seagrass beds (*Zostera capricorni*, *Halophila ovalis* and algae *Caulerpa taxifolia*), and are fringed by mangrove species (*Lumnitzera racemosa* and *Bruguiera gymnorhiza*, respectively). Both marine reserves were established in 1997 and are complete no-take areas managed under 1 government department (QPWS Queensland Parks and Wildlife Service) in accordance with the Marine Parks Act 1982 (Queensland Parliamentary Counsel 1997).

Survey design. No baseline data was available before the implementation of the reserves, so a before–after-control-impact (BACI) experimental design could not be used (Underwood 1994). The 2 marine reserves surveyed in this study were located at opposite ends of Moreton Bay; Tripcony Bight reserve in the north and Willes Island reserve in the south. For each reserve site, 2 nearby and comparable non-reserve (fished) sites were chosen and surveyed to increase comparisons within sites for differences associated with spatio-temporal variability (Garcia-Charton et al. 2000). Non-reserve sites were chosen on the basis of proximity to reserve sites (no more than 7 km north or south of reserves; referred to as boundary non-reserves [NRB] and far non-reserves [NR]), habitat similarities (such as habitat and substrate type and vegetation coverage) and hydrodynamic conditions (such as flow rates, depth and water chemistry).

As surveys of *Scylla serrata* were replicated at the reserve level, any intrinsic differences in habitat and/or location could be reduced by averaging the 2 reserves (R = Reserves; Tripcony Bight [TB] and Willes Island [WI] reserves). Non-reserve sites were also averaged depending on their geographical location and proximity to the reserve (i.e. boundary non-reserves NRB_{TB} + NRB_{WI} and far non-reserves NR_{TB} + NR_{WI}). Each non-reserve site was open to fishing and experienced different levels of fishing pressure. For example, in the non-reserve sites associated with the Tripcony Bight reserve, only recreational fishing is

permitted whereas in the non-reserve sites associated with the Willes Island reserve both commercial and recreational fishing is allowed. Sampling was carried out at all study sites during summer (January–February) and winter (July–August) each year over a 2 yr period from February 2002 to August 2003.

Crab surveys. Sampling within fully protected reserves needs to be non-destructive and at the same time maximize the amount of data collected (Edgar & Barrett 1997). The most non-obtrusive and practical method of sampling S*cylla serrata* is to use catch and release sampling using baited crab pots (Williams & Hill 1982). The crab pots used in this study were
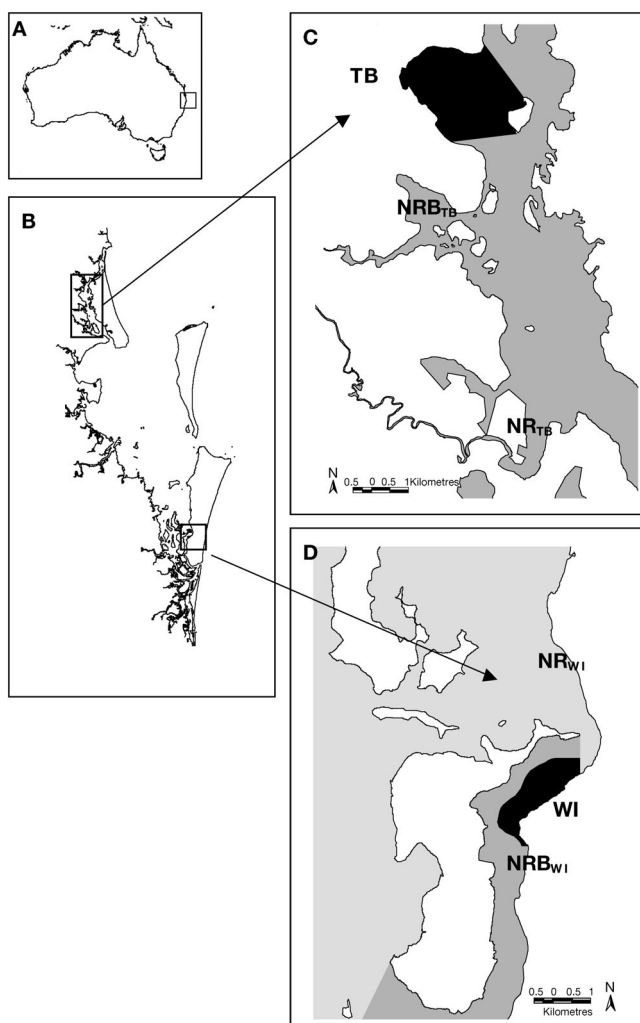

Fig. 1. (A) Map of Australia. Insert shows location of the study area in subtropics. (B) Map of the Moreton Bay Marine Park. Inserts show the 2 marine reserves surveyed in this study. (C) Map of Tripcony Bight reserve (TB) and associated non-reserve sites (NRB_{TB}: boundary non-reserve; NR_{TB}: far non-reserve). (D) Map of Willes Island reserve (WI) and associated non-reserve sites (NRB_{WI}: Boundary non-reserve; NR_{WI}: far non-reserve)

designed to catch large sub-adult/adult feeding crabs (Heasman 1980, Hill et al. 1982, Williams & Hill 1982), which is the same harvest method used by both commercial and recreational fishers in Moreton Bay (Williams 2002). Each day, 11 crab pots were baited with mullet *Mugil cephalus* and set randomly, but at least 50 m apart (Williams & Hill 1982), within the study sites at depths ranging between 1 and 4 m. The pots were checked 24 h after setting and all crabs captured were identified to species, measured, sexed and released. Relative abundance of crabs, expressed as CPUE in this study, was defined as the number of crabs caught per pot. Carapace width (CW, cm) of each crab was measured between the tips of the ninth antero-lateral spines. Pots were then re-baited and reset at random to maximize coverage of sites and to allow pots to 'fish' for 48 h at each study site. This method was repeated at each study site during summer and winter for a 2 yr period (i.e. 44 pot lifts per site per year).

