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REPORT

Batch fecundity of *Lutjanus carponotatus* (Lutjanidae) and implications of no-take marine reserves on the Great Barrier Reef, Australia

R. D. Evans · G. R. Russ · J. P. Kritzer

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Abstract This study investigated body size to fecundity relationships of a reef fish species targeted by line fishing, and examines the potential benefits of increased batch fecundity in no-take reserves compared to fished areas around the Palm, Whitsunday and Keppel Island Groups, Great Barrier Reef, Australia. *Lutjanus carponotatus* batch fecundity increased with fork length in a non-linear relationship that was best described by a power function. Batch fecundity differed by more than 100-fold among individuals, with a range from 7,074 to 748,957 eggs in fish ranging from 184 to 305 mm fork length. Furthermore, egg diameter increased with fish size. Based on underwater visual census, the potential batch fecundity per unit area in all three island groups ranged from 1.0 to 4.2 times greater in the no-take reserves than in the fished areas between 2001 and 2004. In 2002, a mean 2.3-fold difference in biomass between no-take reserves and fished areas converted to a mean 2.5-fold difference in batch fecundity per unit area. Greater batch fecundity, longer spawning seasons and potentially greater larval survival due to larger egg size from bigger individuals might significantly enhance the potential benefits of no-take marine reserves on the Great Barrier Reef.

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Keywords Marine reserves · *Lutjanus carponotatus* · Egg production · Batch fecundity · Great Barrier Reef

Introduction

Increasing size of human populations and frequent decreases in the size of stocks of numerous marine fishes have led many fishery scientists to consider the benefits of no-take marine reserves as fisheries management tools (Pauly et al. 2002). Some fishery managers have begun to support the implementation of such reserves. These no-take areas are established for many reasons. The most notable are conservation of species, ecosystems and bioregions, and in a fishery context, protecting a portion of the spawning stocks of target fishery species. The expected benefits of no-take marine reserves for target fishery species are decreased fishing mortality, increased density, increased average age and size, increased biomass and greater propagule production per unit area (Russ 2002). Numerous empirical studies have provided considerable information on the positive effects of reserves for the first four of these expectations (Russ 2002; Halpern 2003). However, comparisons of propagule production per unit area of target species between fished and no-take areas are rare, and have never been estimated in the world's largest network of no-take marine reserves, Australia's Great Barrier Reef (GBR).

Demonstrating greater egg production per unit area of target species in no-take reserves compared to fished areas is an important prerequisite for reserves to eventually become net exporters of propagules, a major expectation for fishery enhancement. Several studies suggest that marine reserves provide great benefits to the reproductive output of marine invertebrates. Abalone (*Haliotis* *kamschatkama*) had up to 20 times higher reproductive potential in three reserve sites compared to fished areas in British Colombia, Canada (Wallace 1999). In New Zealand, annual egg production of spiny lobster (*Jasus edwardsii*) increased, by 4.8% in shallow sites and 9.1% in the deep sites, in reserves that had been protected for up to 20 years compared to fished areas (Kelly et al. 2000). The reproductive products of the Chilean gastropod (*Concholepas concholepas)* were up to three orders of magnitude higher in marine reserves than fished areas at Las Cruces, central Chile (Manriquez and Castilla 2001). Male Limpets (*Cymbula oculus*) in Dwesa marine reserve, South Africa produced 113 times more sperm, and females produced 182 times more eggs than outside the reserve (Branch and Odenal 2003).

Such results are substantially greater than those quantified to date for most teleost fishes. The reproductive output of rockfish (*Sebastes* spp.) in no-take and fished areas was compared using length-specific fecundity. Two of three no-take marine reserves in the kelp forests in Central California (Hopkins and Pt. Lobos) had larger individuals of *Sebastes atrovirens* and *Sebastes chrysomelas* (Paddack and Estes 2000). Using length-specific fecundity relationships, Paddack and Estes (2000) demonstrated *S. atrovirens* and *S. chrysomelas* had greater batch fecundity in reserves than in nearby fished areas that lacked larger individuals (~2.8 and ~4.5 times, respectively). Lingcod (*Ophiodon elongatus*) had from 3.1 to 4.5 times greater reproductive potential in three no-take reserves compared to three areas open to fishing in the San Juan Islands, USA (Eisenhardt 2001). In a recent attempt to compare the reproductive output of *Lutjanus fulviflamma* in fished and no-take reserves around Mafia Island, Tanzania Kamukuru and Mgaya (2004) estimated batch fecundity in the protected area ranged from 45,200 to 430,200 oocytes per female for individuals between 207 and 293 mm (total length [TL]). However, they were unable to compare batch fecundities between protected and fished areas because they could not find any females in a breeding condition in the fished areas. Length-fecundity relationships were used to show that daily batch fecundity of the temperate snapper *Pagrus auratus* was 11–18 times higher in the Poor Knights no-take reserve than at nearby reference locations after 4 years of full protection in New Zealand (Denny et al. 2004).

The size–fecundity relationship in teleost fishes is generally represented by a power function ($y = ax^b$), and the exponent (b) can be as high as 5 (Jennings et al. 2001). Therefore, fecundity increases rapidly with length. Using Grimes (1987) estimates of the largest and smallest batch fecundity from a population of *L. campechanus*, Plan Development Team (1990) suggested that one 60.5 cm fork length (FL) *L. campechanus* could produce the same number of eggs as 212 42 cm FL individuals. Based on this observation, a protected population with many larger individuals should have a greater reproductive output per unit area than a fished population with proportionally more smaller individuals.

Few studies directly demonstrate substantially higher fish egg production per unit area in no-take reserves. There are at least four reasons for this: (1) few people measure egg production, often assuming that the egg production rises sharply with fish size; (2) estimating true egg production from a no-take reserve would require removal of individuals from that protected area, imposing negative implications for that no-take area; (3) estimating total egg production of a serial pelagic spawner is very difficult because (a) estimating batch fecundity requires capture of samples at time of spawning; (b) spawning frequency is difficult to estimate; (c) not all mature females reproduce every year; and (d) social interactions can affect the number of spawns and eggs produced within a species (see review by Sadovy 2001); and (4) the number of no-take reserves effectively protected for long periods of time (e.g., decades) remains limited.

