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Growth of ornate rock lobsters, *Panulirus ornatus*, in Torres Strait, Australia

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Abstract. Growth (size-at-age) of *Panulirus ornatus* in Torres Strait was calculated from size–frequency data collected during annual population surveys and from the catch of lobster fishermen. Growth varied on both spatial (~100 km) and temporal (yearly) scales, the former probably because of differences in water temperature and/or food availability, and the latter probably because of density-dependent effects. Although an existing growth curve formulated from tag–recapture data was similar to growth of lobsters in the fast growth zones, it may overestimate the growth of lobsters from the area where most of the tag–recapture data were collected.

Introduction

The ornate rock lobster *Panulirus ornatus* (Fabricius) is a tropical spiny lobster that supports a small (~200 t annually) commercial fishery in Torres Strait, north-eastern Australia. Spawning (which occurs outside the Torres Strait fishing grounds) and recruitment of larvae to the Torres Strait fishing grounds are highly seasonal; spawning occurs between November and March (MacFarlane and Moore 1986; Bell *et al.* 1987) with recruitment about 6 months later between May and September (CSIRO, unpublished data). About two years after settlement, almost all 2+ female and most 2+ male lobsters migrate eastward out of the Torres Strait fishing grounds during August–September each year to breed, and do not return (Moore and MacFarlane 1984; Skewes *et al.* 1994).

In recent years, lobster research has been focused mainly on stock assessment objectives. CSIRO has carried out annual surveys of lobster abundance since 1989 (Pitcher *et al.* 1992*a*) providing estimates of the relative abundance of the fishable (mainly 2+) stock and recruiting (1+) lobsters which become the mainstay of the fishery in the following year. The catch is also monitored in June each year to provide catch-per-unit-effort (CPUE) data and catch size frequencies. The results of the monitoring form the basis of annual stock assessments and are used in population modelling.

An important parameter in stock assessment and population models is growth. Previous information on lobster growth in Torres Strait came from a growth curve modelled from tag–recapture data (Phillips *et al.* 1992) and an analysis of size–frequency data from population surveys and catch monitoring (CSIRO, unpublished data).

During the analysis of size frequencies from the two monitoring projects, it was noticed that the size of the modes in the population and catch size frequencies varied both spatially and temporally. This variability makes population modelling of the entire lobster population in Torres Strait difficult; therefore it is important that it be described. This paper uses population and catch size frequencies to describe spatial and temporal variability in size at age, and it compares these results to the tag–recapture growth curve (Phillips *et al.* 1992).

Materials and methods

Study area

Torres Strait, the sea strait between Papua New Guinea and Cape York, Australia, is generally less than 20 m deep, with extensive reefs.

The study area was separated into four zones (Fig. 1) based loosely on differences in average depth, substratum type and epibenthos cover (Pitcher *et al.* 1992*b*) . The north-west (NW) zone was relatively shallow (mean site

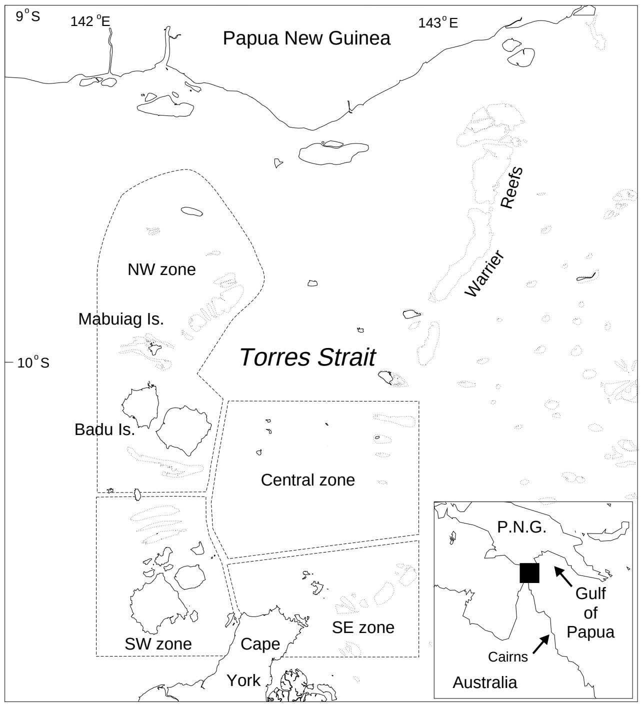

Fig. 1. Map of Torres Strait showing study area and zones used to assess spatial differences in growth.