Due to the selective nature of the mud crab fishery in Moreton Bay, we were also able to assess the impacts of sex-biased fishing by determining the sex ratios of crabs between reserve and non-reserve sites. As only male crabs of ≥15 cm CW made up the *Scylla serrata* fishery in Moreton Bay, only mature male and female crabs were used in the comparison of sex ratios. The maturity of *S. serrata* can be deduced from minimum size limits (MSL). The MSL in a fishery is generally dependent on the size at which the target species matures (Robertson & Kruger 1994). In Moreton Bay, male *S. serrata* moult to adult body form (i.e. maturity) between 14 and 16 cm CW (Heasman 1980). Mating pairs of *S. serrata* in Moreton Bay predominantly comprise females passing through their terminal moult at a mean premoult carapace width of 12.8 ± 0.8 cm, and larger intermoult terminal instar males of mean carapace width 16.5 ± 1.0 cm (Heasman et al. 1985). The mature sizes used in the comparison of sex ratios in this study were, therefore, of mature males (legal-sized, ≥15 cm CW) and mature females (≥12 cm CW).

Crab movement. Commencing in summer 2003 and continuing through to summer 2004, all *Scylla serrata* >10 cm CW caught were also tagged. To document the movement of crabs, plastic T-bar anchor tags (Hallprint) were used to mark the crabs, as described by Hill (1975). The tags were imprinted with a freecall phone number. Hill (1975) found that tagging *S. serrata* did not alter the behavior of crabs and that tags were retained after moulting. The distance moved refers to the distance between the release and the recapture site of crabs (Hyland et al. 1984). In this study, spillover is defined as cross-boundary movement of crabs with no implication for

density-dependence as defined by Kramer & Chapman (1999).

Data analysis. *Catch rates:* Catch rates (CPUE) of *Scylla serrata* were tested for normality (Kolmogorov-Smirnov test, Zar 1984) but as the data were counts and contained many zeros, they did not satisfy the assumptions of normality or homogeneity of variance. The data were, therefore, analyzed with a generalized linear model (GLM) under the assumption of a Poisson distribution. The model was fitted using maximum likelihood methods by the SAS procedure GEN-MOD (SAS 2003). The factors used in the analysis were 'location' (north, south), 'status' (reserve, non-reserve), 'season' (summer, winter) and 'sex' (male, female), which were all treated as fixed factors. Ratios describing the magnitude of differences between the main effects were calculated after non-significant interactions were progressively removed from the model (see Willis et al. 2003 for a more comprehensive explanation of this methodology). Further analysis on the catch rates of male and female *S. serrata* between the 2 marine reserves and 4 non-reserve sites were also carried out (separately) using the same GLM.

Size: As the mean size (per pot) data of *Scylla serrata* had a non-normal distribution, differences between reserve and non-reserve sites were tested using non-parametric tests (Zar 1984). A Kruskal-Wallis 1-way ANOVA was used to test the mean size of crabs between the reserve and non-reserve sites (using factor status). The mean sizes of all crabs (males and females) were tested as were male and female *S. serrata* data sets. Length–frequency distributions (%) of *S. serrata* from both reserves and non-reserve sites (total catch) were then compared using a chi-square goodness of fit test (Zar 1984). Separate tests were also performed on size distribution data for male and female crabs.

Sex ratio: As the factor sex interacted with all measures tested (i.e. CPUE and mean size), we looked at the sex ratio among and between study sites. Mature sizes used in the comparison of sex ratios in this study were of mature males (legal-sized, ≥15 cm CW) and mature females (≥12 cm CW). Sex ratios were compared between reserve and non-reserve sites using a chi-square goodness of fit test for departure from 1:1 (Zar 1984).

Crab movement: The total number of *Scylla serrata* tagged within both marine reserves and non-reserve sites was recorded, and recaptures were expressed as a percentage for each site. The total time from release to recapture, and the distance moved from the capture site, were recorded for each recapture. The growth of crabs will not be discussed in this paper due to the short time frame of this tagging study.

Table 1. *Scylla serrata*. Summary of relative abundance (n) and mean size (cm CW) with SE (±1) for total mud crabs and male and female crabs caught between study sites (seasons pooled). Total catch and male mud crabs also include the percentage of legal-sized crabs (≥15 cm CW) caught. TB: Tripcony Bight reserve; NRB$_{TB}$: Tripcony Bright boundary non-reserve; NR$_{TB}$: Tripcony Bright far non-reserve; WI: Willes Island reserve; NRB$_{WI}$: Willes Island boundary non-reserve; NR$_{WI}$: Willes Island far non-reserve

Location	Site	Total				Male				Female		
		n	Size	SE (±1)	% legal	n	Size	SE (±1)	% legal	n	Size	SE (±1)
North	TB	133	15.7	0.135	52	97	15.4	0.149	71	36	16.4	0.265
	NRB$_{TB}$	98	14.7	0.180	14	56	14.1	0.201	25	42	15.6	0.273
	NR$_{TB}$	30	15.8	0.335	20	14	14.7	0.387	43	16	16.8	0.405
South	WI	130	16.1	0.139	59	94	16.2	0.173	82	36	15.8	0.213
	NRB$_{WI}$	43	15.5	0.263	9	18	14.2	0.305	22	25	16.5	0.251
	NR$_{WI}$	38	15.4	0.285	24	20	14.8	0.398	45	18	16.0	0.360

RESULTS

Catch rates and sex

Over the 2 yr period of this study, a total of 472 mud crabs were recorded from the 2 marine reserves and non-reserve sites. A summary of total catch rates (n)

Table 2. *Scylla serrata*. Likelihood ratio statistics for CPUE (no. of crabs per pot) of total mud crabs, and male and female crabs caught at 2 marine reserves (Tripcony Bight and Willes Island) and 4 non-reserve sites surveyed 4 times over a 2 yr period. Location: north, south; Status: reserve, non-reserve; Season: summer, winter; Sex: male, female. Non-significant (p > 0.05) interaction terms have been removed from the model