On the inshore coral reefs of the Great Barrier Reef (GBR) the stripey seaperch (*L. carponotatus*) is a secondary target of the commercial fishery, but is commonly caught by recreational fishers. It has significantly greater biomass in the no-take reserves than in the fished areas on the inshore coral reefs of the GBR (Evans and Russ 2004; Williamson et al. 2004). On the GBR, *L. carponotatus* is a gonochoristic serial spawner, with a peak spawning period from October to December, with some larger individuals probably spawning over a longer period (Kritzer 2004). This study aimed to estimate batch fecundity of *L. carponotatus* and compare estimates of batch fecundity per unit area (BFUA) for fished and protected populations on the inshore reefs of the GBR after 14 years of fisheries protection. Batch fecundity per unit area was estimated assuming that all mature fish per 1,000 m^2 would spawn once. In the absence of information about annual spawning frequency, this study only estimated the BFUA of *L. carponotatus*, and did not extrapolate batch fecundity estimates to total egg production.

Materials and methods

The Great Barrier Reef Marine Park (GBRMP) in Australia was established in 1975, and Marine Park zoning was first formally implemented by the GBRMP Authority in 1981 in the Capricornia (southern) section of the park. No-take protection of reefs in this study was implemented by 1987 (Williams and Russ 1994). Thus at the time of the field surveys (see below) these reefs had been protected for

14–17 years. The multiple-use zoning plan for the entire GBRMP changed on 1 July 2004. This re-zoning entailed an increase in no-take reserves (reserves) from 4.5% of the marine park to 33.4%. In terms of the actual number of coral reefs, the protection increased from approximately 21 to 30% of 2,900 individual coral reefs in the GBRMP.

Surveys

Underwater visual census (UVC) was conducted at the Palm Islands during March–April from 2001 to 2003, the Whitsunday Islands during November–December from 2001 to 2003, and in the Keppel Islands during October in 2002 and May in 2004 (Fig. 1). The Keppel Island group was not surveyed in 2001 and 2003 due to bad weather. Fish and benthic data were collected at all three island groups in 2002. Thus, this was the only year for which formal (statistical) spatial comparisons of *L. carponotatus* populations from all three island groups were made. This study was part of a larger long-term project surveying 12 sites each in fished and reserves at all island groups. However, only 6 sites each were surveyed in fished and reserve areas in the Keppel Islands in 2002. Therefore, to balance the data sets, 6 sites each were randomly removed from the 12 fished and reserve sites in the Palm and Whitsunday Islands. The reef flats at all three island groups are exposed at lowest astronomical tide, and the reef slope, which ranges from gentle to vertical walls, has high structural complexity. The bottom of the reef slope varied in depth from 5 to 20 m. Data on the abundance of fish and benthic organisms were collected by UVC along the reef slope at a depth of 4–9 m.

The abundance and individual size of *L. carponotatus* were estimated at each site on five replicate transects measuring 50 m × 6 m (300 m^2). Fish were assigned to 5 cm size classes (i.e., 0–5, 5.1–10, 10.1–15 cm FL etc., up to 35.1–40 cm). For ease of presentation, size classes are presented as the largest length in each size class (5, 10, 15, 20 cm). Target species biomass did not correlate with measured habitat variables (Evans and Russ 2004), so habitat variables were not included in the present study. A spatial and temporal comparison of the biomass of *L. carponotatus* in the no-take and fished areas is presented to illustrate effects of zoning on the target species in this study.

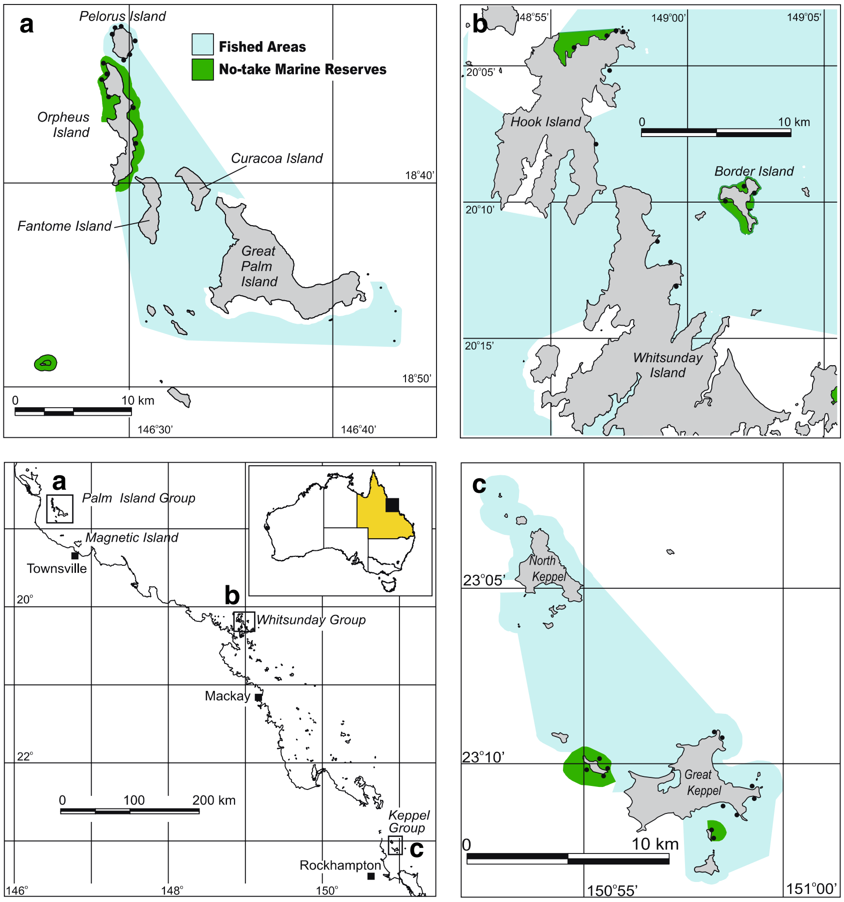

Fig. 1 Map of the Queensland coast and the three island groups: **a** Palm, **b** Whitsunday and **c** Keppel Islands. *Black dots* indicate sampling sites

Batch fecundity

The *L. carponotatus* samples were collected from Pelorus Island (Palm Islands) by divers using scuba and spear guns in the last quarter moon phase of October 1997 and from the first quarter to the full moon in October 2001. To date, no unequivocal evidence has shown that *L. carponotatus* spawn at any particular time of the month during the peak spawning season. Preliminary evidence suggests that fish sampled over the new moon at Lizard Island had larger gonads than fish captured in the last quarter at Pelorus Island (Kritzer 2004). However, this may have been a regional difference, as it was also noted that samples collected in the same study at Lizard Island had higher proportions in the larger size classes (Kritzer 2002).

