

## Demography, fishery yield and potential management strategies of painted spiny lobster (*Panulirus versicolor*) at Northwest Island, Great Barrier Reef, Australia

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**Abstract.** Quantification of demographic parameters is important for understanding how populations interact with their environment and for developing sustainable harvest strategies. Our aims were to quantify demographic parameters and yield of painted spiny lobster (*Panulirus versicolor*) at Northwest Island, Great Barrier Reef and review fishery management regulations in view of the findings. Using catch-curve analysis and an intensive mark–recapture program, the local lobster population was found to be sparsely distributed ( $\sim 1.3 \text{ ha}^{-1}$ ), with low rates of natural mortality ( $0.25\text{--}0.28 \text{ year}^{-1}$ ) and immigration ( $0.05 \text{ ha}^{-1} \text{ year}^{-1}$ ). Under current management regulations (no minimum size limit; MSL), yield-per-recruit peaked at  $0.38 \text{ kg}$  when fishing mortality was  $0.4 \text{ year}^{-1}$ . Implementation of a 100-mm (carapace length) MSL is recommended because it provides the best compromise between yield and stock size and has minimal impact on existing fishing practices. Revocation of the prohibition on possessing egg-bearing females is also recommended because it would reduce wastage of lobsters that are inadvertently killed by spear-fishers and because there appears to be little chance of localised recruitment overfishing. This study provides the first estimate of mortality rate for *P. versicolor* and highlights the importance of this parameter for understanding demographic processes and optimising management regulations.

**Additional keywords:** coral reefs, fishery management, mortality, population dynamics, yield per recruit.

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### Introduction

Spiny lobsters (Family Palinuridae) are a highly esteemed seafood, not just in places where they are captured, but all over the world. Consequently, spiny lobsters are a high-value commodity and commercial, recreational and artisanal fisheries have developed wherever these animals are abundant (Pitcher 1993; Phillips 2006). Due to the increasing size and wealth of the human population, the future worldwide demand for spiny lobsters is expected to increase. However, most of the world's spiny lobster fisheries are now considered to be either fully exploited or over exploited (Phillips and Melville-Smith 2006). The need for effective management of spiny lobster populations is therefore critical.

Effective management of lobster populations requires knowledge about the fishery (e.g. catch per unit effort), biology of the target species (e.g. size at first maturity) and demography of the unit stock. One of the most important demographic parameters is mortality rate, because it is requisite for development of almost all fishery harvest models (Vetter 1988). Total mortality rate ( $Z$ ) is the sum of deaths caused by natural mortality ( $M$ ) and fishing mortality ( $F$ ). Surprisingly,  $Z$ ,  $M$

and  $F$  are unknown for most species of spiny lobster, primarily because age determination is hindered by moulting (ecdysis). As such, mortality rates of spiny lobster populations are most often estimated by length-converted catch curve (LCCC) analysis (Morgan 1980; Pitcher 1993), which involves conversion of length frequencies to age frequencies using von Bertalanffy growth parameters (Pauly 1983). However, LCCC analysis is often unreliable because of errors associated with variable recruitment, size-specific gear selectivity and the poor empirical relationship between lobster length and age (King 1995). Another method for estimating mortality rate of spiny lobster populations is multiple mark–recapture. The Jolly–Seber mark–recapture model is particularly useful because it can simultaneously estimate population size, mortality rate and recruitment (or immigration) rate and the model allows each of these parameters to vary with time (Krebs 1999).

Once mortality rate and other demographic parameters have been adequately quantified, yield of lobster fisheries can be investigated via yield-per-recruit (YPR) analysis (Ebert and Ford 1986; Pitcher 1993). The YPR model examines the trade-off between capturing a larger number of young (or small)

individuals versus capturing a smaller number of old (or large) individuals and is dependent upon growth, natural mortality, fishing mortality and size at first capture (Beverton and Holt 1957). In practice, the latter two parameters are manipulated, at least hypothetically, to help identify management schemes that maximise sustainable yield.

Much of what is known about spiny lobsters comes from studies of three commercially important species (*Panulirus argus*, *Panulirus cygnus* and *Jasus edwardsii*), which together comprise ~70% of the total world catch (Lipcius and Eggleston 2000; Phillips and Melville-Smith 2006). Much less is known about other exploited species, particularly those that inhabit the tropical west-Pacific region (Pitcher 1993; Munro 2000). One consequence of this knowledge gap is that the lesser-known species may be inadequately managed, leading to over exploitation (King 1995; Phillips and Melville-Smith 2006). At present, there are no knowledge-based management schemes in place for any stock in the entire tropical west-Pacific region, apart from *Panulirus ornatus* in the Torres Strait (between Australia and Papua New Guinea) (Munro 2000).

The painted spiny lobster (*Panulirus versicolor*) inhabits coral reefs of the Indo-West Pacific Ocean (George 1974), including Australia's Great Barrier Reef (GBR), where it is sought after by recreational fishers (Frisch *et al.* 2008). *P. versicolor* is reluctant to enter traps (the standard fishing gear for temperate palinurids), so they are extracted from their coral shelters (dens) using rubber-propelled spears. By world standards, the total catch of *P. versicolor* on the GBR is small (6000–8000 kg year<sup>-1</sup>; A.J. Frisch and J.-P.A. Hobbs unpubl. data). However, individuals of *P. versicolor* inhabit predictable places (Frisch 2008) and maintain strong associations with small reef areas for long periods of time (Frisch 2007b), which together predispose this species to over-exploitation. This highlights the need to better understand the demography of *P. versicolor* when developing management strategies for this species.