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depth 8.5 m) with a variable seabed ranging from sand to rock. Epibenthos cover (sponges, gorgonians, hard and soft corals) was often dense; seagrass was very dense in places, and algae (*Sargassum* spp.) were common. The south-west (SW) zone was deeper (mean site depth 11.5 m) also with a variable seabed but with less rock substratum than the NW zone. Epibenthos cover was highly variable from dense to none; algae, particularly *Sargassum*, were often abundant. The central zone was deeper again (mean site depth 18.1 m) with mostly a sand or rubble seabed. Epibenthos cover was generally sparse but with dense patches; seagrass, particularly *Halophila spinulosa*, was sparse but common, and algae were rare. The south-east (SE) zone was the deepest (mean site depth 19.9 m) with generally a rock or rubble seabed. Epibenthos cover was often dense, but seagrass and algae were rare.

Annual population surveys

A large-scale survey of lobster abundance was carried out in Torres Strait in June 1989 (Pitcher *et al.* 1992*a*) and smaller annual surveys have been carried out at 100 sites in June each year since 1990. Size frequencies from the surveys for each year, zone and sex were analysed with the size–frequency modal analysis program MIX (Macdonald and Pitcher 1979) to estimate the mean size (with standard errors) and proportions of the component 1+ and 2+ year classes. The analysis procedure was the same for each size frequency. We fitted both two and three modes to each size frequency and the result with the lowest χ^2 value (most significant) was used. The starting values for the analysis were the long run means for each year class from previous size–frequency analyses. Generally the 1+ and 2+ modes are well separated and the analysis was straightforward; however, small sample sizes for some areas and zones meant that the modal analysis could not be successfully resolved without constraints being placed on starting parameters. To avoid the subjectivity that might be inherent in the setting of constraints during modal analysis, we used only the results of MIX analyses that did not require constraints on parameters to achieve a significant fit.

The mean size of lobsters in each year class was tested for significant differences by zone, sex, year and age, using the results of the modal analysis in a four-factor ANOVA. Only main effects could be tested because there was only one data value available for each cell (Zar 1984).

Commercial catch

Lobsters from the catch of lobster fishermen were measured in June each year from 1988 to 1994. The lobsters were caught within the NW zone and landed at Mabuiag and Badu Island (Fig. 1). Size frequencies from the catch for each year and sex were analysed with MIX to estimate the mean size (with standard errors) and proportions of the component 1+ and 2+ year classes.

The mean size of 2+ female lobsters was tested for significant differences between years by using the mean and variance estimates from the modal analysis in a one-way ANOVA. The size of 2+ females in the catch was the best measure of differences in the size of lobsters between years for four reasons: the 2+ lobsters were fully recruited to the fishery; the lobsters in the catch were caught from the same limited area of the fishery, therefore reducing spatial variability; the catch size–frequency data-sets were larger and offered greater precision in the MIX estimation of mean size than can be gained from the smaller survey data-sets; and all female lobsters migrate in August or September each year when they are 2+ (Skewes *et al.* 1994), whereas a small proportion of male lobsters do not and therefore small but variable numbers of 3+ male lobsters in the catch make estimates of the average size of 2+ males less reliable.

A possible link between year-to-year variation in the size of lobsters in the commercial catch and abundance was tested by multiple regression. The measure of abundance was the CPUE in numbers of lobsters caught per hour, measured concurrently with the catch size–frequency measurements. Several regression models were tested, including various combinations of CPUE of 2+ lobsters, CPUE of 2+ lobsters the previous year, survey 2+ abundance and survey 1+ abundance. CPUE 2+ includes small numbers of 3+ male lobsters — for the purpose of testing density-dependent effects on growth, their effect is the same as 2+ lobsters.