The individual ripe females were divided into four size classes: 15.1–20 cm FL ($n = 13$), 20.1–25 cm FL ($n = 26$), 25.1–30 cm FL ($n = 15$), and 30.1–35 cm FL ($n = 2$). Gonads were weighed (gram wet weight) immediately after removal and placed in the gonad fixative Formaldehyde, Acetic Acid, Calcium Chloride (FAACC). The sex of *L. carponotatus* cannot be determined by external features underwater so all individuals above 16 cm (approximate size of first maturity determined by Kritzer 2004) were targeted for collection. This random sampling of mature individuals (>15 cm) provided the necessary estimate of female to male ratio per size class required to estimate BFUA of the females in the population.

The *L. carponotatus* gonads can be sexed and staged macroscopically, except for determination between ripe (stage IV) and running ripe (stage V) gonads (Kritzer 2004). Stage IV and V gonads were sectioned at 5 μm, stained with haematoxylin and eosin and histologically examined to determine the exact stage of development of the gonad.

Histological staging was based on Ganias et al. (2004) to ensure that the individuals with the correct yolk globule stages were chosen for batch fecundity estimates. Ganias et al. (2004) found that the oocyte spawning batch of *Sardina pilchardus sardina* begins to separate in size from the smaller oocytes at the secondary yolk globule stage, and a well-developed size-difference occurs at the tertiary yolk-globule stage. This size difference at the secondary yolk globule stage was observed in *L. carponotatus* gonads (Fig. 2). To allow for cutting artefacts, multiple measurements were made of oocytes on all the histological sections ($n = 56$) to determine which size oocytes to include in the batch fecundity counts. The maximum size of primary yolk globule stage oocytes (which had a nucleus) was less than 0.30 mm diameter. Therefore, all oocytes greater than 0.30 mm diameter were in the secondary yolk globule stage and were included in the study. Macroscopically, these oocytes had a very distinct colour difference from less developed oocytes. The oocytes more mature than and including secondary yolk globule stages (SY/TY and HO) (Fig. 2b) were dark yellow compared with the whitish/pale yellow of the inactive oocytes (YV and PO; Fig. 2b).

Few females had hydrated oocytes, and approximately 40% had tertiary yolk development. To determine if batch fecundity estimates could be determined using secondary yolk stage gonads the size class specific batch fecundity of 3 to 23 randomly selected females with secondary and tertiary yolk-staged gonads was estimated and compared in an ANOVA. Batch fecundity estimates for females, with secondary or tertiary yolk development, in the three size classes analysed had no significant difference. No analysis was performed on the fourth size class (greater than 30 cm) as both samples had secondary yolk development. Therefore, all samples at the secondary yolk-globule stage and above were included in the study ($n = 56$ fish).

Batch fecundity was determined using gravimetric techniques (Hunter et al. 1985). Batch fecundity estimates have not previously been made for *L. carponotatus*. Thus, the amount of gonad tissue examined and where in the gonad to remove the tissue, needed to be determined. To account for the gonad wall during weighing of the entire gonad, a small tissue sample from the gonad wall was included in sections of two sizes (0.005, 0.010 g). These were removed from the anterior, median and posterior regions of both lobes of three gonads in the 20, 25 and 30 cm FL size classes and from only two gonads of the 35 cm size class ($n = 2$). There was a significant difference in batch fecundity among size classes ($F_{3,84} = 146$; $P < 0.0001$). However, there was no significant difference in batch fecundity based on the size of section, the location of the lobe, and between gonad lobes. For consistency, estimates were only taken from the left lobe sections weighing 0.005 g. Once the oocytes were separated from the surrounding tissue, they were photographed using a photomicroscope. The resulting images were loaded into the software package Image Tool to count and measure all of the oocytes in the sample. The batch fecundity per individual per size class, the average number of eggs per gram of gonad, and the egg diameter per size class were determined.

Batch fecundity per unit area

The population was divided into four size classes: ≤20 cm (FL) ($n = 13$); 20.1–25 cm (FL) ($n = 26$); 25.1–30 cm (FL) ($n = 15$); and >30 cm (FL) ($n = 2$). The overall female to male sex ratios of the samples collected in 2001 from the Palm Islands was 1.06:1. On the GBR, Kritzer (2004) observed the same female to male ratios at Lizard Island, but recorded a female biased ratio of 1.3:1 in the Palm Islands from 1997 to 1998. Kritzer (2004) concluded