The GBR extends for 2300 km along the north-east coast of Australia and comprises over 2900 individual reefs (Hutchings *et al.* 2008). Due to the long duration and extensive dispersal potential of palinurid larval stages (Dennis *et al.* 2001; Phillips *et al.* 2006), *P. versicolor* on the GBR probably represent a single unit stock. Given that 20% of reefs in the region are protected from fishing (Fernandes *et al.* 2005; Day 2008) and many more are inaccessible to recreational fishers (Blamey and Hundloe 1993), conceivably there is a large unexploited breeding population. Thus, it is reasonable to assume that local overfishing would have little impact on the breeding potential of the unit stock. The management significance of this is that there is little risk of recruitment overfishing of individual reefs because the source of recruitment is unlikely to be local. The main biological concern for management, then, should not be protection of breeding females, but optimisation of yield from the local stock (e.g. by implementing an appropriate minimum size limit; MSL). However, current management of *P. versicolor* on the GBR is antithetical; ovigerous and spermatophoric females are protected, but size limits are non-existent (Anon. 2008). For these reasons, as well as the high value, low abundance and site fidelity of *P. versicolor* (Frisch 2007b, 2008), the conservation status of this species is insecure.

Our first objective was to estimate total mortality rate ( $Z$ ) of *P. versicolor* using a Jolly–Seber, multiple mark–recapture model. For comparison, mortality rate was also quantified using LCCC analysis. In both cases, estimates were based on adult individuals (>90 mm carapace length;  $L_c$ ) because juveniles are virtually absent from the study site (Frisch 2008). The second objective of this study was to estimate potential fishery yield of *P. versicolor* and to explore potential management strategies that enhance sustainability of this important fishery resource. *P. versicolor* is sparsely distributed throughout its range and is extraordinarily difficult to catch alive and uninjured on coral reefs, so the sample size for this study was necessarily small despite intensive sampling effort. Nonetheless, the results reported here are presented with an adequate level of confidence due to a high recapture rate of tagged individuals and relatively low variability in the data.

## Materials and methods

### Study site

The study was conducted on the coral reef at Northwest Island (23°18'S, 152°43'E) in the southern section of the Great Barrier Reef (GBR), Queensland, Australia (see Frisch 2007b; for a map of the study area). Northwest Island is adjacent to two small coastal cities (Rockhampton and Gladstone) and it supports a recreational fishery for *Panulirus versicolor* and other seafoods (authors' personal observation). Although *P. versicolor* inhabits the entire GBR, Northwest Island was chosen only for logistical reasons. However, the reef at Northwest Island is typical of other reefs in the region, so results and conclusions from this study may be applicable to other parts of the GBR and perhaps beyond.

The reef at Northwest Island has a high diversity and coverage of scleractinian corals and modest quantities of adult *P. versicolor* can usually be found wherever suitable dens exist. Although the total area of coral reef at Northwest Island was estimated to be 1100 ha, the study site (i.e. search zone) was confined to an area of ~60 ha because: (1) intensive searching of a relatively small area ensured an adequate number of tagged lobsters were recaptured; and (2) this small area was avoided by local fishers which enabled estimation of natural mortality (see below). The study site was adjacent to the exposed reef crest (1–4 m in depth) and was relatively homogeneous, consisting of scattered coral 'bombras' with interspersed sand patches (locally known as a 'bommie' field). There were no obvious barriers to movement within or across the boundaries of the study site, although nearby rubble barrens (beyond the reef edge) and tracts of sand (in the lagoon) were devoid of suitable dens.

### Mark–recapture surveys

Lobsters were captured by hand (with the aid of SCUBA) and transferred to a shallow, water-filled box onboard a nearby support vessel. Carapace length ( $L_c$ ; between the supra-orbital ridge and the posterior, dorsal edge of the carapace) was measured to the nearest 0.5 mm with Vernier calipers. Lobsters were uniquely marked in the abdominal musculature with elastomer implants (Northwest Marine Technology, Shaw Island, WA, USA) and then photographed ventrally to facilitate subsequent identification based on polymorphic, exoskeletal, colour patterns (Frisch and Hobbs 2007). Previous studies indicate this

marking and identification system is reliable (i.e. the frequency of misidentification is nil or negligible) and was not likely to affect survival or movement of spiny lobsters in the wild (Woods and James 2003; Frisch and Hobbs 2006). The entire tag-and-measure process, from capture to being returned to the den, was completed in ~5 min.

The study site was surveyed for 10 consecutive days on six occasions: December 2003, June 2004, December 2004, June 2005, December 2005 and December 2006 (June and December occur during the austral winter and summer respectively). Lobsters were captured during the first five surveys (December 2003–December 2005) and recaptured during the last five surveys (June 2004–December 2006). Thus, time-at-liberty ranged from 0.5–3 years depending on when each individual lobster was captured and recaptured. Data from the same pool of lobsters were used for both the Jolly–Seber and LCCC analysis, except that data from recaptured lobsters were excluded from the LCCC analysis to ensure independence.

#### Jolly–Seber analysis

Jolly–Seber formulae for estimating population size, survival rate and immigration rate are described by Krebs (1999). As recommended by Seber (1973), a correction factor was included in the analysis to rectify bias in small samples. To enable a comparison with results from the catch-curve analysis, finite survival rates ( $\Phi_t$ ) were converted to instantaneous mortality rates ( $Z$ ) using the equation:

$$Z = -\log_e(\Phi_t^2), \quad (1)$$

where the exponent '2' represents a conversion from bi-annual to annual rate. The overall annual mortality rate for the 3-year study was calculated as the arithmetic mean of the respective mortality rates for each census (Krebs 1999).