Comparison of size-at-age with tag–recapture growth curve

The coefficients k and L_∞ of the von Bertalanffy growth curve (Fabens 1965)—

$$l_{(t)} = L_\infty\left\{1 - e^{-k(t-t_0)}\right\} \quad (1)$$

where $l_{(t)}$ represents size, L_∞ represents the asymptotic maximum size, k represents the rate of growth, t is time or age and t_0 positions the curve along the age axis — were previously calculated for *P. ornatus* with a random coefficient model (Phillips *et al.* 1992) from tag–recapture data from Torres Strait. A value for t_0 was calculated to compare the growth curve with size-at-age data from the annual population surveys; this was done by substituting the size and age at settlement, about 6 mm CL at 0.5 years old (CSIRO, unpublished data), into equation (1), and solving for t_0 (t_0 = 0.423 and 0.421 for males and females respectively).

Results

Annual population surveys

The size–frequency distributions of lobsters caught during population surveys in June showed two modes (Fig. 2). Using January as the mean hatching time (MacFarlane and Moore 1986; Bell *et al.* 1987), the two year classes represent 1+ (17 months old) and 2+ (29 months old) lobsters (Pitcher *et al.* 1992*a*). The male lobster population had small but variable numbers of 3+ (41 months old) lobsters (Skewes *et al.* 1994), the relative proportion of which was usually not large enough to be adequately resolved by modal analysis.

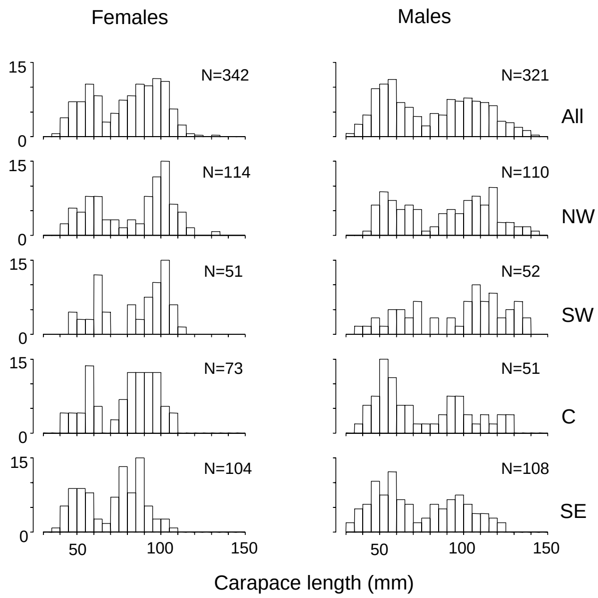

Fig. 2. Size–frequency distributions for *Panulirus ornatus* from an abundance survey in 1989 (Pitcher *et al.* 1992*a*) of all Torres Strait, split into four zones (NW, SW, Central, SE) to illustrate spatial differences in growth.

Table 1. Results of a four-factor main effects ANOVA testing the effects of year, quadrant, sex, and age on size, using the mean size of each component distribution of size–frequency distributions from modal analysis

No interaction terms could be tested because there is only one data value per cell

Effect	df	SS	*F*	*P*
Zone	3	678.07	30.94	<0.0001
Year	5	449.77	12.31	<0.0001
Age	1	13353.60	1827.85	<0.0001
Sex	1	132.13	18.09	<0.0001
Error	60	431.03		
Total	69	15963.97		