Source	df	Total		Male		Female	
		χ^2	p	χ^2	p	χ^2	p
Location	1	5.3	0.02	4.1	0.04	1.3	0.2
Status	2	125.2	0.0001	131.2	0.0001	16.1	0.0003
Season	1	15.0	0.0001	4.1	0.04	14.0	0.0002
Sex	1	34.0	0.0001	–		–	
Location × Status	2	17.7	0.0001	17.4	0.0002	3.1	0.2
Location × Season	1	4.5	0.03	3.2	0.07	1.3	0.2
Status × Sex	2	22.6	0.0001	–		–	

Fig. 2. *Scylla serrata*. Total catch rates (no. of crabs per pot) (±1 SE) of mud crabs (male and female crabs) between the 2 reserves (TB: Tripcony Bight; WI: Willes Island) and corresponding non-reserve sites (NRB: boundary non-reserve; NR: far non-reserve) (seasons pooled)

and mean size of *Scylla serrata* between all study sites (seasons pooled), and between male and female mud crabs is displayed in Table 1.

The log-linear model fit to catch rates of total crabs (male and females) resulted in significant interactions between location and status, location and season, and status and sex (Table 2). At both locations, catch rates of *Scylla serrata* were 2-and-a-half times higher in the reserves compared to non-reserve sites (Fig. 2). The only exception were the catch rates of crabs in the Tripcony Bight boundary non-reserve site (NRB$_{TB}$) which were only marginally lower than catch rates within the Tripcony Bight reserve and much higher than catch rates of crabs within the corresponding non-reserve sites (Table 1). A seasonal pattern in catch rates of *S. serrata* was evident in both reserves, with higher catch rates of crabs in summer compared to winter months. Catch rates of *S. serrata* also appeared to peak in summer 2003 in the northern sites (TB, NRB$_{TB}$) compared to the southern sites over the same season (see Fig. 4A). Catch rates of crabs within the non-reserve sites were more variable throughout the seasons.
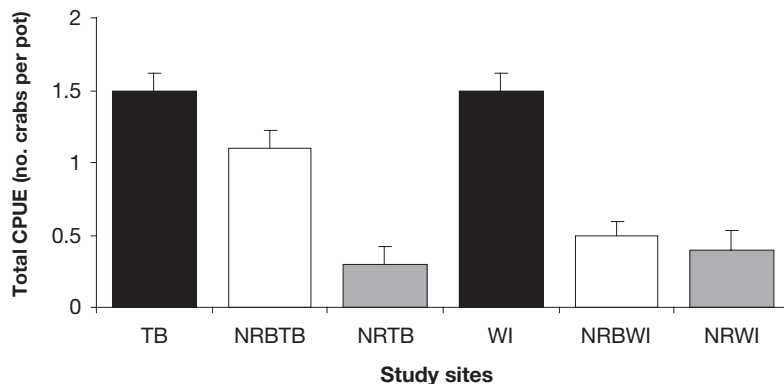
The best statistical model for catch rates of male *Scylla serrata* resulted in a significant interaction between location and status, with no significant interactions with season (Table 2). Higher catch rates of male crabs were recorded in both marine reserves compared to the non-reserve sites (Fig. 3A). Catch rates between the non-reserve sites did not differ greatly, with the exception of catches in the Tripcony Bight boundary
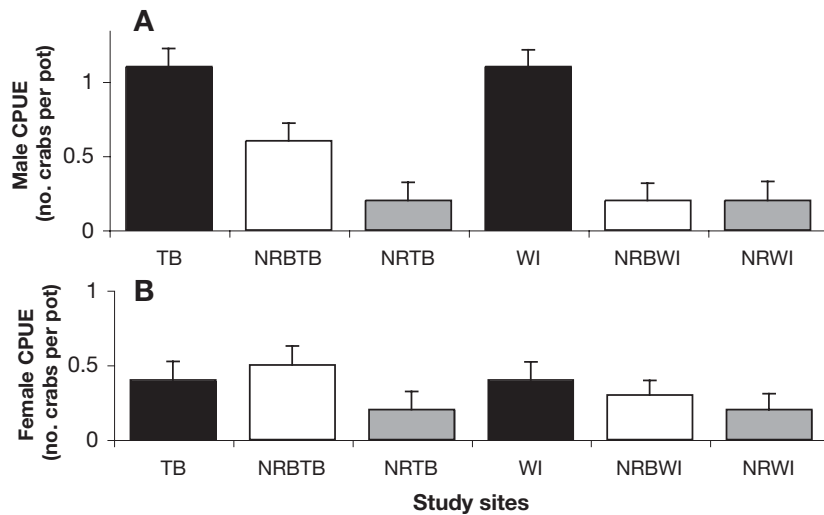
Fig. 3. *Scylla serrata*. Catch rates (no. of crabs per pot) (±1 SE) of mud crabs between the 2 reserves (TB: Tripcony Bight; WI: Willes Island) and corresponding non-reserve sites (NRB: boundary non-reserve; NR: far non-reserve) (seasons pooled) for (A) males and (B) females
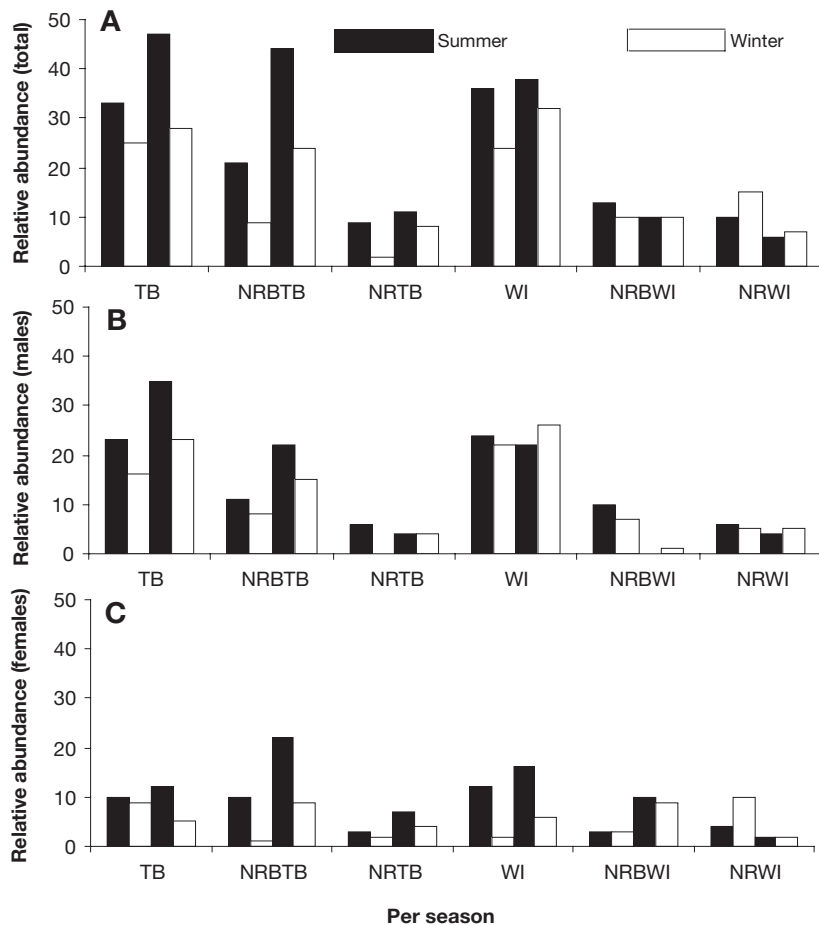