The assumptions of the Jolly–Seber model are that: (1) sampling time is negligible relative to sampling interval; (2) tags are not lost or overlooked; (3) every tagged individual has the same probability of survival; and (4) every individual has the same probability of being captured, regardless of whether or not it is tagged (Krebs 1999). Given the short duration of the sampling period (10 days every 6–12 months) and the effectiveness of the tagging technique (Frisch and Hobbs 2006, 2007), assumptions (1) and (2) were demonstrably satisfied. Evidence from other lobster species suggests that injury (autotomy) is the most likely factor to differentially affect survival of tagged lobsters (Parsons and Eggleston 2005; Brouwer *et al.* 2006). However, occasional autotomy has no significant effect on survival rate of *P. versicolor* (Frisch and Hobbs 2011), so assumption (3) was probably satisfied. With respect to assumption (4), equal catchability of lobsters was verified *a priori* using Leslie's test ( $\chi^2_5 = 6.8$ ,  $P > 0.1$ ). Although it is possible that some tagged lobsters emigrated from the study area (and biased the results), this was considered unlikely because individual *P. versicolor* maintain strong associations with small reef areas for long-term periods (Frisch 2007b, 2008).

#### Length-converted catch curve analysis

The mean size of male and female lobsters was compared using a parametric *t*-test after confirmation that relevant statistical

assumptions (normality and homoscedasticity) were satisfied (Zar 1999). If no gender differences were identified, then the data were pooled across groups.

The  $L_c$  of each lobster was assigned to a 5-mm length class to construct a length–frequency distribution. The relative age ( $t$ ) of each length class ( $L_t$ ) was estimated using the inverse of the von Bertalanffy growth equation:

$$t = (-1/K) \times \log_e(1 - L_t/L_\infty), \quad (2)$$

where  $K = 0.27 \text{ year}^{-1}$  and  $L_\infty = 144.7 \text{ mm}$  (Frisch 2007a). The time taken for *P. versicolor* to grow through a particular length class ( $\Delta t$ ) was calculated as the difference in relative ages between two adjacent length classes. Next, the natural logarithms of the frequency of each length class divided by the change in age ( $\log_e(\text{frequency}/\Delta t)$ ) were plotted against mean relative age. Lastly, a regression line was fitted to the data, excluding length classes with small sample sizes ( $n < 5$ ) or that exceeded  $L_\infty$  (King 1995). The significance of the regression line was tested by analysis of variance (ANOVA) after confirmation that relevant statistical assumptions (linearity, normality and homoscedasticity) were satisfied (Zar 1999). Total mortality rate ( $Z$ ) was estimated as the slope of the regression line.

#### Natural vs fishing mortality

Although the 60-ha study site was 'open' to fishing, it received little or no fishing pressure because it was located on the exposed side of the reef where wave energy was high and difficult to access (even in calm weather) due to a barrier-like, inter-tidal rampart of rocky reef that prevented vessel navigation whenever tide height was at or below mean sea level. Interviews with local fishers confirmed that they do not spear-fish within the 60-ha study area. No fishing was observed at the study site during the 70+ days that the authors were present. The inaccessibility of the study site, in combination with the small home-range of *P. versicolor* (Frisch 2007b, 2008), suggests that  $F$  was probably negligible (and  $M \approx Z$ ) for lobsters within the study area. Although it is possible to separate  $F$  and  $M$  using extensive catch and effort records (Morgan 1980; King 1995), this was considered beyond the scope of the present study because recreational fishery data are difficult to obtain because there are no reporting requirements for recreational fishers in Queensland and recreational landings are spatially and temporally dispersed.

#### Fishery yield

Yield per recruit (YPR) was estimated as per the model described by Beverton and Holt (1957):

$$\text{YPR} = W_\infty F e^{-M(t_c - t_r)} \sum_{n=0}^3 [U_n e^{-nK(t_c - t_0)} / (F + M + nK)],$$

where  $U_0 = 1$ ,  $U_1 = -3$ ,  $U_2 = 3$ ,  $U_3 = -1$ ,  $W_\infty$  = mean asymptotic weight (see below),  $F$  = hypothetical fishing mortality rate,  $M$  = natural mortality rate ( $M \approx Z$ ; see above),  $K$  = growth co-efficient ( $0.27 \text{ year}^{-1}$ ; Frisch 2007a),  $t_0$  = hypothetical age at zero carapace length ( $-0.18 \text{ year}$ ; Frisch 2007a),  $t_c$  = estimated age of lobster when they reach the hypothetical minimum size limit (MSL) and  $t_r$  = estimated age of lobster when they first become vulnerable to the fishing gear. The latter parameter was

**Table 1. Mark–recapture data for *Panulirus versicolor* at Northwest Island**  
(Data are cast in a ‘Method B’ table, as per Krebs 1999)

Time of last capture	Time of capture					
	Dec. 2003	June 2004	Dec. 2004	June 2005	Dec. 2005	Dec. 2006
Dec. 2003	–	8	1	3	2	0
June 2004	–	–	20	6	3	2
Dec. 2004	–	–	–	12	6	1
June 2005	–	–	–	–	7	8
Dec. 2005	–	–	–	–	–	7
Total marked	0	8	21	21	18	18
Total unmarked	17	42	11	11	4	4
Total caught	17	50	32	32	22	22

