Higher water temperature leads to precocious maturation of western rock lobsters (*Panulirus cygnus*), but are things that simple?

*R. Melville-Smith, [1]S. de Lestang and [1]D. J. Johnston

*Curtin University of Technology, Department of Envrionment and Agriculture, GPO Box 6845, Perth, Western Australia, Australia, *E-mail: roy.smith@curtin.edu.au*

Western Australian Fisheries and Marine Research Laboratories, P.O. Box 20, North Beach WA6020, Australia.

Abstract

During a rock lobster post-puerulus grow out project, western rock lobsters from three different cohorts (post-puerulus, year-1 and year-2) were held for 12 months under two temperature regimes (ambient and 23°C) and two feed delivery treatments (the same ration of pelleted diet fed once nightly and in the alternate treatment, thrice nightly). At the end of the trial, 43% of females from the largest cohort (2-year post settlement) in the 23°C treatment, had ovigerous setae. However, none of the animals held at ambient temperatures showed signs of maturity. Feed delivery did not influence the presence or absence of ovigerous setae. Male maturity responded to elevated temperature in the same way as for females, as indicated by merus/carapace length ratios. The response of female size at maturity to 23°C was compared to a similar trial in the 1970s in which 2-year post settlement animals were held at 25°C. Maturity of females in that study was one year later than in the trial reported here, indicating that there may have been a decrease in age at maturity since the 1970s. The conclusion from this and research on other rock lobster species, is that size/age at maturity is likely to be a complex response to a range of contributing factors of which temperature is an important one.

Keywords: Maturity, life history, aquaculture, Bergmann's rule

Introduction

It has long been recognized that western rock lobsters (*Panulirus cygnus*) mature at a smaller size in the northern regions of their coastal distribution and at the offshore Abrolhos Islands of Western Australia (Chittleborough, 1976a; Grey, 1979; Chubb, 1991; Melville-Smith and de Lestang, 2006). Therefore, at least superficially, temperature, which is warmer in the northern coastal regions and especially the offshore Abrolhos Islands, would seem to offer a reasonable explanation for regulating the onset of maturity at either a smaller size or earlier age.

Small western rock lobster females carry one brood per year and large females two (de Lestang and Melville-Smith, 2006). Recently it was shown that as with size at maturity, the size at which a female carries two broods per year (*i.e.* is a double breeder) is smaller in the north and at the Abrolhos Islands than in the southern regions of the distributional range (de Lestang and Melville-Smith, 2006).

Plasticity in size at maturity is generally attributed to environmental conditions, lobster density and/or fishing pressure, but the specific factor or factors causing these differences is often difficult to identify (Gardner *et al*., 2006; Maxwell *et al*., 2009). Size at maturity and by implication, size at double breeding, has been shown to be decreasing over time in most parts of the western rock lobster fishery (de Lestang and Melville-Smith, 2006; Melville-Smith and de Lestang, 2006). In some regions, particularly the southern part of the fishery, these changes have been very marked. One explanation for these observations, proposed by Caputi *et al.* (2010), is that there has been a warming trend in the south-eastern Indian Ocean over the last 50 years of an average of about 0.02°C per year (Pearce and Feng, 2007).

The response of most ectotherms to temperature is well known: in most species there is an increase in adult body size with a decrease in environmental temperature as shown by the reviews across a range of species by Ray (1960) and Atkinson (1994)). These observations in ectotherms are commensurate with the intraspecific version of Bergmann's rule, first proposed for endotherms in the mid-1800s (Bergmann, 1847). Therefore, in the context of western rock lobsters, the increase in water temperature over the last 50 years might be expected to have affected life history parameters such as growth rates and age at maturity.

Another explanation for the changes in size at maturity in this fishery is that the selective fishing practices such as the knife edge selection resulting from the legal minimum size combined with high exploitation rates. This might have selected for heritable characteristics which led to these observed changes (Melville-Smith and de Lestang, 2006; Allendorf *et al.*, 2008).