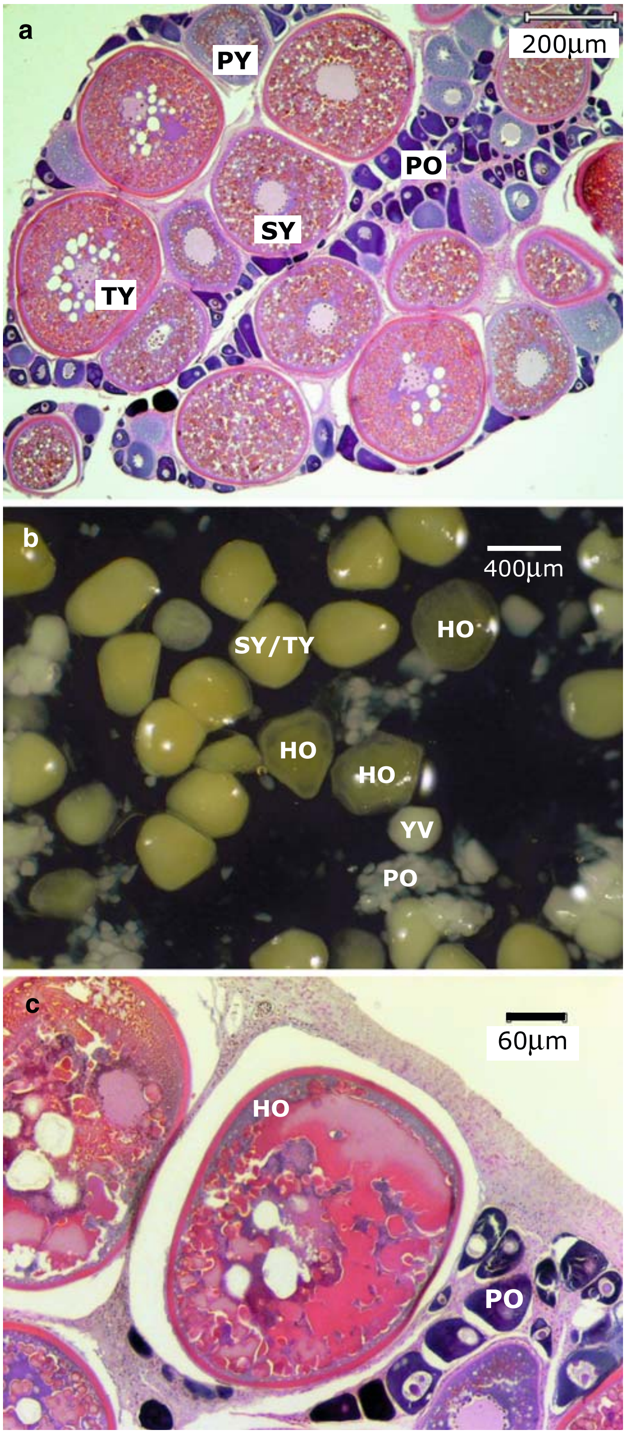

Fig. 2 Photographs of the oocytes of *Lutjanus carponotatus*. **a** Histological photograph (4×) of the tertiary yolk globule stage indicating the group-synchronous pattern of oocyte development. **b** Macroscopic photo of Hydrated Oocyte stage and **c** histological photo (10×) of hydrated Oocyte stage. *YV* yolk vesicle stage; *PY* primary yolk globule stage; *SY* secondary yolk globule stage; *TY* tertiary yolk globule stage; *PO* primary oocytes; *HO* hydrated oocytes

that the results for the Palms in 1997–1998 were not representative as they did not conform to what would be expected for a gonochore lacking complex mating interactions such as defence of females or territories. The sex ratios (female to male) in the four size classes were: ≤20 cm (FL) (1:1.4), 20.1–25 cm (FL) (1.4:1), 25.1–30 cm (FL) (1.2:1), and >30 cm (FL) (1:1). The batch fecundity/individual/size class was multiplied by the size-specific sex ratios and density data collected between 2001 and 2004 in the Palm, Whitsunday, and Keppel Islands.

Assumptions

A number of assumptions were made to generate the results. These assumptions include: (1) the sex ratios of *L. carponotatus* at Pelorus Island (Palm Islands) were the same as those at Orpheus Island (no-take protected area in the Palm Islands), whereas sex ratios of 1:1 were used in the Whitsunday and Keppel Island Groups, as suggested by Kritzer (2004); (2) all individuals above minimum reproductive size spawn (in the absence of any estimate of annual spawning frequencies for *L. carponotatus* we do not extrapolate beyond the BFUA); (3) all of the secondary yolk-globule oocytes were spawned.

Analysis

Due to the different sampling years for the Keppel Islands (compared to the Palm and Whitsunday Islands), the temporal data were analysed in two sets, the Palms and Whitsunday Islands (2001–2003) and the Keppel Islands individually (2002 and 2004). The biomass data contained many zero estimates at the transect level, and often did not conform to the assumptions of ANOVA. Thus, all data were pooled to site level (five transects per site). Since the focus of this study was on variation between fished and no-take areas and between island groups, rather than between or within sites, pooling did not affect the comparisons of major interest. Thus, the spatial data were analysed with a two-factor orthogonal design ANOVA, using two zones (no-take and fished), three island groups (Palm, Whitsunday, and Keppel Island groups), and six nested sites as replicates within each combination of zone and island group.

To meet the assumptions of ANOVA in the spatial comparison, the *L. carponotatus* biomass data had to be square root transformed. The temporal Whitsunday and Palm Island data were log10(x) transformed to meet the assumptions of repeated measures ANOVA (normal distribution, homogeneity of variance, sphericity). Comparisons between batch fecundity per size class (square root transformed to meet Levene's test of homogeneity of variance) and egg diameter per size class were analysed using a fixed factor one-way ANOVA using four fish size classes and either batch fecundity or egg diameter as the replicates.

The BFUA was analysed in a two-factor orthogonal ANOVA using the data from all three island groups in 2002. In addition, BFUA was subjected to a repeated measures ANOVA across time. The analyses were divided into two groups to allow for the different sampling times in the Keppel Islands, as indicated above. The spatial data (2002) for *L. carponotatus* were log10(x) transformed. The temporal Palm and Whitsunday Island data for *L. carponotauts* were log10(x) transformed to pass the homogeneity of variance assumption of ANOVA.

Results

Biomass per unit area

In all three island groups combined in 2002, the overall mean biomass per unit area of *L. carponotatus* in the reserves (4.9 kg 1,000 m^{-2}) was approximately 2.3 times greater than that in the fished areas (2.2 kg 1,000 m^{-2}) (Fig. 3a). Although there was some variability in biomass per unit area within each zone at each island group among years (Fig. 3b), there was no significant effect of year for the combined Whitsunday and Palm group analysis or the Keppel Island group analysis (Table 1). The only significant factor in any analysis was zone (Table 1).