**Table 2. Jolly–Seber population estimates ( $\pm$ s.e.) for *Panulirus versicolor* at Northwest Island**

Time <sup>A</sup>	Population size <sup>B</sup>	Density (ha <sup>-1</sup> )	Mortality rate ( $Z$ ) (year <sup>-1</sup> )	Immigration (year <sup>-1</sup> )
June 2004	100 $\pm$ 31	1.7 $\pm$ 0.5	–0.07 $\pm$ 0.08 <sup>C</sup>	–
Dec. 2004	71 $\pm$ 11	1.2 $\pm$ 0.2	0.46 $\pm$ 0.04	–16 <sup>C</sup>
June 2005	75 $\pm$ 14	1.3 $\pm$ 0.2	0.32 $\pm$ 0.08	28
Dec. 2005	60 $\pm$ 18	1.0 $\pm$ 0.3	0.41 $\pm$ 0.13	–2 <sup>C</sup>
Mean	76 $\pm$ 10	1.3 $\pm$ 0.2	0.28 $\pm$ 0.18	3

<sup>A</sup>Estimates for December 2003 and December 2006 were not possible.

<sup>B</sup>Per 60 ha (the size of the study area).

<sup>C</sup>Negative estimates were artefacts of sampling error (see Krebs 1999).

assumed to be 1.8 years, based on the lower size limit of *P. versicolor* that were captured by spear-fishing at Palau (60 mm  $L_c$ ; MacDonald 1982). Size and age were inter-converted using the von Bertalanffy growth equation, as described by Frisch (2007a). Population biomass per recruit (BPR) was estimated as per Jennings *et al.* (2001) using the same input parameters as for YPR. Three hypothetical MSLs (80, 90 and 100 mm  $L_c$ ) were chosen for exploratory analysis, based on the dual criteria of size at first maturity (65–82 mm  $L_c$ ; George and Morgan 1979; MacDonald 1982) and ease of compliance by recreational fishers.

To establish a length-weight conversion formula for *P. versicolor* (and thus estimate  $W_\infty$ ), the weights of 20 captured lobsters were measured ‘at sea’ using a standard spring-balance ( $\pm 25$  g). To improve the accuracy of the predicted relationship, the sample size was bolstered by inclusion of 20 additional samples that were either donated by recreational fishers or collected later by the authors. These additional samples were measured ‘on land’ using an electronic balance ( $\pm 0.001$  kg). Any animal that was missing a substantial portion of its body or appendages was excluded from the analysis. The length-weight formula was calculated by least-squares regression analysis using the generalised equation:

$$\text{bodyweight} = a \times L_c^b, \quad (4)$$

where  $a$  and  $b$  are constants, weight is expressed in kilograms and  $L_c$  is expressed in millimetres (Kulbicki *et al.* 2005). As above, the significance of the regression line was tested by

ANOVA after confirmation that relevant statistical assumptions (normality and homoscedasticity) were satisfied (Zar 1999).

#### Statistical analyses

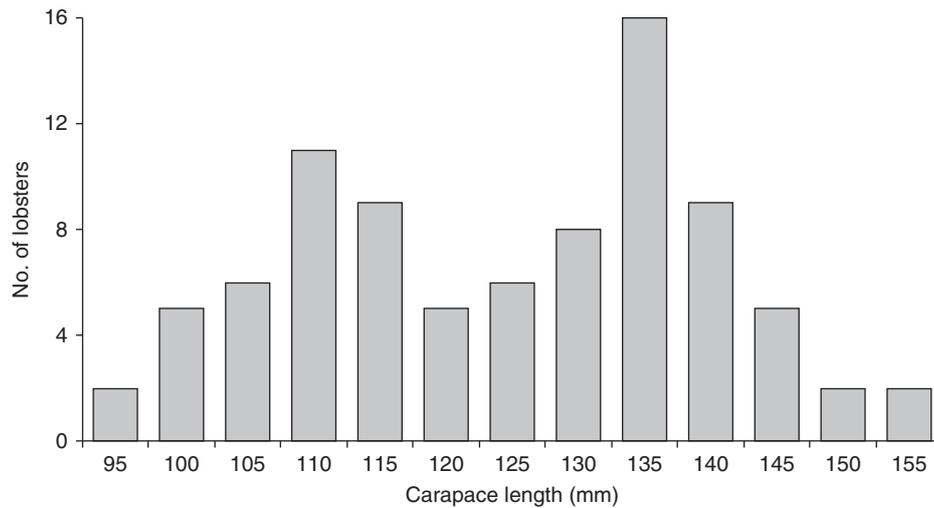
Jolly–Seber analyses were performed using ‘simply tagging’ computer software (Pisces Conservation, Hants, UK). All other statistical analyses were performed using SPSS computer software (SPSS, Chicago, IL). All error terms reported in the text and figures refer to one standard error (s.e.).