Fig. 4. *Scylla serrata*. Relative abundance (n) of mud crabs between the seasons (summer and winter) over 2 yr (2002–2003) between the 2 reserves (TB: Tripcony Bight; WI: Willes Island) and corresponding non-reserve sites (NRB: boundary non-reserve; NR: far non-reserve) for (A) total crabs, (B) males and (C) females. Closed bars represent summer and open bars denote winter for 2002 and 2003, respectively

non-reserve site (NRB$_{TB}$) which peaked in summer 2003 (Table 1, Fig. 4B). Catch rates of male *S. serrata* appeared to be slightly higher in the summer months compared to winter months, particularly in the reserve sites (Fig. 4B). The results of the model fit for catch rates of female *S. serrata* revealed no significant interactions; significant results were only obtained for factors status and season (Table 2). Catch rates for female crabs were similar between the reserve and non-reserve sites (Fig. 3B). In most cases, catch rates of female crabs were slightly higher in the summer months than in the winter months for all study sites, with a peak in the Tripcony Bight non-reserve site (NRB$_{TB}$) in summer 2003 (Fig. 4C).

Size and sex

The Kruskal-Wallis 1-way ANOVA for mean size of all *Scylla serrata* (males and females) revealed significant differences in the mean size of crabs between the reserve and non-reserve sites (status, p < 0.000) (Table 3). Multiple comparisons revealed that the mean size of *S. serrata* was also significantly different between the non-reserve sites (Tables 1 & 3). The mean size of crabs did not change greatly between the seasons, whereas the mean size of crabs caught in non-reserve sites was more variable depending on the season. The size distributions of *S. serrata* were not found to be significantly different between the 2 reserves or between the Tripcony Bight reserve and the far non-reserve site (NR$_{TB}$); however, all other comparisons between the reserves and non-reserve sites (and between non-reserve sites) were found to be significantly different (p < 0.0001).

The Kruskal-Wallis 1-way ANOVA for the mean size of male *Scylla serrata* revealed that there were significant differences between the reserve and non-reserve sites (status, p < 0.0001) (Table 3). Multiple comparisons revealed there was no significant difference in the mean size of male crabs between the non-reserve sites (Tables 1 & 3). Of the male crabs caught in each

Table 3. *Scylla serrata*. Kruskal-Wallis 1-way ANOVA of mean size (per pot) of total mud crabs, and male and female crabs caught between the marine reserves (R: reserves: Tripcony Bight and Willes Island) and 4 non-reserve sites (NRB: boundary non-reserve; NR: far non-reserve) with multiple comparisons of mean ranks for all groups within the factor Status (reserve, non-reserve)

Factor	df	χ^2	p	Total Comparisons		χ^2	p	Male Comparisons		χ^2	p	Female Comparisons	
Status	2	74.4	0.000	R vs. NRB	0.000	87.5	0.000	R vs. NRB	0.000	10.24	0.006	R vs. NRB	1.0
				R vs. NR	0.000			R vs. NR	0.000			R vs. NR	0.1
				NRB vs. NR	0.01			NRB vs. NR	0.2			NRB vs. NR	0.1

of the study sites, over 70% of the crabs within the marine reserves were equal to or greater than legal-size (15 cm CW) compared to fewer than 50% within the non-reserve sites (Table 1). The size distributions of male *S. serrata* were found to be significantly different between the reserve and all of the non-reserve sites (p < 0.0001), with no significant difference found between the boundary non-reserve sites (NRB_{TB} and NRB_{WI}) and the Tripcony Bight non-reserve sites (NRB_{TB} and NR_{TB}) (Figs. 5A & 6A).

Although the Kruskal-Wallis 1-way ANOVA for female *Scylla serrata* revealed a significant difference between the reserve and non-reserve sites (status, p < 0.006), no significant difference was detected by the multiple

comparisons between the sites (Table 3). The mean size of female *S. serrata* did not differ greatly between the study sites (Table 1). Female size distribution was found to be significantly different between the reserve and the non-reserve sites (p < 0.0001), with only 1 non-significant result detected between the Tripcony Bight non-reserve sites (NRB_{TB} and NR_{TB}) (Figs. 5B & 6B).