Batch fecundity

Batch fecundity of *L. carponotatus* increased with FL, best described by a power function:

$$F = 0.0054 \times \mathrm{FL}^{5.28} \left(r^2 = 0.64\right),$$

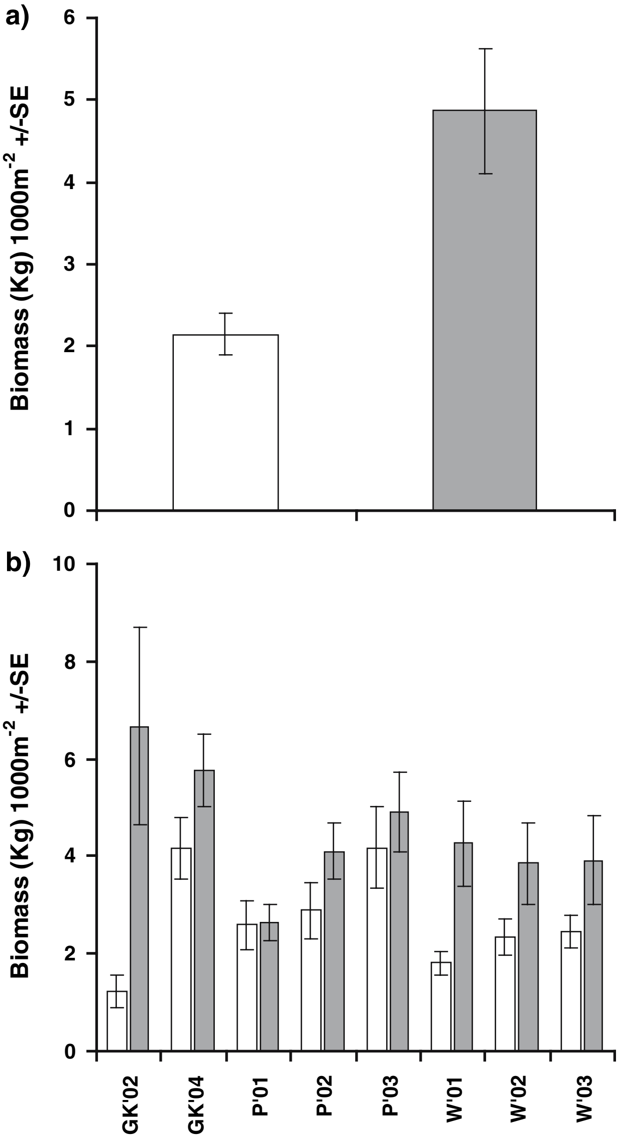

Fig. 3 **a** Spatial and **b** temporal comparisons of *L. carponotatus* biomass in no-take and fished areas in the Palm, Whitsunday and Keppel Islands from 2001 to 2004. *GK* Great Keppel Islands, *P* Palm Islands, *W* Whitsunday Islands, *White bars* Fished, *Grey bars* No-take reserves. The year is designated by '01, and so on

Table 1 Results of ANOVA and repeated measure ANOVAs of biomass/unit area for *Lutjanus carponotatus* in the Palm, Whitsunday and Keppel Island Groups between 2001 and 2004

Source of variation	Year × Zone × Island (*df*)	Year × Island (*df*)	Year × Zone (*df*)	Year (*df*)	Zone × Island (*df*)	Island (*df*)	Zone (*df*)
L. carponotatus 2002	–	–	–	–	2.923 (1.30) NS	0.107 (1.30) NS	12.258 (1.30)***
L. carponotatus W&P	0.86 (2.40) NS	1.72 (2.40) NS	0.14 (2.40) NS	2.93 (2.40) NS	0.21 (1.20) NS	0.15 (1.20) NS	4.62 (1.20)*
L. carponotatus KI	–	–	1.627 (1.10) NS	0.450 (1.10) NS	–	–	8.16 (1.10)*

W&P Whitsunday & Palm Islands, *KI* Keppel Islands, *NS* not significant

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

where F is batch fecundity and FL is fork length (cm). For statistical analysis of the regression, the raw data were logged ($F_{1,56} = 110.8$; $P < 0.001$), but the raw data were plotted to demonstrate the length–fecundity relationship. The large exponent in this relationship may be influenced substantially by the two largest fish in the study (Fig. 4a). However, if these two data points are removed, the exponent was still greater than 5.

The highest individual batch fecundity recorded was 748,957 eggs (FL = 305 mm) and the lowest was 7,074 (FL = 184 mm). This represents a more than 100-fold difference (Fig. 4a). The average batch fecundity per individual in each size class ranged from 33,621 eggs in the 20 cm size class up to 698,394 eggs in the 35 cm size class (Fig. 4b). Thus, fish in the largest size class produced on average 20 times more eggs than fish in the smallest size class. Batch fecundity significantly increased with size classes ($F_{3,52} = 32.9$; $P < 0.001$) (Fig. 4b). The 35 cm size class had significantly greater batch fecundity than all other size classes (Tukey's HSD $P < 0.0001$ in all cases), while the 20 cm size class had significantly less batch fecundity than the two intermediate size classes (Tukey's HSD $P = 0.002$ and $P < 0.001$). Batch fecundity did not statistically differ between the two middle size classes. For statistical analysis of the regression, the raw data were logged ($F_{1,2} = 48.3$; $P = 0.02$), but the raw data were plotted to demonstrate the size class–fecundity relationship.