## Results

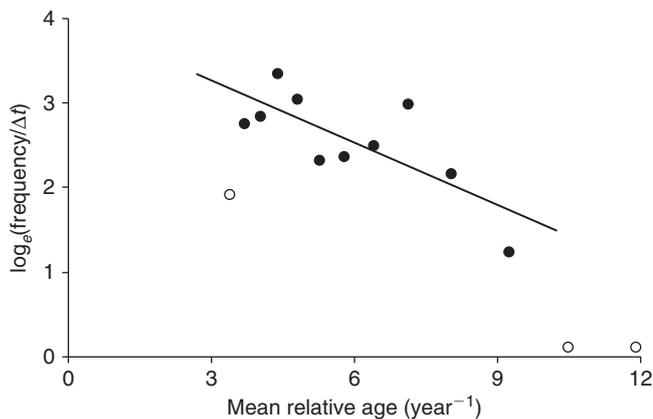
### Jolly–Seber analysis

Eighty-five lobsters (37 males, 48 females; size range 93–156 mm  $L_c$ ) were tagged and released between December 2003 and December 2005. Fifty-one (60%) of these lobsters were recaptured after 0.5–3 years (mean time at large = 540 days).

During each of the six censuses, 17–50 lobsters were captured and 8–21 lobsters were recaptured (Table 1). The proportion of marked lobsters in the population increased throughout the study and ranged from 16% during the second census to 82% during the final census. According to the Jolly–Seber model, there was a mean of 76  $\pm$  10 *P. versicolor* in the study area (60 ha) during each census (June 2004–December 2005), which is equivalent to a density of 1.3  $\pm$  0.2 individuals ha<sup>-1</sup> (Table 2). Assuming a similar density of *P. versicolor* on the surrounding areas of coral reef, the total abundance of lobsters at Northwest Island was estimated to be 1400  $\pm$  185 individuals. From June 2004 to December 2005, the mean instantaneous total mortality



**Fig. 1.** Length–frequency distribution of *Panulirus versicolor* that were captured at Northwest Island between December 2003 and December 2006. The  $x$ -axis labels are size-class midpoints.

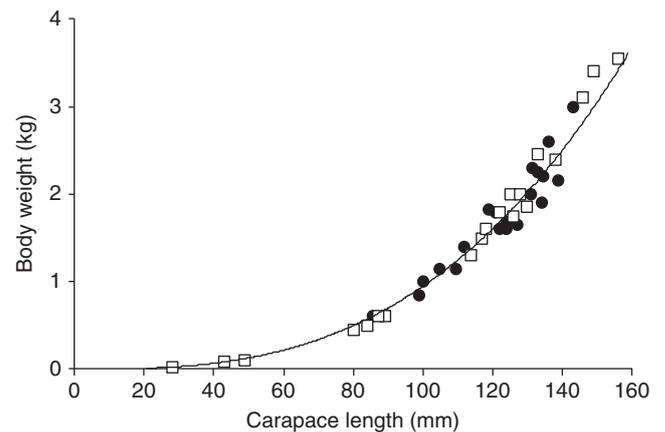


**Fig. 2.** Length-converted catch curve (LCCC) for *Panulirus versicolor* at Northwest Island. Data included in the regression analysis are shown as black circles. The instantaneous mortality rate ( $Z$ ), which is estimated from the slope of the line regression line, is  $0.25 \pm 0.08$  (s.e.)  $\text{year}^{-1}$  ( $r^2 = 0.56$ ).

rate ( $Z$ ) was estimated to be  $0.28 \pm 0.04 \text{ year}^{-1}$  and the mean number of immigrants to the study area was estimated to be  $3 \text{ year}^{-1}$ , which is equivalent to  $0.05 \text{ ha}^{-1} \text{ year}^{-1}$  (Table 2).

#### Length-converted catch curve analysis

The mean size of captured males ( $124 \pm 2 \text{ mm } L_c$ ) and females ( $125 \pm 2 \text{ mm } L_c$ ) at Northwest Island was not significantly different ( $t$ -test,  $t_{83} = 0.37$ ,  $P = 0.71$ ). Consequently, the data for both genders were pooled for analysis ( $n = 85$ ). The resulting length–frequency distribution was bi-modal (mode 1 =  $107.5\text{--}112.5 \text{ mm } L_c$ , mode 2 =  $132.5\text{--}137.5 \text{ mm } L_c$ ; Fig. 1). There was a significant relationship between  $\log_e(\text{frequency}/\Delta t)$  and mean relative age (ANOVA,  $F_{1,8} = 10.4$ ,  $P = 0.012$ ; Fig. 2). The slope of the regression line, which is the estimated  $Z$ , was  $0.25 \pm 0.08 \text{ year}^{-1}$  and the coefficient of determination ( $r^2$ ) was 0.56.



**Fig. 3.** Length–weight relationship for 20 *Panulirus versicolor* that were captured within the 60-ha study area (black circles). Twenty additional samples (white squares) were either donated by the public or collected later by the authors. Both groups of samples were used to calculate the regression line (bodyweight =  $10^{-6} \times L_c^{2.98}$ ).