Sex ratio

The results of the chi-square analysis revealed significant differences in the sex ratios of *Scylla serrata* between both marine reserves and their corresponding
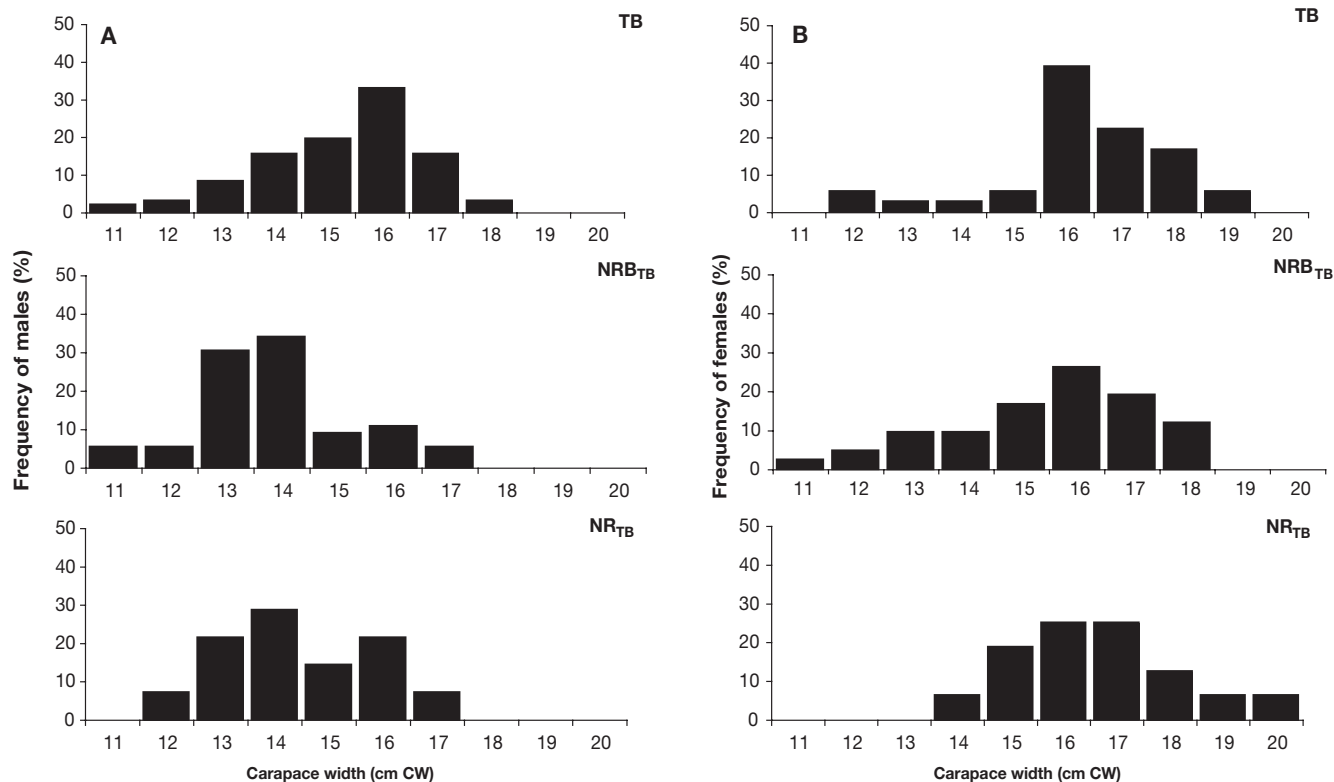

Fig. 5. *Scylla serrata*. Length–frequency (%) data of mud crabs between Tripcony Bight reserve (TB) and the northern non-reserve sites (NRB_{TB}, NR_{TB}) (pooled seasons) for (A) males and (B) females. Male crabs ≥15 cm CW are of legal size and female crabs ≥12 cm CW are of mature size in Moreton Bay
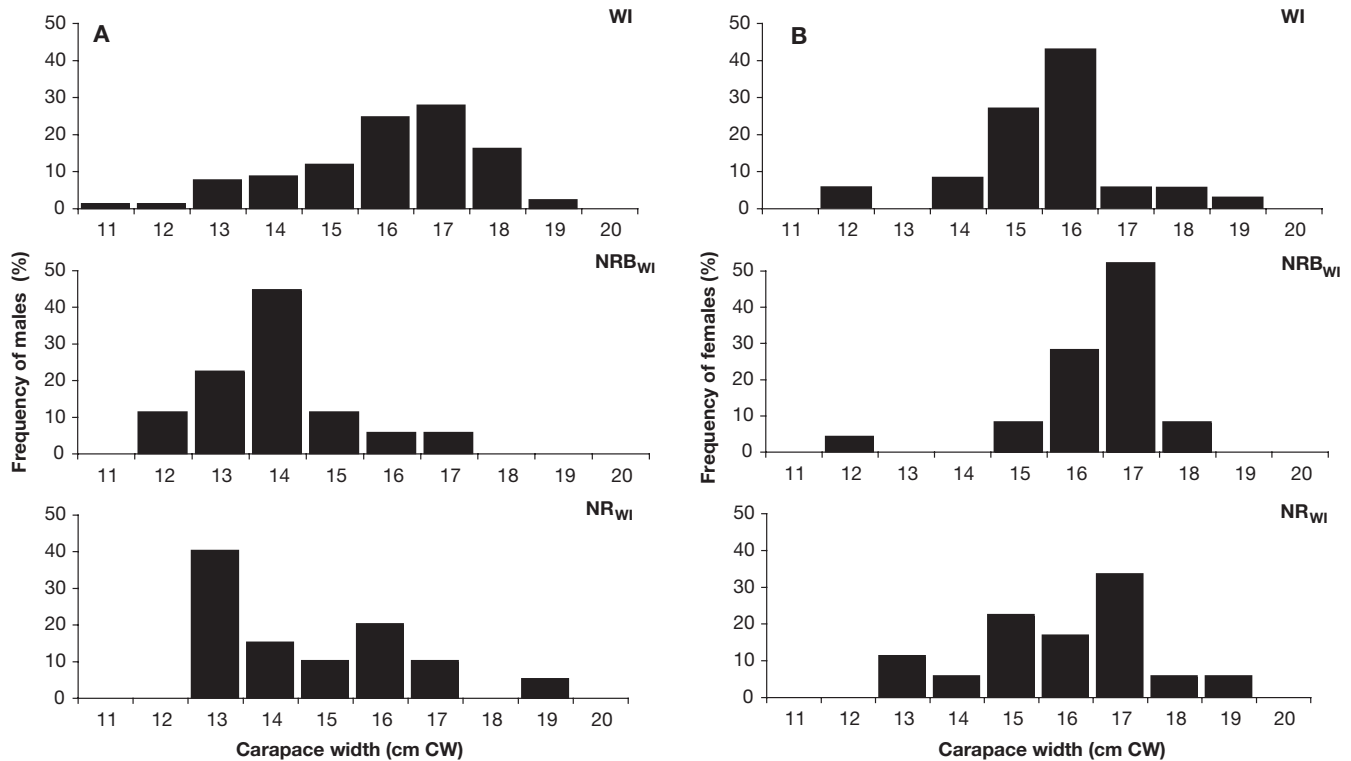
Fig. 6. *Scylla serrata*. Length–frequency (%) data of mud crabs between Willes Island reserve (WI) and the southern non-reserve sites (NRB$_{WI}$, NR$_{WI}$) (pooled seasons) for (A) males and (B) females. Male crabs ≥15 cm CW are of legal size and female crabs ≥12 cm CW are of mature size in Moreton Bay