This paper shows the effect of water temperature on precocious maturity as part of a wider study on the aquaculture grow out of western rock lobsters (Johnston *et al.,* 2008). We have reviewed published western rock lobster research to compare historical reproductive characteristics recorded in the literature with recent data. The objective was to further investigate cause-effect relationships in western rock lobster reproductive life history patterns to understand current egg production estimates and in so doing, improve advice to management.

Material and Methods

Lobsters for this study were collected in November 2004, off Seven Mile Beach, Dongara, Western Australia. Pueruli and early post pueruli (mean length at capture: 8.7 ± 0.3 mm carapace length (CL)) were collected from puerulus collectors, while one-year (mean length at capture 38.3 ± 0.3 mm CL) and two-year (mean length at capture 52.2 ± 0.2 mm CL) post settlement animals were collected using baited mesh pots and were aged by their size range conforming to those for one- and two-year cohort size frequency modes. The grow out trial was run for 12 months (December 2004 to December 2005).

Animals from the three cohorts (post-pueruli, year 1 and year 2) were randomly assigned into 12*60 L, 12*250 L, and 12*350 L tanks, respectively, at densities of post pueruli 50 m^{-2}; year 1 juveniles 23 m^{-2} and year 2 juveniles 19 m^{-2}. Six of the 12 tanks were supplied by preheated flow through seawater (mean $\pm$ S.E., 23.0 ± 0.35 $^{\circ}$C) and 6 by flow through water piped from storage tanks at ambient temperatures (between 15.6°C and 23.1 $^{\circ}$C, mean $\pm$ S.E., 19.0 ± 0.07 $^{\circ}$C). The upper temperature limit of the ambient tanks, which was similar to that of the heated tanks, was recorded for a relatively short period (around 1-2 months in mid-summer).

Three tanks in each temperature treatment and for each year-class were fed daily at 1700 hours. All other tanks were fed three times per night by auto feeders, at 1800 hours, 0000 hours and 0500 hours. The same daily ration of pelleted diet, formulated for tropical lobster *Panulirus ornatus* (Smith *et al.*, 2005) with fresh mussels fed on weekends, was provided to tanks within each size class irrespective of feeding regime. Photoperiod was maintained on a 12 hours fluorescent light: 12 hours dark cycle.

Periodic sampling throughout the experiment allowed the calculation of survival rates, growth rates, weight gain and feed conversion rates. Those data are presented elsewhere (Johnston *et al.,* 2008). Any stress on the lobsters was minimized by not handling the lobsters outside of these sampling events, or tagging. The data presented here were collected during the final drain down in December 2005 at the completion of the grow out trial. On that occasion, unlike any of the previous 2-monthly drain downs that had been conducted throughout the trial, several year-2 post settlement cohorts were observed to be ovigerous. This observation was considered unusual enough for the breeding condition of all the experimental animals in this year-class to be recorded. For both sexes, weight was recorded; the carapace length measured and any missing, damaged or regenerated appendages were noted. For females, the presence or absence of ovigerous setae was noted and the condition of the ovary and external ova if present, were visually assessed. For males, the length of the merus of the second pereiopod was measured.

Criteria used to assign females into a particular reproductive state are strongly influenced by time of year. In the natural environment, breeding occurs from October through January, with highest abundance of ovigerous females during November (Chubb, 1991). In this study, the maturity of females, whether they were breeding or carrying more than one batch of eggs in the season, was established according to the characteristics outlined in Melville-Smith and de Lestang (2005).

Male maturity was indicated using the relationship between carapace length and the length of the merus of the second pereiopod (ML) to determine the morphometric size change associated with onset of male maturity. The disproportionate length of the first and second pereiopods compared to the rest of the animal is a secondary sexual characteristic in mature males (Melville-Smith and de Lestang, 2006).

Analyses: Although data were available for post-pueruli and year-1 cohorts, none of those animals showed any evidence of maturity and therefore all further analyses have been restricted to the year-2 cohort year classes.