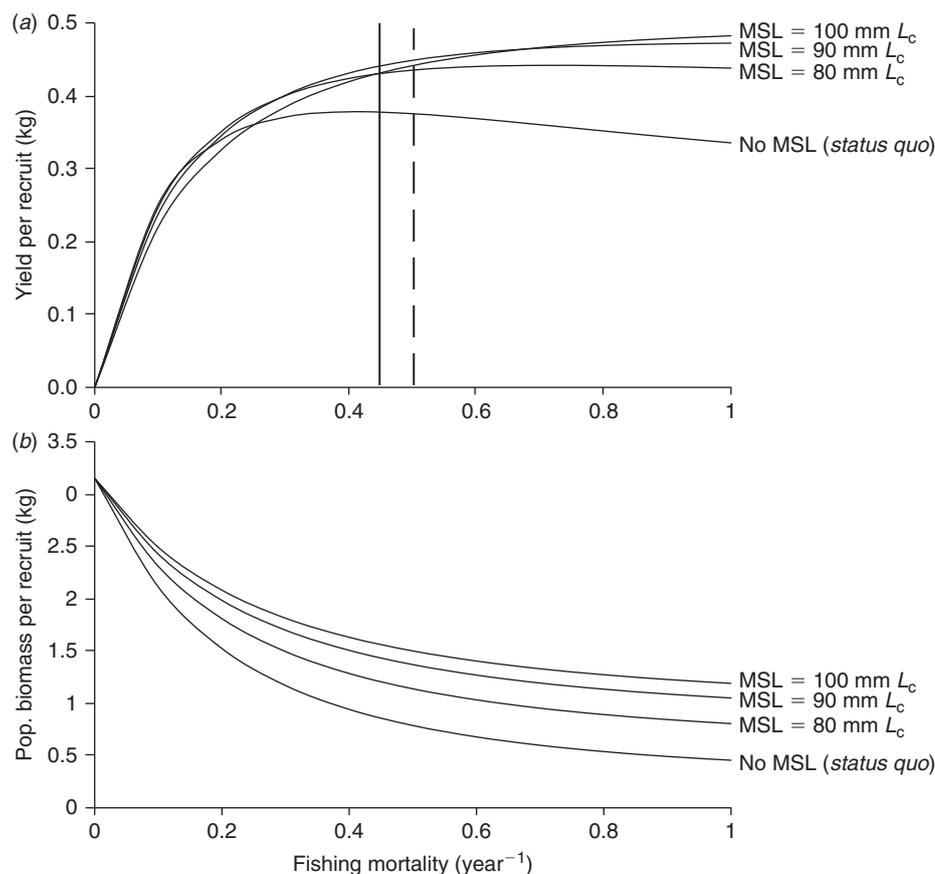
#### Fishery yield

The bodyweight of *P. versicolor* increased allometrically with  $L_c$  (Fig. 3). This relationship was significant ( $F_{1,38} = 5638$ ,  $P < 0.001$ ) and was well described ( $r^2 = 0.99$ ) by the equation:

$$\text{bodyweight (kg)} = 10^{-6} \times L_c \text{ (mm)}^{2.98}. \quad (5)$$

If the mean asymptotic length ( $L_\infty$ ) of *P. versicolor* is 144.7 mm (Frisch 2007a), then the mean asymptotic weight ( $W_\infty$ ) is estimated to be 2.74 kg. This statistic was subsequently used as an input to the YPR model.

Under current management regulations (i.e. no minimum size limit, MSL), YPR was found to be maximal (0.38 kg) at an instantaneous fishing mortality rate ( $F$ ) of  $0.4 \text{ year}^{-1}$  (Fig. 4a),



**Fig. 4.** (a) Yield per recruit and (b) population biomass per recruit for a single cohort of *Panulirus versicolor* that were subject to various potential fishing mortality rates ( $F$ ) and hypothetical minimum size limits (MSL). The solid and dashed vertical lines in (a) show  $F_{0.1}$  for MSLs of 90-mm and 100-mm carapace lengths respectively. Results were for individuals aged 1–13 years and a natural mortality rate ( $M$ ) of 0.28 year<sup>-1</sup> (assumes  $M \approx Z$ ; see Table 2). Mean age at recruitment to the fishery ( $t_r$ ) was assumed to be 1.8 years (carapace length ~60 mm).

which corresponds to a finite  $F$  of 33%. If the lobster population at Northwest Island is 1400 (see above), then the potential fishery yield was estimated to be 462 lobsters per annum. Implementation of a hypothetical MSL (80, 90 or 100 mm  $L_c$ ) increased YPR relative to the *status quo* (no MSL), but only when  $F$  was moderate to high ( $>0.4$  year<sup>-1</sup>). The utility of a MSL will therefore depend on the level of  $F$  which, although not presently known, may be very high at some locations. YPR was relatively insensitive to introduction of a MSL (80, 90 or 100 mm  $L_c$ ), regardless of  $F$  (Fig. 4a). However, implementation of a MSL substantially increased population biomass (Fig. 4b). When  $F = 0.5$  year<sup>-1</sup>, this increase was 44–90%, depending on the choice of MSL.

The YPR trajectories for hypothetical MSLs of 90 and 100 mm  $L_c$  were asymptotic (Fig. 4a). Under these circumstances, optimum  $F$  is typically assumed to be the value at which the slope of the YPR trajectory is one-tenth of its initial slope (i.e.  $F_{0.1}$ ) (King 1995). For *P. versicolor*,  $F_{0.1}$  is equivalent to 0.45 or 0.50 year<sup>-1</sup> for MSLs of 90 and 100 mm  $L_c$  respectively (Fig. 4a). Thus, it would be appropriate to cap fishing effort (e.g. by implementing catch limits) at a level that corresponds to a fishing mortality of 0.45–0.5 year<sup>-1</sup>, which is equivalent to

removing ~36–39% of legal-sized lobsters annually. Given an estimated population size of 1400, the maximum recommended harvest at Northwest Island is 507–551 lobsters per year, depending on the choice of MSL.