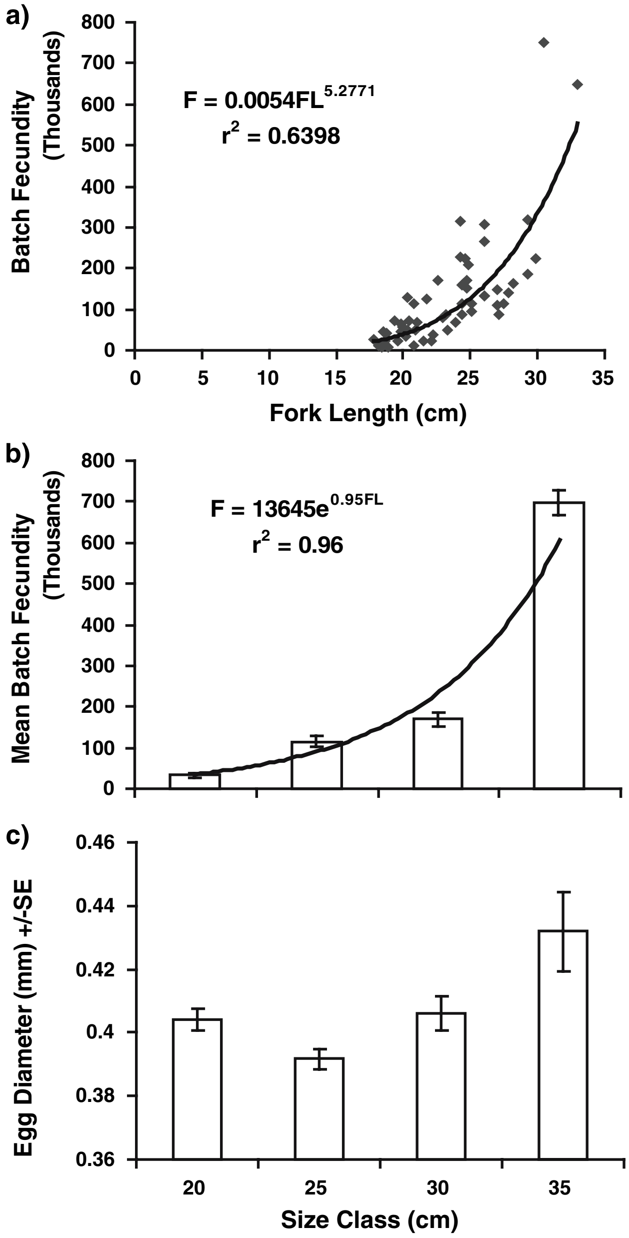

Fig. 4 Batch fecundity data from *L. carponotatus*. **a** Fork Length vs batch fecundity; **b** Average batch fecundity/individual/size class with a power curve fitted, and **c** Average egg diameter/size class. *F* fecundity, *FL* fork length

There was no overall relationship for egg diameter (Fig. 4c); however, the largest size class (35 cm) had significantly greater egg diameter than the 25 cm size class (Tukey's HSD, $P = 0.03$) (Fig. 4c). The other size classes recorded no statistical differences between them.

Batch fecundity per unit area

In all three island groups combined in 2002, the overall mean batch fecundity per unit area BFUA of *L. carponotatus* in the reserves (1,077,130 eggs 1,000 m^{-2}) was approximately 2.5 times greater than that in fished areas (429,379 eggs 1,000 m^{-2}) (Fig. 5a). The inter-annual variability in BFUA within each zone at each island group among years was comparable to the variability in biomass (Figs. 3b, 5b). There was no significant effect of year for the combined Whitsunday and Palm group analysis or the Keppel group analysis (Table 2). The only significant factor in any analysis was zone (Table 2).

Comparing biomass per unit area to BFUA

An average 2.3-fold difference in biomass between no-take reserves and fished areas converted to an average 2.5-fold difference in batch fecundity per unit area. Therefore, the difference in batch fecundity per unit area between zones was 9% greater than the difference estimated for biomass per unit area. However, this result is surprisingly small considering the difference between the exponents for the length to body weight conversions ($b \sim 3$) and the length to fecundity relationships ($b \sim 5$). Three of the eight surveys conducted in the three Island groups produced estimates of BFUA that were equal to or less than biomass per unit area differences when comparing no-take to fished areas

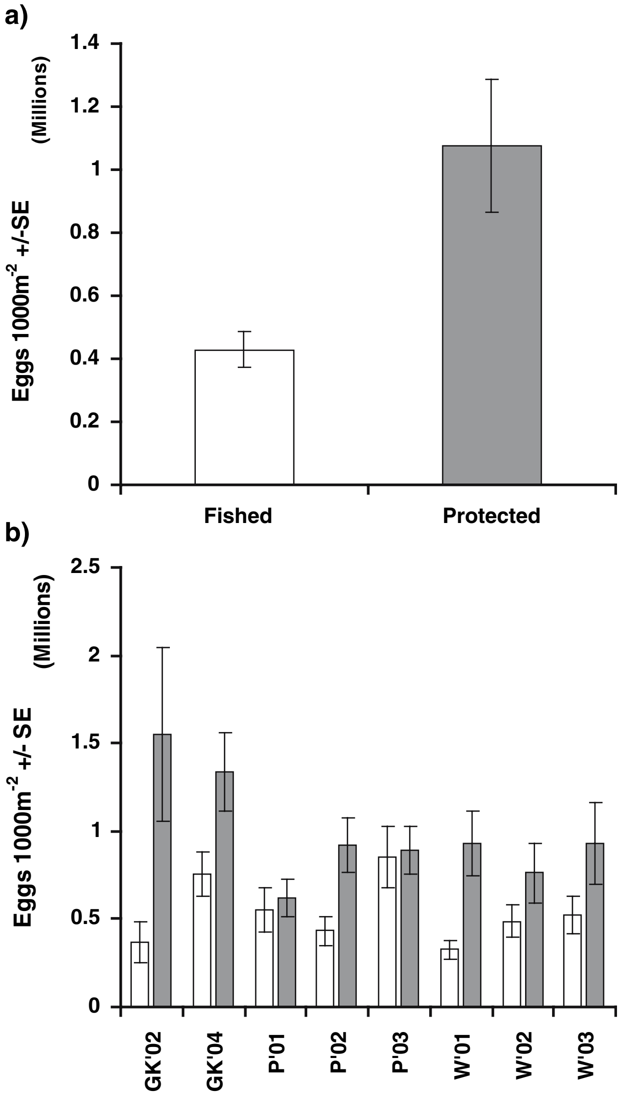

Fig. 5 **a** Spatial and **b** temporal comparison of batch fecundity per unit Area of *L. carponotatus* in the no-take and fished areas of the Palm, Whitsunday and Keppel Islands from 2001 to 2004. *GK* Great Keppel Islands, *P* Palm Islands, *W* Whitsunday Islands, *White bars* Fished, *Grey bars* No-take reserves. The year is designated by '01, and so on

(Table 3). The minimal increase from biomass per unit area to BFUA is put into perspective by examining the relative contributions of the different size classes in the no-take and fished areas. The 25 cm size class in the fished areas, with relatively high abundance and medium size, produced the highest proportional contribution (45%) to the BFUA in the fished areas (193,000 eggs 1,000 m^{-2} from the total 429,000 eggs 1,000 m^{-2}) (Fig. 6). However, the least abundant size class (35 cm) produced the highest proportional contribution (47%) to the BFUA in the no-take areas (504,000 eggs 1,000 m^{-2} from the total 1,077,000 eggs 1,000 m^{-2}) (Fig. 6). In fact, the BFUA of the relatively few 35 cm size class individuals in the no-take areas (504,000 eggs 1,000 m^{-2}) was more than the total mean estimate of all size classes in the fished areas (429,000 eggs 1,000 m^{-2}) (Fig. 6).