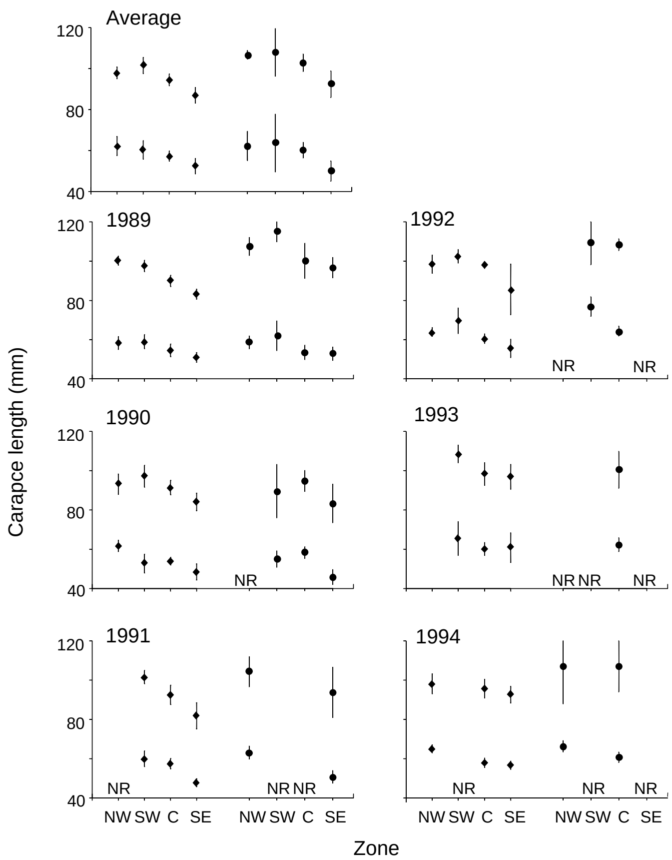

Fig. 3. Results of modal analysis of the size frequencies of the *Panulirus ornatus* population in each of four zones: average carapace length (error bars are 95% CI) of the 1+ and 2+ lobsters for each year between 1989 and 1994, for (◆) females and (●) males. Only the results of modal analysis resolved with no constraints were used (NR, not resolved).

The four-factor ANOVA, using the results of MIX modal analysis, showed a significant difference in the average size of lobsters between zones (Table 1). Because no interaction terms could be tested in the ANOVA, main effects should be interpreted cautiously. However, lobsters in the SE zone were generally smaller than those in the NW and SW zones, and lobsters in the central zone were intermediate (Figs 2 and 3). On average, 1+ lobsters were 10.32 mm CL (± 4.40 mm, 95% CI) smaller, and 2+ lobsters were 11.15 mm CL (± 4.19 mm, 95% CI) smaller, in the SE than the NW. For 2+ lobsters this is about 12.7% by CL and equivalent to about 41% by tail weight.

The four-factor ANOVA also showed a significant difference in the average size of lobsters between years (Table 1). However, year-to-year comparisons were difficult because of spatial variability in the size of the lobsters.

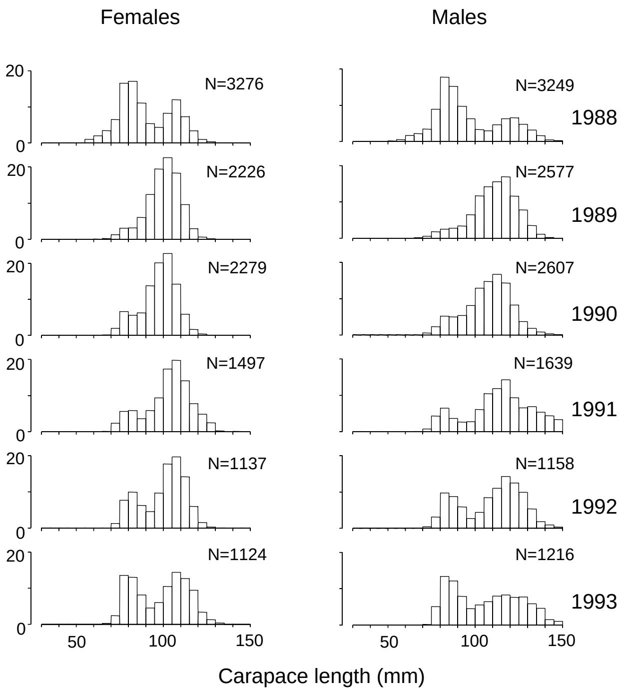

Fig. 4. Size–frequency distributions of *Panulirus ornatus* from the catch of Torres Strait lobster fishers every June between 1988 and 1993.