## Discussion

### Demography and yield

The total number of *P. versicolor* at Northwest Island was estimated to be  $1400 \pm 185$ , which is equivalent to  $1.3 \pm 0.2$  individuals ha<sup>-1</sup> of shallow reef habitat, or  $51 \pm 8$  individuals per kilometre of reef edge. Other estimates of palinurid density in the tropical west-Pacific are 10 individuals per hectare of reef habitat (*P. ornatus*, Pitcher *et al.* 1992) and 95 individuals per kilometre of reef edge (*P. penicillatus*, Ebert and Ford 1986). The density of *P. versicolor* at Northwest Island is thus very low, even by tropical Pacific standards. Consequently, the local stock can be expected to sustain only relatively light fishing pressure.

Jolly–Seber and LCCC estimates of (instantaneous) total mortality rate ( $Z$ ) for *P. versicolor* were  $0.28 \pm 0.04$  and  $0.25 \pm 0.08$  year<sup>-1</sup> respectively. In finite terms, ~22–24% of

the population died or was removed during each year of the study. This is considerably less than for exploited populations of other palinurids, which typically have  $Z$  values of 0.4–1.6 year<sup>-1</sup> (33–80% in finite terms) depending on the degree of exploitation (Morgan 1980; Pitcher 1993; Muller *et al.* 1997; Pitcher *et al.* 1997). In general, models for estimating mortality rates are less robust than models used to estimate other population parameters such as growth rate (King 1995). Consequently, fishery scientists are often uneasy about their estimates of  $Z$ , even in the most intensively studied fisheries (Jennings *et al.* 2001). With respect to the estimates of  $Z$  presented here, some level of confidence is gained by the fact that both the Jolly–Seber and LCCC-derived estimates of  $Z$  were similar in magnitude, despite being derived by independent methods.

As the 60-ha study site received little or no fishing pressure, it was assumed that fishing mortality rate ( $F$ ) was probably negligible and that  $Z$  approximates natural mortality rate ( $M$ ). The observed length–frequency distribution of *P. versicolor* provides further support for the validity of this assumption. Modal size classes were 107.5–112.5 and 132.5–137.5 mm  $L_c$  and 33% of lobsters were >135 mm  $L_c$  (Fig. 1). In comparison, *P. versicolor* from an exploited population in Palau (Micronesia) had a modal size class of only 95–105 mm  $L_c$  and 100% of the catch was ≤135 mm  $L_c$  (MacDonald 1982). Furthermore, 100% of *P. versicolor* in samples collected from Western Australia and India were ≤120 mm  $L_c$  (George and Morgan 1979; Kuthalingam *et al.* 1980).

In general, tropical palinurids spawn and recruit continuously, with the result that length–frequency distributions tend to be unimodal (Pitcher 1993). It is therefore unusual that the length–frequency distribution of *P. versicolor* at Northwest Island was bimodal. This result was neither an artefact of biased sampling (since adult lobsters are equally vulnerable to hand-capture) nor gender-related (because male and female lobsters were similar in  $L_c$  and homogeneously distributed among size classes) (Frisch 2007a). The only reasonable explanation for a bi-modal length–frequency distribution is that the population contained one or two unusually strong cohorts, as is common among temperate palinurids (Caputi *et al.* 2003; Butler *et al.* 2006). We noted that immigration of *P. versicolor* to the study area varied considerably among censuses (Table 2). In this context, immigration may actually represent recruitment of subadult individuals to Northwest Island, since juveniles probably recruit to coastal areas and then migrate offshore as they approach maturity, as occurs in many other palinurids (Butler *et al.* 2006). If immigration (recruitment) is episodic, then the estimated immigration rate presented here (0.5 ha<sup>-1</sup>year<sup>-1</sup>) should be interpreted with caution.

The potentially episodic nature of immigration (recruitment) at Northwest Island has implications regarding interpretation of both the length-converted catch curve (LCCC) and the YPR analyses, because both models assume a stable size structure (Beverton and Holt 1957; Pauly 1983). With respect to the LCCC analysis, it is unclear if or how episodic recruitment may have biased the estimated mortality rate because it is not known whether the first, second or both modal size classes were over represented (Fig. 1). However, any potential bias is likely to be small because the mortality estimates derived via both LCCC and Jolly–Seber models are concordant. For the YPR analysis,

episodic recruitment can potentially influence the trade-off between size and quantity of lobsters available for harvest. However, episodic recruitment does not directly affect YPR model outputs because neither recruitment nor size structure are inputs to the YPR model. Thus, practical application of model outputs (i.e. implementation of management regulations) can be adapted as required according to local recruitment dynamics.

Assuming  $F \approx 0$  within the 60-ha study area, then  $M$  is estimated to be 0.28 year<sup>-1</sup>, based on the Jolly–Seber analysis (Table 2). Only two other estimates of  $M$  are available for any palinurid in the tropical west-Pacific region; these are 0.36–0.48 year<sup>-1</sup> for *P. penicillatus* at Marshall Islands (reanalysis of Ebert and Ford 1986) and 0.69–0.91 year<sup>-1</sup> for *P. ornatus* at Torres Strait (Pitcher *et al.* 1997). Given that *P. penicillatus*, *P. ornatus* and *P. versicolor* have similar growth parameters (cf. Ebert and Ford 1986; Skewes *et al.* 1997; Frisch 2007a) and that  $M$  is primarily governed by predation (Kanciruk 1980; Morgan 1980), it may be inferred that estimates of  $M$  reflect the relative intensity of predation on each of the three species. Factors that influence predation rates include the quality and quantity of shelter (dens), the relative abundance of conspecifics and the density of predators (Smith and Herrnkind 1992; Mintz *et al.* 1994). It is hypothesised, therefore, that the relatively low  $M$  of *P. versicolor* at Northwest Island was due to specific behaviour and habitat characteristics. In particular, we suggest that strong fidelity to shallow water (Frisch 2007b) and an abundance of high quality coral dens (Frisch 2008) reduced exposure of *P. versicolor* to large predators (e.g. sharks and teleosts). In other locations, mortality rate may be amplified because palinurids often have limited access to shelter (Herrnkind *et al.* 1997; Sharp *et al.* 1997; Briones-Fourzán and Lozano-Alvarez 2001).