Discussion

The aim of this study was to compare the BFUA between no-take and fished areas of inshore GBR coral reefs based on underwater visual census of fished and no-take marine reserves. This study provides preliminary evidence that a fishery target species in no-take areas has a greater BFUA than fished areas on the inshore reefs of the GBR. However, the BFUA estimates are lower than might be expected given that fecundity increases with length more rapidly than biomass. In other words, fecundity of larger fish is a greater proportion of body size than smaller fish, which corroborates Kritzer's (2004) finding that the gonadosomatic index increases with body size in *L. carponotatus*. Despite this disproportionately greater fecundity of large fish, the relative difference in BFUA between protected and fished areas was only slightly higher than the relative difference in biomass.

Larger fish generally have greater egg production per spawning event (Berkeley et al. 2004). The frequently cited comparison of individual fish fecundity for red snapper (*L. campechanus*; Plan Development Team 1990) has often been used to justify the expectation that, since no-take reserves produce more fish and bigger fish, they will enhance egg production per unit area even more than they enhance biomass (Palumbi 2004). Given this expectation, one might expect larger differences in BFUA between no-take and fished areas in this study, such as the 11-fold to 18-fold differences reported for *Pagrus auratus* in New Zealand by Denny et al. (2004), but this was not the case. Relative differences in BFUA were more modest, and were

Table 2 The no-take marine reserves/fished areas ratios of biomass and batch fecundity/unit area (BFUA) in the Palm and Whitsunday Islands in 2001, 2002, 2003 and Keppel Island in 2002 and 2004

	Palms			Whitsundays			Keppels	
	2001	2002	2003	2001	2002	2003	2002	2004
L. carponotatus biomass	1.0	1.4	1.2	2.4	1.6	1.6	5.4	1.4
L. carponotatus BFUA	1.1	2.1	1.0	2.8	1.6	1.7	4.2	1.8

Table 3 Results of the ANOVA and repeated measure ANOVAs of the batch fecundity/unit area of *L. carponotatus* in the Palm, Whitsunday and Keppel Island Groups

Source of variation	Year × Zone × Island (2,40 *df*)	Year × Island (2,40 *df*)	Year × Zone (*df*)	Year (*df*)	Zone × Island (*df*)	Island (*df*)	Zone (*df*)
L. carponotatus 2002	–	–	–	–	2.44 (2.30) NS	0.20 (2.30) NS	13.32 (1.30)***
L. carponotatus W&P	0.97 (2.40) NS	0.66 (2.40) NS	0.36 (2.40) NS	1.95 (2.40) NS	0.16 (1.20) NS	0.01 (1.20) NS	7.87 (1.20)*
L. carponotatus KI	–	–	0.86 (1.10) NS	0.08 (1.10) NS	–	–	8.33 (1.10)*

W&P Whitsunday & Palm Islands, *KI* Keppel Islands, *NS* not significant

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

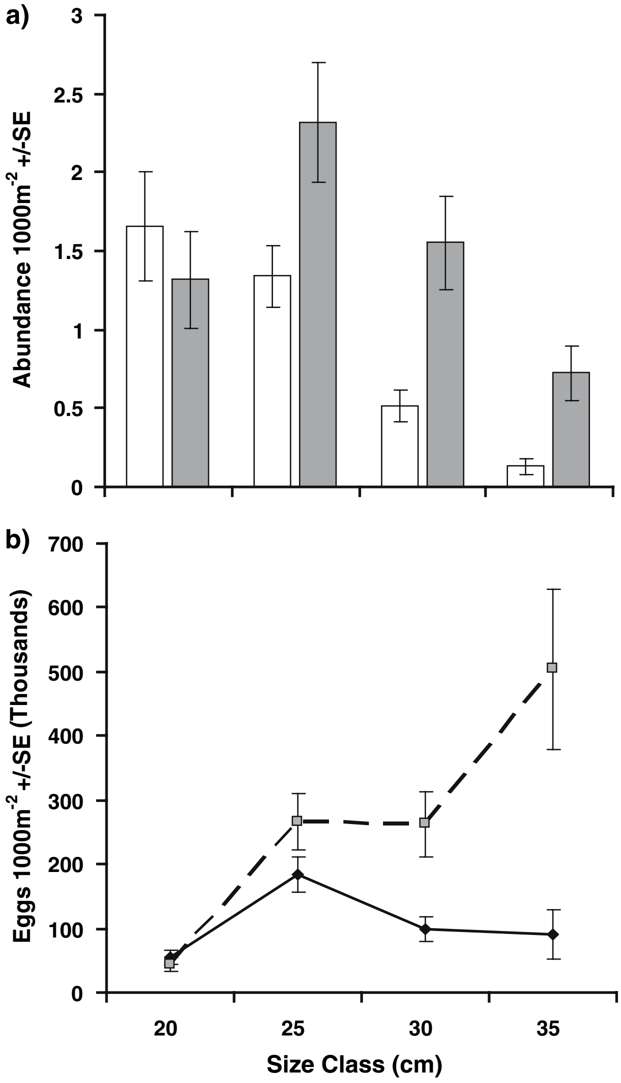

Fig. 6 Density of *L. carponotatus* females and the mean batch fecundity per size class in each zone in the Palm, Whitsunday and Keppel Islands 2002. *White bars* Fished, *Grey bars* No-take reserves; *Dash line* Protected; *Solid line* Fished

similar to those estimated for *Sebastes* in California by Paddack and Estes (2000). Individuals in larger size classes that would have the greatest effect on the relative increases in BFUA were comparatively less abundant in some no-take reserves, due to natural mortality schedules, lack of recruitment in previous decades, or potential poaching within these no-take areas (Davis et al. 2004).