Commercial catch

The catch of lobsters in Torres Strait during June each year from 1989 and 1994 consisted mainly of 2+ lobsters with varying, but usually smaller, proportions of larger 1+ lobsters (Fig. 4). The 2+ year class is fully recruited to the fishery by June. Owing to a minimum legal size that was imposed about half-way through 1988, lobsters smaller than ~72 mm CL were not represented in the commercial catch. Only larger 1+ lobsters are represented in the catch.

The size of 2+ female lobsters differed significantly between years (ANOVA, $P < 0.0005$, Table 2). The difference in size between the smallest (1990) and the largest (1988) was 7.8 mm CL (± 0.7 mm, 95% CI) – about 8% by CL and equivalent to 25% by tail weight.

The regression model with the highest r^2 relating the average size of 2+ female lobsters to year class abundances

Table 2. The CPUE of the 2+ lobsters in the catch and the modal size of the 2+ females in the catch, for each year between 1988 and 1994

Year	CPUE 2+ (lobs h^{-1})	Mean size 2+ females CL (mm)	s.e.	*N*
1988	2.30	107.9	0.3	1154
1989	8.98	101.7	0.3	2005
1990	4.56	100.1	0.2	1980
1991	2.95	106.1	0.4	1215
1992	3.54	105.9	0.3	849
1993	2.69	106.9	0.4	704
1994	3.74	109.9	0.4	443

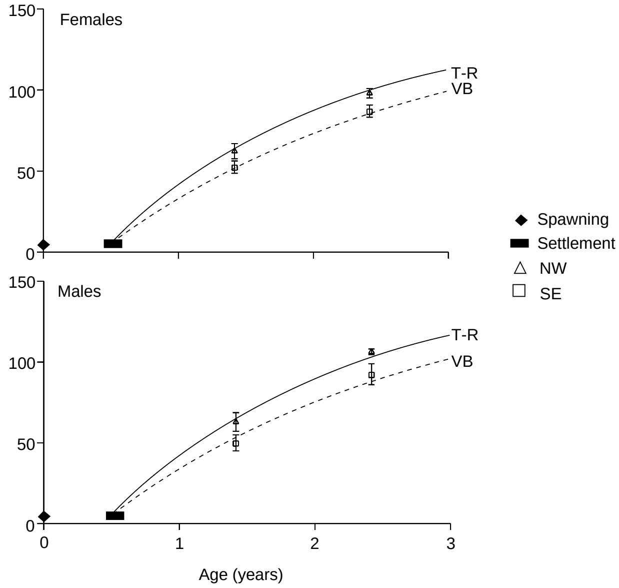

Fig. 5. Growth curves modelled from field tag–recapture growth curves (T–R) for *Panulirus ornatus* (Phillips *et al.* 1992), the von Bertalanffy growth curve with the coefficient $k = 0.44$ year $^{-1}$ (VB) and the average size of the 1+ and 2+ lobsters (with 95% CI) in the NW and SE zones of Torres Strait from modal analysis of size frequencies from population surveys.

included the relative abundance of the 2+ lobsters in the same year (CPUE of 2+ lobsters) and the relative abundance of the 2+ lobsters in the previous year (CPUE 2+ lobsters previous year) (Table 2). The mean size of 2+ females was smaller when 2+ lobsters were more abundant in the same year, and when 2+ lobsters were more abundant the previous year (i.e. the preceding year class) ($r^2 = 0.95$, $P < 0.01$).

Comparison of size-at-age with tag–recapture growth curve

The tag–recapture growth curve (Phillips *et al.* 1992), with t_0 calculated using the size and age at settlement, agreed with the size at age data for the NW zone, and overestimated growth in the SE zone (Fig. 5). The curve better represented growth in the SE zone when we reduced the coefficient k in the tag–recapture curve from 0.573 year^{-1} to 0.44 year^{-1} (Fig. 5).