Demographic parameters such as  $M$  are not known for most spiny lobster species in the tropical west-Pacific region, so there are correspondingly few estimates of YPR available in the literature. Thus, it is possible only to compare the present estimate of YPR (i.e. 0.38 kg when hypothetical  $F = 0.4$ ) with that of two other species in the region: these are (unexploited) *P. penicillatus* at Marshall Islands, for which YPR was estimated to be 0.22 kg when hypothetical  $F = 0.5$  year<sup>-1</sup> (Ebert and Ford 1986) and (commercially exploited) *P. ornatus* at Torres Strait, for which YPR was estimated to be 0.032–0.056 kg when  $F = 0.4$  year<sup>-1</sup> (Pitcher *et al.* 1997). For palinurids in other parts of the world, YPR is typically 0.1–0.7 kg, depending on the level of  $F$  (Morgan 1980; Annala and Breen 1989). Thus, the YPR of *P. versicolor* is higher than the YPR of other tropical west-Pacific palinurids (for reasons which are yet to be determined), but it is well within the range reported for palinurids globally.

#### Fishery management

At present, management strategies for *P. versicolor* on the GBR are based solely on precautionary principles rather than quantitatively-derived population parameters, because many of these are yet to be determined. As such, current management regulations are limited to: (1) a catch limit of five *P. versicolor* per person (or 10 per boat); and (2) a prohibition on possessing females in ‘mated’ (spermatophoric) or ‘egg-bearing’ (ovigerous) condition. Numerous small ‘no take’ marine reserves have

also been established with the general aim of conserving biodiversity (Fernandes *et al.* 2005), but their effectiveness for protecting spiny lobsters remains unknown. Based on the results of this study and assuming that a large proportion (i.e. 20–50%) of the GBR and hence a large proportion of the *P. versicolor* stock, remains inaccessible or protected by ‘no take’ reserves, two changes to current management are recommended. First, the current prohibition on possession of spermatophoric and ovigerous females should be revoked. This is because *P. versicolor* must be caught using spears (they cannot be coaxed from their dens and they will not enter traps) and it is almost always impossible to assess the reproductive status of individuals before capture because the abdomen is typically concealed deep inside the den. Consequently, large numbers of breeding female lobsters are inadvertently killed or severely injured by the fishery (Frisch *et al.* 2008), which renders the current management regulation highly ineffective. Eliminating the requirement to discard breeding females would greatly reduce wastage of stock and potentially reduce the overall quantity of lobsters that are killed by the fishery (i.e. catch limits may be attained sooner). Furthermore, owing to extensive larval dispersal capabilities and the presence of a large unexploited breeding population on the GBR, there appears to be little chance of localised recruitment overfishing and hence there is little need to protect breeding females at a local level.

The second proposed change is to implement a MSL of 100 mm  $L_c$ . The basis of this recommendation is that a 100-mm  $L_c$  MSL will: (1) optimise yield, thereby reducing the risk of growth overfishing (Fig. 4a); (2) maintain a greater population biomass (Fig. 4b), thereby enhancing other potential income-generating opportunities for sustainable use of the resource, such as dive tourism (Kragt *et al.* 2009); and (3) give every lobster in the population an opportunity to breed at least once before capture, thereby reducing the effects of fishing selection on the gene pool (Dunlop *et al.* 2009). Importantly, a 100-mm  $L_c$  MSL would not greatly impact current fishing practices because the mean size of lobsters currently caught by recreational fishers is 120 mm  $L_c$  (Frisch *et al.* 2008). Stakeholder opposition to the proposed MSL is therefore anticipated to be minimal. From a fisher’s perspective, it is far easier to comply with regulations pertaining to size rather than reproductive status because it is relatively easy to estimate  $L_c$  of individual lobsters before capture (i.e. the carapace is usually visible to the spear-fisher).

This study was undertaken over a small spatial scale, thereby introducing the possibility that the estimated parameters may not represent lobster populations beyond Northwest Island. This is because biological characteristics of single species often vary among regions (MacDiarmid and Sainte-Marie 2006; Wahle and Fogarty 2006). Should this be the case and the current data were used to formulate management strategies for *P. versicolor* populations beyond Northwest Island, such strategies may be suboptimal. In fisheries elsewhere in the world, this type of deficiency has provided enough justification to preserve *status quo* with respect to management regulations, thereby increasing risk of over-fishing (Chubb 2000; Walters and Martell 2004). However, the current management scheme for *P. versicolor* across the GBR is ‘data-less’ and is therefore based entirely on precautionary principles rather than on any sound

knowledge of the species’ demography. Under this circumstance, ‘data-limited’ management is not just a valid alternative, but is a management imperative (Johannes 1998).

In conclusion, this study provides the framework for implementation of sound, knowledge-based management strategies that help to ensure this important fishery resource is harvested on a sustainable and rational basis. In doing so, it underscores the utility of basic demographic information (particularly mortality rate) for understanding spiny lobster ecology and for optimising fishery management, even when the resource is seemingly well protected by non-specific management tools such as marine reserves.

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