non-reserve sites. In the Tripcony Bight reserve, 69 mature male *S. serrata* were caught compared to 36 mature female crabs, resulting in a sex ratio of 2:1 ($\chi^2 = 10.37$, p < 0.001). In the boundary non-reserve site (NRB$_{TB}$), 14 mature male crabs were caught compared to 41 mature female crabs resulting in a sex ratio of 0.34:1 ($\chi^2 = 13.25$, p < 0.001), with a similar sex ratio of 0.38:1 ($\chi^2 = 4.54$, p < 0.03) observed in the far non-reserve site (NR$_{TB}$), with 6 mature males caught compared to 16 mature female crabs. Within the Willes Island reserve, a total of 77 mature male *S. serrata* were caught compared to 36 mature females, resulting in a sex ratio of 2:1 (males to females) ($\chi^2 = 14.87$, p < 0.001). In the boundary non-reserve site (NRB$_{WI}$), 4 mature male crabs were caught compared to 25 mature females, resulting in a sex ratio of 0.16:1 ($\chi^2 = 15.2$, p < 0.001) and in the far non-reserve site (NR$_{WI}$), 9 mature male crabs were caught compared to 18 mature female crabs, resulting in a sex ratio of 0.5:1 ($\chi^2 = 3.0$, p < 0.08).

Crab movement

A total of 203 *Scylla serrata* were tagged within the Tripcony Bight reserve; 42 crabs were tagged within the boundary non-reserve site (NRB$_{TB}$) and 11 within the far non-reserve site (NR$_{TB}$). Of those *S. serrata* tagged within the Tripcony Bight reserve, 19 crabs were recaptured, a 9% recapture rate. Over 50% of *S. serrata* recaptured inside the Tripcony Bight reserve were recorded by the authors (S.P.) (n = 10). Most of these crabs were recorded within 1 to 4 d of being tagged. Movement within the Tripcony Bight reserve was estimated to be 50 m, which was the average distance between pots. Nine crabs tagged inside the reserve (all male) were recaptured outside the reserve by recreational anglers, resulting in a 4% recapture rate of crabs moving outside the reserve. Crabs were at liberty for 80 d on average (ranging from 8 to 223 d). The distance traveled from the reserve boundary was approximately 2 km, predominantly in an easterly direction with no dominant north or south direction recorded. One crab was recaptured from the boundary non-reserve site (NRB$_{TB}$) and although the crab was at liberty for 62 d, no movement outside this site was recorded. There was also a difference in the mean size of crabs recaptured outside the Tripcony Bight reserve compared to crabs caught in the corresponding non-reserve sites. The mean size of male crabs tagged inside the Tripcony Bight reserve and recaptured outside the reserve was 17% larger (16.6 cm CW) than crabs caught in both non-reserve sites (14.2 cm CW).

Within the Willes Island reserve, a total of 135 *Scylla serrata* were tagged; 9 crabs were tagged in the boundary non-reserve site (NRB$_{WI}$) and 4 in the far non-reserve site (NR$_{WI}$). The majority of crabs tagged in the reserve were recaptured inside the reserve boundary, resulting in a 13% recapture rate (n = 17). Most of the crabs recaptured (88%) inside the reserve were recorded within 2 to 5 d of being tagged (by S.P.). However, 2 *S. serrata* were recaptured 163 and 164 d after the initial tagging. The distance moved within the reserve was approximately 50 m, which was the average distance between pots. Only 1 *S. serrata* (large male, 17 cm CW) was recaptured outside the Willes Island reserve (a recapture rate of <1%); this was a long-term recapture with the crab at liberty for 300 d. The crab was recaptured by a commercial crab fisher, approximately 25 m outside the reserve boundary.

DISCUSSION

Overall, our results indicate that when a species is imposed with sex-limits in a fishery the implementation of a marine reserve has the potential to reverse the effects of fishing and benefit the exploited species as well as the 'dominant' sex. Catch rates of adult *Scylla serrata* were higher in both marine reserves compared to all corresponding non-reserve sites. The CPUE of *S. serrata* also differed between seasons, with higher catches recorded in summer compared to winter months. This seasonal pattern was particularly strong in catches of crabs from the marine reserves, whereas high fishing pressure in the non-reserve sites probably reduced seasonal changes in catches. Previous studies of *S. serrata* in Moreton Bay have found higher catches of crabs in summer compared to winter (Williams & Hill 1982). Our results are consistent with similar studies in which increases in catch rates (CPUE) of invertebrates have been detected in reserves worldwide (gastropod and sea urchin, Castilla 1996; gastropod, sea urchin and limpet, Castilla & Fernandez 1998; abalone and lobster, Edgar & Barrett 1999; lobster, Kelly et al. 2000, Davidson et al. 2002). Interestingly, the catch rates of *S. serrata* were almost identical between both marine reserves despite the Tripcony Bight reserve being 3 times larger in size than the Willes Island reserve. This result is consistent with numerous studies showing the benefits to exploited species despite small reserve size (see extensive review by Halpern 2003).