One-way ANOVA was used to test for differences at the end of the one-year growout experiment, in the sizes of lobsters held at ambient temperature compared to those held at 23°C. Carapace length of individuals was used as a standardized measure of length with the data for males and females analysed separately to remove any confounding sex-related influences.

The percentage of mature females in each 2 mm size class in the 23°C tanks was graphed to visually assess differences in the proportions that were mature in the size classes of the largest cohort.

The merus length of males was standardized against carapace length prior to the data being used to determine maturity. One-way ANOVA was then used to test for differences between the ML/CL of male lobsters in 23°C *vs.* ambient temperature tanks. Plots of the estimated marginal means and 95% confidence intervals were constructed for all ANOVAs that detected significant differences among factor groups. To visually assess the differences between lobsters in the two groups, frequency histograms of carapace lengths were plotted (5 mm increments) as well as ML/CL ratio (rounded to the nearest 0.01).

Table 1. Summary of the number of 2-year post settlement male and female *P. cygnus* at the end of the one-year trial in 12 tanks. Numbers of females that had ovigerous setae, spermatophores and/or that were ovigerous is provided for each tank. All females with ovigerous setae were regarded as mature. The temperature and feeding treatments use the abbreviations H and A for heated (23°C) and ambient and 1 or 3 for once and thrice-daily feeding

Tank	Males (n)	Females (n)	Females with ovigerous setae (n)	Females with spermatophores (n)	Females ovigerous (n)	Treatment temperature	Feeding frequency (times/day)
1	7	10	7	7	2	H	1
2	5	9	4	4	3	H	3
3	10	3	2	0	0	H	3
4	7	7	3	0	0	H	1
5	8	10	2	1	0	H	1
6	8	5	1	2	1	H	3
7	7	11	0	0	0	A	3
8	7	9	0	0	0	A	3
9	11	8	0	0	0	A	1
10	10	8	0	0	0	A	1
11	11	8	0	0	0	A	3
12	8	8	0	0	0	A	1

Results

Both sexes: Mean lobster size for both sexes was significantly (p = 0.001) larger in tanks that were heated, compared to those under ambient conditions. The mean ± S.D size of males was 68.3 ± 1.0 mm in heated tanks compared to 65.1 ± 0.9 mm in the ambient tanks, and for females, 65.0 ± 1.0 mm compared to 62.4 ± 0. 9 mm.

Females: There were obvious differences between the proportions of sexually mature females in the heated compared to ambient tanks; 43% of the animals across all six heated tanks had ovigerous setae and were therefore mature, whereas none of the females in the six ambient tanks had ovigerous setae. In four of the six replicate tanks there were females with spermatophores, but in two tanks, one where feeding was once-daily and another where it was thrice-daily, there was no evidence of mating (Table 1). Furthermore, only three of the four tanks in which there were females that had been mated, had ovigerous individuals (Table 1).

There was no observable correlation between size and state of maturity for females in the heated tanks. The proportions of mature individuals within 2 mm size classes ranged between 25 and 50%, except in the two smallest size classes which each had a single mature individual (Fig. 1).
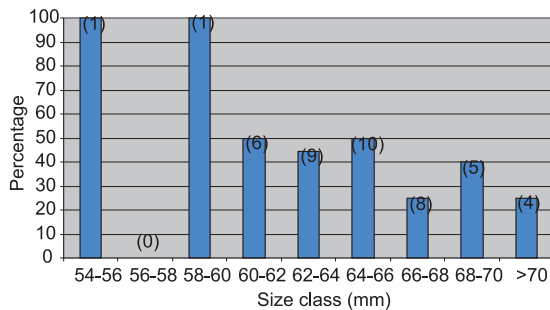

Fig. 1. Percentage of western rock lobster year-2 cohort females in 2 mm size classes held in heated (23°C) tanks for a year, that were mature at the end of the experiment. The bracketed value on each bar = n

Males: Given CL and ML for a sufficiently large range of size-classes, the inflection point in the relationship between these variables can be used to estimate size at maturity in male western rock lobsters. This procedure was attempted, but the

restricted size range of males in this study did not produce a clear inflection point. However, the ratio of ML/CL could provide an indication of maturity, with a high ratio indicating a disproportionately long merus length and therefore likelihood that the animal was mature. The ML/CL ratios of lobsters held at 23°C were larger than those from the ambient temperature tanks (one-way ANOVA, p = 0.05).