Discussion

Size–frequency data can be used to produce reliable estimates of size-at-age for *Panulirus ornatus* in Torres Strait because the modes are well separated and easily resolved — a consequence of seasonal settlement, rapid growth, and the emigration of nearly all 2+ lobsters in August–September each year. Nevertheless, small numbers of 3+ male lobsters in the population makes modal analysis of 2+ males size frequencies less reliable than for 2+ females. Further, the usefulness and resolution of population size–frequencies was improved after the spatial variability in the size of lobsters was identified.

The spatial differences in the size of lobsters in the four zones is caused by differences in the growth rate rather than in the timing of settlement. If the timing of settlement was different between zones, then the size difference in lobsters would be greater for 1+ lobsters than for 2+ lobsters (for von Bertalanffy growth, the size difference is reduced as lobsters near L_∞), whereas the average difference in the size of lobsters between the NW and SE zones is almost the same for 1+ and 2+ lobsters (10.32 mm CL and 11.15 mm CL for 1+ and 2+ lobsters respectively). This can occur because with changes in growth rate, lobster growth diverges at first but then converges again as the lobsters near the asymptotic size, L_∞ (Fig. 5). Also, it is unlikely that the timing of settlement varies between the zones in Torres Strait because they are less than 100 km kilometres apart and the same processes drive recruitment for the region.

The cause of this difference in growth in the two zones could be partly attributable to differences in food availability and quality (Hartnoll 1982; Joll and Phillips 1984) and temperature (Aiken 1980; Hartnoll 1982). The NW and SW zones had more seagrass and algae, which generally increases the productivity of the epibenthos by providing food and shelter for the small molluscs and crustaceans that the lobsters eat (Joll and Phillips 1984; Joll and Phillips 1985). In terms of temperature, the SE zone had lower water temperatures during the annual lobster survey in June 1992 (average temperature = 25.7° C) than the NW zone (average temperature = 27.1° C) and lower temperatures are likely to result in lower growth rates (Hartnoll 1982).

Temporal (interannual) differences in size-at-age may be a result of density-dependent interactions because of the significant inverse relationship between size and abundance; i.e. increased abundance of a year class will slow its growth, as will increased abundance of the preceding year class. Higher abundance increases competition for food and shelter, which could slow growth, as has been suggested for *P. cygnus* (Jernakoff *et al.* 1994), *P. marginatus* (Polovina 1989) and *Jasus tristani* (Pollock 1991).

Given the spatial variability in growth, it is not surprising that the tag–recapture growth curve showed a "high variability in individual growth rates" (Phillips *et al.* 1992), since the data used to model the curve were collected over a wide geographic range, from Mabuiag Island in Torres Strait to Roberts Pt, 330 km south of Torres Strait. The tag–recapture growth curve (Phillips *et al.* 1992) best reflected the growth rate we observed in the NW zone. However, only 6% of the tag–recapture data came from lobsters in the NW zone; most (78%) of the tag–recapture data came from lobsters in the SE zone or from further south along the Queensland coastline (Bell *et al.* 1987). Therefore the tag–recapture growth curve may overestimate the growth of the lobsters in the area from which most of the tag–recapture data came. A possible cause of this may be slower early growth in the SE zone. As the tag–recapture data used to produce the growth curve did not include lobsters smaller than 38 mm CL, the curve may overestimate growth. The environmental differences between zones such as the abundance of algae and seagrass and water temperature may well affect the very young lobsters most strongly. Lobsters held in aquaria often show slow early growth resulting in sigmoidal growth curves (Phillips *et al.* 1992). Another possible reason that the tag–recapture growth curve may overestimate average growth is by selective recapture of faster growing lobsters biasing the data. While there may be some capture selectivity towards larger lobsters by commercial fishermen, most of the recaptures were collected by CSIRO divers. Also the tagged lobsters were from a wide size range, and were at large for a wide range of times. These factors would reduce possible selectivity bias.

This study shows that lobster growth can vary over relatively small spatial scales and from year to year because of differences in environmental factors and/or lobster density. Documenting differences in growth in zones has implications for fishery models that use growth rate as an input. Information from this study will be incorporated into future stock assessment modelling resulting in improved fishery status advice for managers. Identifying the factors that affect growth in the wild also provides useful information for the potential aquaculture of this species.

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