Using data from commercial catches of *Scylla serrata* in Moreton Bay, we were also able to compare catch rates between fished and unfished areas on a larger scale. Fisheries data (CHRIS 2003) available on the commercial harvest (i.e. biomass) of *S. serrata* in Moreton Bay showed approximate catches of 300 g of crab per pot. This is based on commercial catch data (113.3 t in 2003), number of days fished (7743 d in 2003) and a maximum number of 50 crab pots per license (Queensland Fisheries Legislation, Williams 2002). Using our unpublished data (S.P.) of length/weight measurements of *S. serrata* in Moreton Bay, the biomass of crabs caught in the marine reserves was approximately 900 g per pot, suggesting that the reserves in Moreton Bay have 3 times the biomass (estimated by catch rates) of *S. serrata* relative to the commercial fishery.

Sex-related differences in the catch rates of male and female *Scylla serrata* were obvious between the marine reserves and non-reserve sites. Male *S. serrata* dominated catches in both marine reserves, with 5 times more male crabs caught in the reserves compared to the non-reserve sites. The only exception was catches of male crabs in the Tripcony Bight boundary non-reserve site (NRB$_{TB}$) in summer 2003, which were unexpectedly high (as were female numbers at this site during this season), perhaps due to a single heavy rainfall event. Heavy and prolonged rainfall has the potential to change water temperature and salinity, which in turn can influence catch rates of *S. serrata* (Williams & Hill 1982). Although heavy rainfall occurred in all study sites, it only appeared to influence crab catches in the boundary non-reserve site (NRB$_{TB}$), which is most likely due to a small creek located near this site which commonly floods after heavy rainfall (i.e. increasing crab catches). As marine reserves are commonly chosen on the basis of their 'uniqueness', the exact compatibility between reserve and non-reserve sites is almost impossible and we acknowledge this in our study. In terms of seasonal catch rates of male *S. serrata*, the highest catches in the reserves were in summer. In contrast, more variable catches of male crabs were recorded between the seasons in the non-reserve sites, perhaps due to consistent fishing pressure throughout the year. We expected an increase in catch rates of male *S. serrata* in the reserves because they are protected in the reserves and not outside.

In comparison, catch rates of female *Scylla serrata* did not reveal such strong patterns between the reserve and non-reserve sites. Catch rates of female crabs did not differ between the reserves and boundary non-reserve sites; however, there were twice as many female crabs caught in the reserves compared to the far non-reserve sites. Catch rates of female crabs between reserve and non-reserve sites were not expected to be very different because female *S. serrata* are totally protected (inside and outside the marine reserves). Interestingly, the catch rates of female *S. serrata* were almost always higher in the reserve

compared to the non-reserve sites. Again, the only exception were catch rates of female crabs in the Tripcony Bight boundary non-reserve site (NRB$_{TB}$), which as mentioned previously could be the result of a one-off prolonged rainfall event. The higher catch rates of female *S. serrata* in both marine reserves could be due to several reasons. These include increased habitat quality and ecosystem function offered by total protection in reserves (Ward et al. 2001), non-compliance to fishery regulations outside the reserves (particularly in far non-reserve sites) or the possibility that female crabs may be attracted to areas with an abundance of large male crabs. Seasonal changes in water temperature in Moreton Bay were also reflected in catch rates of female crabs, with higher catch rates in summer compared to winter at all study sites.

The mean size of *Scylla serrata* was also significantly higher in both marine reserves compared to non-reserve sites. Within the reserves, the mean size of crabs did not change dramatically between the seasons whereas the mean size of crabs caught in non-reserve sites was more variable depending on the season. Again, sex-related differences were detected in the average size of *S. serrata*; male crabs were on average 10% larger in both marine reserves compared to the non-reserve sites, which was expected due to the protection offered by the reserves. Not only were male crabs larger in size, but within both marine reserves, legal-sized male *S. serrata* made up >70% of the total male catch in both reserves, whereas within non-reserve sites, <50% of male crabs were of legal size. The skewed size distribution of male crabs in both marine reserves in this study further reflects the impact the mud crab fishery has in Moreton Bay. Increases in the average size of crustaceans have also been detected in marine reserves for spiny lobster *Jasus edwardsii* in New Zealand (Kelly et al. 2000, Davidson et al. 2002) and American lobster *Homarus americanus* in Newfoundland (Rowe 2002). In contrast, the average size of female *S. serrata* in our study did not differ greatly between the reserve and non-reserve sites which is probably due to the total protection offered to female crabs at all study sites.

It is clear from our results that the sex-biased fishery in Moreton Bay impacts heavily on the catch rates and mean size of *Scylla serrata*. Within both marine reserves, almost identical proportions of mature male and female crabs were caught resulting in a sex ratio of 2:1 (male:female). The opposite sex ratio was displayed in the non-reserve sites, skewed towards more females. The only records documenting sex ratios of *S. serrata* in the Moreton Bay fishery are population estimates carried out by fisheries agencies more than 10 yr ago which revealed that although there were seasonal variation in sex ratios, adult female *S. serrata*

often outnumbered adult male crabs (Coates 1993), no doubt a result of the male-only fishery. Consequently, due to the nature of the mud crabs fishery in Moreton Bay, a skew in sex ratios between reserve and non-reserve sites was predicted. However, it was not expected that the sex ratio in both marine reserves would be so skewed towards males. If both sexes were totally protected by the marine reserves, it was anticipated that the sex ratio would be almost equal.