ML/CL ratios have been rounded to two decimal places and plotted separately for the ambient and 23°C tanks (Fig. 2). A 4-point running mean indicates the distribution of the ratios for the two tanks was different, with the males in the 23°C tanks appearing to have a greater proportion of the individuals with larger ML/CL ratios. High ML/CL ratios for males in the heated tanks did not correspond with large CL values, indicating that it was not necessarily the large males, which displayed the sexual characteristic of a disproportionately long merus. In the ambient tanks there was a weak correlation between ML/CL ratios compared to carapace length, despite the fact that there was no evidence that any of these males were mature.
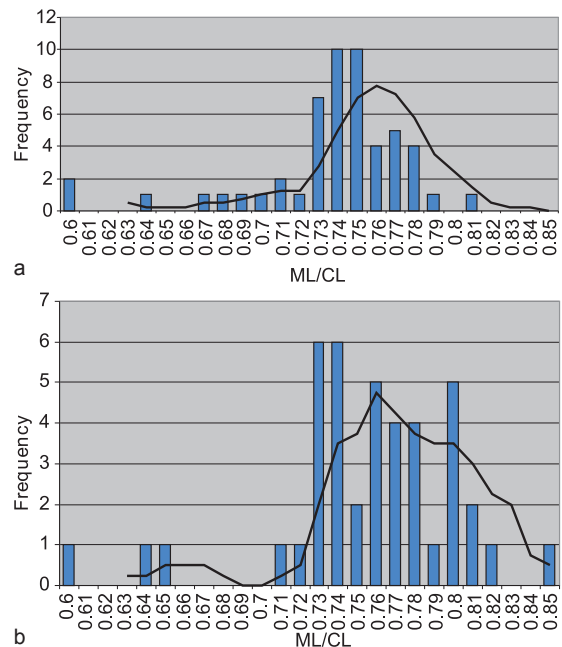

Fig. 2a and b. Comparative frequency distribution of merus/ carapace length (ML/CL) for year-2 cohort male western rock lobsters in ambient (A) and 23°C (B) tanks at the end of the 1-year experiment. The bold lines are 4-point running means of the ML/CL data

Discussion

None of the lobsters that were held at ambient temperatures in this study were mature at the end of the one-year experiment, despite the fact that it was within the breeding season for the species (de Lestang and Melville-Smith, 2006). If these animals were following the same breeding cycle as those in the wild and if they were to be ovigerous in the breeding season one year later, they would have moulted to a setose condition five to six months later (in May or June). Since the lobsters held in the ambient tanks would have had to at least moult once before to become setose and therefore mature, it follows that they would have undoubtedly had a larger mean size at maturity than the females held in the heated tanks. These results show clearly therefore, that western rock lobsters respond to constant elevated water temperature by both maturing earlier and at a smaller size, than those held at ambient temperatures.

Annala *et al.* (1980) showed similarly, that size at maturity of *Jasus edwardsii* in New Zealand is negatively correlated to water temperature, but they also considered it likely that size at maturity is related to other factors interacting with temperature, such as growth rate, age, metabolic rate, population density and food availability. In contrast to the result of Annala *et al*. (1980) result, Gardner *et al.* (2006) found that the relationship between size at maturity and water temperature for *J. edwardsii* in Tasmania to be the reverse of that described for the species in New Zealand, supporting Annala *et al's* (1980) belief that size at maturity in *J. edwardsii* may be determined by factors other than just temperature.