Larger individuals, as there are typically so few, often have relatively little effect on reproductive output, and only become important when there is a shift in population structure toward older and larger age and size classes (Kritzer and Davies 2005). The results of this study tend to support their claims. After 15 years of protection, there were consistently more larger fish in all size classes affected by the fishery (Fig. 6). In the no-take areas in this study, the largest size class contributed nearly 50% of the BFUA with relatively few individuals. In contrast, nearly 50% of the BFUA in the fished areas was provided by the greater numbers of mid-sized fish (<25 cm), not yet recruited to the fishery (Fig. 6). Furthermore, the mean BFUA for all size classes in the fished areas was approximately 429,000 eggs 1,000 m^{-2}. The mean BFUA for the largest size class in the no-take areas was approximately 504,000 eggs 1,000 m^{-2}. Therefore, the contribution to BFUA, by only the largest size-class in the no-take areas, is greater than the mean of all the size classes in the fished areas of this study. This demonstrates the value of long-term protection to enable the build up of larger individuals.

Batch fecundity alone does not determine the relative reproductive output of individuals within a population. Age and size of a fish may determine the number of times an individual spawns, as well as the quality of eggs produced (Berkeley et al. 2004). Kritzer (2004) determined that larger *L. carponotatus* have longer spawning seasons and therefore may also spawn more times in a year than smaller individuals. Older and larger rockfishes (*Sebastes* spp.) produced larger eggs that may result in faster larval growth, higher survival rate in the plankton and greater recruitment success (Berkeley et al. 2004). Therefore, larger fish tend to produce more eggs that are bigger, and presumably may be more viable (Ojanguren et al. 1996; Pepin et al. 1997; McCormick 1998). The present study detected a pattern of increased egg diameter from smaller to larger individuals of *L. carponotatus*. If there are a greater number of larger individuals producing more viable offspring in the no-take areas, the increased BFUA should provide greater benefits than the present results suggest. That is, recruitment potential may also be higher from these protected populations than from a fished population with smaller and younger fish. However, more investigation is required as these issues are still unresolved due to the ambiguity of the results in the smaller size classes of this study. Furthermore, information on spawning frequency of different age and size classes is required for more accurate estimates of egg production per unit area.

Recent advances have enabled direct estimates of self-recruitment within local populations of coral reef fishes. By tagging the demersal eggs of *Amphiprion polymnus* with tetracycline, Jones et al. (2005) found 30% self-recruitment to one population of anemones in Kimbe Bay, Papua New Guinea (PNG). Furthermore, they used microsatellite markers to determine that some individuals actually settled to within 100 m of their natal anemone after a 10-day pelagic period. Almany et al. (2007) demonstrated up to 60% self-recruitment of *Chaetodon vagabundus* (30–40 day pelagic period) and *Amphiprion percula* (~11 day pelagic period) to Kimbe Island in Kimbe Bay, PNG. Based on these figures, more than 40% of larvae settling in that area originated from reefs up to 10 km away. Thus, greater BFUA in the no-take reserves on the inshore reefs of the GBR has the potential to effectively replenish nearby no-take and fished areas. Just how far the larval fish on the GBR disperse requires a multi-disciplinary approach incorporating larval tagging, genetics and biophysical modelling.

Increased egg production from no-take areas may be irrelevant if recruitment is already at saturation levels, and post-recruitment processes such as food availability and predation determine adult populations. On the GBR where fish stocks are exploited, but not overly so, increased levels of egg production from no-take areas may have slightly less benefits than on heavily depleted reefs elsewhere in the world. In such over-fished areas, increased density of larger size classes in a network of no-take reserves could provide huge benefits to surrounding fished and protected reefs (Russ 2002). Potential recruitment benefits from increased export from reserves should be assessed on a regional basis depending on reef fish stock status, exploitation levels and connectivity of populations.

Greater biomass of *L. carponotatus* in the no-take areas compared to fished areas around the same inshore island groups of the GBR has been recorded in other years of sampling (Williamson et al. 2004). The temporal consistency reported in the present study strengthens the conclusions of Williamson et al. (2004) that there is a significant influence of reef zoning on the biomass of species targeted by fishing. In contrast, Kritzer (2002) found that density and biomass of *L. carponotatus* were greater in the fished area in the Palm Island group than in the no-take area in 1999. He speculated that fishing pressure might not be high enough to affect differences, or that release from competition with, or predation by, preferred target species (larger serranids and lutjanids) might be advantageous to *L. carponotatus* in fished areas. Another possibility is that these studies are detecting a transition in the effects of protection at the Palm Island group. At the time of Kritzer's (2002) sampling in 1999, the site had been protected for 12 years. By the end of the sampling in the present study, the site had been protected for 16 years, approximately the maximum longevity of individuals in the species at the Palm Island group (Kritzer 2002, 2004). Therefore, these studies may have occurred during a progressive accumulation of reserve effects and are capturing the state of the system at different points along that increasing trajectory. It is notable that Kritzer's (2002) estimates of biomass per km^2 for the fished site (3,139 and 3,890 g, using different approaches, for Pelorus Island) is intermediate among those estimated in this study, but his estimates for the no-take site (1,966 and 2,235 g for Orpheus Island) are below any estimated herein. Furthermore, biomass at the no-take site shows a continual increase from Kritzer's (2002) data through the final year of this study that is not seen for the fished site.

In conclusion, this study and several others (Graham et al. 2003; Evans and Russ 2004; Williamson et al. 2004) show that no-take marine reserves in the inshore regions of the Great Barrier Reef had a greater biomass of species targeted by fisheries than nearby fished areas. This study also demonstrated greater batch fecundity per unit area for *L. carponotatus* in no-take marine reserves compared to the fished areas. Recent research on the connectivity of fish populations within the Great Barrier Reef (e.g., Jones et al. 1999) suggests that the greater batch fecundity per unit area in reserves should benefit the no-take area itself, but should also be of benefit to surrounding fished areas. Two key areas of research require immediate attention to improve our understanding of marine reserve connectivity: (1) measurement of reef fish larval dispersal to determine connectivity regimes to ground truth the predictions from models; and (2) research on spawning frequency of synchronous-batch pelagic spawners, such as lutjanids, to determine the benefits of increased mean body size and to establish annual egg production estimates for no-take and fished areas. This study is the first on the Great Barrier Reef to attempt the estimation of BFUA of reef fish stocks in no-take marine reserves. The results have shown that marine reserves are effectively protecting fish stocks on the inshore reefs of the GBR, allowing for greater biomass and potentially more egg production than in surrounding fished areas.

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