Ward et al. (2001) argues that only examining sex ratios can be misleading as the sex ratio can disguise the fact that structural change to the population is being induced through fishing; therefore, it is not clear how sex ratios in such adapted populations would respond in a marine reserve. The only study we are aware of noting the sex ratio of *Scylla serrata* in a 'protected' situation is the study of Hill (1975) who studied *S. serrata* in 2 South African estuaries. One was open to the sea whilst the second estuary was closed by a sandbar providing 'protection'. Neither of the estuaries was impacted by fishing. Analysis of the sex ratios of *S. serrata* from the 'open' estuary showed that approximately 14% of crabs larger than 13 cm CW were female. Hill suggested this low proportion of females was probably due to a migration of female crabs out of the estuary to spawn at sea. A similar migration could not occur from the 'closed' estuary and the proportion of females remained relatively constant at approximately 43% throughout the size range of 11 to 16.9 cm CW. As previously mentioned, if both sexes were totally protected by marine reserves, or in this case by physical closure, it was anticipated that the sex ratio would be almost equal. Sex ratios were almost equal in the 'protected' estuary in Hill's (1975) study; however, the sex ratios of fully protected *S. serrata* in our study were skewed towards males. The results of our study demonstrate that reserves have the potential to allow exploited species to recover from the effects of fishing and to return to their 'natural' state. In Moreton Bay, the 'natural' state revealed by the 2 marine reserves was a sex ratio of 2:1 (male:female).

Documenting the movement of economically important species is important to determine whether the existing marine reserves are effective in conserving stocks from harvest. There is good evidence from tagging studies that fisheries species have benefited from reserves through 'spillover' (density-dependence) of juveniles and adults to adjacent fishing grounds (e.g. Attwood & Bennett 1994, Johnson et al. 1999, Roberts et al. 2001, Griffiths & Wilke 2002). In this study, the term 'spillover' relates to the cross-boundary movement of *Scylla serrata*, with no implications for density-dependence as defined by Kramer & Chapman (1999). This is due to the crab recapture rates outside the reserves not being inversely proportional to the rela-

tive abundance inside the reserves. Tagging studies on crustaceans within marine reserves are limited; however, recent studies in Japan (on crabs), New Zealand and Newfoundland (on lobsters) have revealed movements of invertebrates between reserves and fished sites (e.g. Yamasaki & Kuwahara 1990, Kelly 2001, Rowe 2002). Due to the sedentary nature of *S. serrata* (with the exception of female mud crabs during spawning, Hill 1994), movement outside of reserves was expected to be minimal. This was evident in our study, with the majority of *S. serrata* recaptured in the same areas, and with only a 4 % recapture rate outside the Tripcony Bight reserve and less then a 1 % recapture rate outside the Willes Island reserve. Hill (1975) showed that *S. serrata* are capable of considerable movement but seem to remain in the same area for long periods. Hyland et al. (1984) also found that most *S. serrata* tagged in Moreton Bay were recaptured in the same area where they had been released. Even though only small numbers of crabs were tagged (and therefore recaptured) within this study, recapture information is still noteworthy as no similar tagging studies have been carried out on *S. serrata* within marine reserves in Australia.

It appears that invertebrate species with small home ranges, such as *Scylla serrata*, have limited potential for spillover (cross-boundary movements) from reserves. Generally, the extent to which spillover occurs, and its timing, is related to the design and size of the reserve, the biological characteristics of the species involved, and the management system in place to enforce marine reserves (Ward et al. 2001). Although the tagging data in this study demonstrated the limited movement of *S. serrata* within 2 small marine reserves, it also revealed this species' ability to move outside reserve boundaries into adjacent fishing areas. Interestingly, all crabs tagged within the reserves which were later caught in fished sites were at least 10 % larger than the MSL for this species. Furthermore, the results of this study agree with the popular notion that marine reserve effectiveness largely depends on the mobility of the target species, with the more sedentary animals, such as crustaceans, most likely to be protected (and show significant differences) in reserves of a small size (Edgar & Barrett 1999, Griffiths & Wilke 2002).

It is also interesting to note that the large differences observed in crabs between the reserve and non-reserve sites could also be related to the short life cycle of *Scylla serrata*. The 2 marine reserves surveyed in this study are a fairly recent addition to the Marine Park (established in 1997), yet *S. serrata* are short-lived. We may not have found such large differences between reserve and non-reserve sites with a long-lived species. As well as being short-lived, *S. serrata* are also highly fecund (2 to 8 million eggs) and are

capable of multiple-spawning (Heasman 1980, Heasman et al. 1985). Increases in the abundance (density) and size of reproductive individuals within marine reserves has important consequences in maximizing the reproductive capacity of natural populations (Manriquez & Castilla 2001) as well as having the potential to export larvae to surrounding areas, known as 'seeding grounds' (Fernandez & Castilla 1997). Although these 2 concepts are beyond the scope of this paper, we can make predictions based on the biology and patterns displayed by adult *S. serrata* to marine reserve protection in Moreton Bay. We predict that the reproductive output from the reserves is likely to be higher than outside fished areas due to higher numbers of large males being more likely to successfully fertilize female mud crabs (see Davidson et al. 2002, lobsters). In terms of 'seeding' adjacent fishing grounds (i.e. non-reserve sites), it is believed that adult female *S. serrata* migrate offshore to spawn (Hill 1994), so the potential for female mud crabs to 'seed' non-reserve sites in our study would be low. Further research into the fecundity and larval biology of *S. serrata* and coastal oceanography within Moreton Bay would be necessary to support this prediction. Again, this highlights the importance of knowing the biology of the species targeted for protection to adequately design and manage effective marine reserves.

CONCLUSION

Empirical testing of marine reserves still remains one of the most critical aspects in improving the design and management of future marine reserves. The results of this study add to the growing body of empirical evidence that small marine reserves (<6 km^2) can provide conservation and fisheries benefits for exploited species (particularly for less mobile invertebrate species). Our results strengthen the case for the implementation of more marine reserves in the Moreton Bay Marine Park, especially for the future protection of *Scylla serrata* populations. In particular, networks of small marine reserves (between 2 and 10 km^2 in area) are recommended to provide both fisheries and conservation benefits to *S. serrata* in subtropical Australia.

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