In this study, there was no relationship between carapace size and size at maturity for females from the year-2 post settlement cohort held in heated tanks. This suggests that size at maturity is more likely to be age-specific rather than size-specific and is consistent with that conclusion made by Pollock (1987) for the South African west coast rock lobster, *Jasus lalandii*. It is relevant in this context, to also note that the size range of females in ambient tanks, where none were mature, was similar to those in the heated tanks where many were mature and that therefore within the size ranges held in both tanks, there were large non-mature females held at ambient temperatures and small mature females held at elevated temperatures. To limit stress effects, handling of the animals was minimized, which unfortunately prevented information being collected on frequency of moulting.

The disproportionate growth of the first and second pereiopods of male western rock lobsters is a trait that is subtle in small animals and increasingly obvious with size. The ratio of ML to CL is therefore an incremental, not a presence-absence feature, which is why this relationship was not conclusive in determining the maturity of the males in the experiment.

The absence of any spawning activity in all the ambient and two of the heated treatment tanks does not necessarily preclude the presence of mature males in those tanks. Although the results of the maturity analyses for males across the tanks in the different treatments generally corroborate that of the females, they remain ambiguous in the absence of a definitive mature/immature designation for individuals. The fact that there were setose females in the two heated treatment tanks that were without mated/ovigerous females does not point to the absence of spawning activity being a tank effect, although this possibility cannot be excluded.

Relationships between size at maturity and growth in western rock lobsters: Published data on spatial and temporal differences in western rock lobsters sampled in the wild are limited. Chittleborough (1976b) compared growth rates of juveniles in the wild from four different areas in the fishery, with laboratory reared individuals. There was high variability between sites, with one of the northern, warm water areas (Cliff Head) producing growth rates equivalent to laboratory reared individuals that he considered to have grown at optimal levels. The three other areas showed substantially slower growth rates, with one of the northerly warm water areas (Seven Mile Beach) showing significantly slower growth than the southern-most and therefore the coolest area (Garden Island). He concluded that these differences were due to competition for limited food resources.

Juvenile growth data obtained from the grow out trials reported in this paper have been reported extensively elsewhere (Johnston *et al*., 2008). The tanks stocked at similar densities were fed for formulated feed to satiation which eliminated any possible influence of density dependence effects on growth rates that possibly influenced Chittleborough's (1976b) field-based data. The tank experiments showed that all cohorts grew faster at 23°C than at ambient temperatures, particularly in the first year after settlement when weight gain by animals in the heated tanks was almost double that of the ambient treatment (Johnston *et al*., 2008).

A less direct method of showing spatial differences in juvenile growth rate has been through fine scale predictions of catch based on puerulus settlement rates (de Lestang *et al.*, 2009). That study has shown that the proportions of 3 and 4-year old lobsters, the age at which they first recruit to the fishery, vary markedly across the distributional range. In the southern areas <25% of the recruits were three year olds, whereas in the northern areas the proportion was ~75%, suggesting that growth for sub-legal sized animals is faster in the warmer water.

With the exception therefore of the Chittleborough's (1976b) results which showed an inconclusive latitudinal, temperature-related, decline in juvenile growth rates, all the other western rock lobster published data point to juvenile growth being fastest at elevated temperatures.

We suggest that the observed pattern in the commercial western rock lobster fishery of a generally small size structure of the population and small size at maturity in the warm northern regions of the distributional range and a larger size distribution and size at maturity in the cooler southern areas, is largely due to differential growth rates. Under this scenario, the lobsters are growing faster in the northern areas of the distribution and maturing at a smaller size. After maturity, the growth rate of western rock lobsters slows (Melville-Smith *et al*., 1997) which would lead to those populations having a smaller size structure compared to that in the cooler water further south. This pattern is typical of many other ectotherms (Berrigan and Charnov, 1994; Sibly and Atkinson, 1994).

Selective fishing pressure as a possible driver of change in western rock lobster size at maturity: Chittleborough (1974) reared western rock lobsters from puerulus to adulthood. For the first year after settlement they were held at ambient temperatures, in the second year they were kept at raised temperatures (20-29°C) and from the third year onwards they were held at 25°C. Maturity occurred from 4.1 to 4.9 years post settlement which Chittleborough (1974) considered as not different from the wild.

A key difference in our results compared to those of Chittleborough's (1974), is that many of the breeding animals in this study were 3-years post-settlement, which is at least 12 months (25%) earlier than that of the earliest maturing female in his study. This is suggestive of maturity possibly occurring in the fishery at an earlier age now than in former years.

The spread of both mature and immature females across all size ranges in the heated tanks in this study, suggests that there may be a substantial degree of individual variability in size and age at first maturity within the species. This apparent intrinsic variability could provide a high degree of plasticity for size and age at maturity to respond to selection pressure.

In its title this paper has acknowledged that temperature affects the size at sexual maturity and that has been clearly confirmed by the results presented. Temperatures across the Australian marine environment are predicted to increase under future climate change scenarios (Poloczanska *et al.,* 2007) and our study as well as other recent research (Caputi *et al.*, 2010), provide useful pointers as to effects on the species that might result from temperature change. However, as has been shown, 'things' are not that simple and serious consideration need to be given to other potential factors influencing size at maturity, in particular selective fishing pressure. Teasing the contribution of factors influencing life history parameters apart is a non-trivial exercise, but one which is extremely important to the future management of the fishery.

Acknowledgements

References

Allendorf, F. W., P. R. England, G. Luikart, P. A. Ritchie and N. Ryman. 2008. Genetic effects of harvest on wild animal populations. *Trends Ecol. Evol.*, 23: 327-337.

Annala, J. H., J. L. McKoy, J. D. Booth and R. B. Pike. 1980. Size at the onset of sexual maturity in female *Jasus edwardsii* (Decapoda: Palinuridae) in New Zealand. *N. Z. J. Mar. Freshwat. Res.,* 14: 217-227.

Atkinson, D. 1994. Temperature and organism size – a biological law for ectotherms? *Adv. Ecol. Res.*, 25: 1-58.

Bergmann, C. 1847. Ueber die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. *Gottinger Studien*, 3: 595-708.

Berrigan, D. and E. L. Charnov. 1994. Reaction norms for age and size at maturity in response to temperature: a puzzle for life historians. *Oikos*, 70: 474-478.

Caputi, N., R. Melville-Smith, S. de Lestang, A. Pearce and M. Feng. 2010. The effect of climate change on the western rock lobster (*Panulirus cygnus*) fishery of Western Australia. *Can. J. Fish. Aquat. Sci.*, 67: 85-96.

Chubb, C. F. 1991. Measurement of spawning stock levels for western rock lobster, *Panulirus cygnus*. *Rev. Invest. Mar.,* 12: 223-233.

Chittleborough, R. G. 1974. Western rock lobster reared to maturity. *Aust. J. Mar. Fresh. Res.*, 25: 221-225.

Chittleborough, R. G. 1976a. Breeding of *Panulirus longipes cygnus* George under natural and controlled conditions. *Aust. J. Mar. Fresh. Res.*, 27: 499-516.

Chittleborough, R. G. 1976b. Growth of juvenile *Panulirus longipes cygnus* George on coastal reefs compared with those reared under optimal environmental conditions. *Aust. J. Mar. Fresh. Res.*, 27: 279-295.

de Lestang, S. and R. Melville-Smith. 2006. Interannual variation in the moult cycle and size at double breeding of mature female western rock lobster *Panulirus cygnus*. *ICES J. Mar. Sci.*, 63: 1631-1639.

de Lestang, S., N. Caputi and R. Melville-Smith. 2009. Using fine-scale catch predictions to examine spatial variation in growth and catchability of *Panulirus cygnus* along the west coast of Australia. *N. Z. J. Mar. Freshwat. Res.,* 43: 443-455.

Gardner, C., S. D. Frusher, N. S. Barrett, M. Haddon and C. D. Buxton. 2006. Spatial variation in size at onset of maturity of female southern rock lobster *Jasus edwardsii* around Tasmania, Australia. *Sci. Mar.*, 70: 423-430.

Grey, K. A. 1979. Estimates of the size at sexual maturity of the western rock lobster, *Panulirus cygnus*, using secondary sexual characteristics. *Aust. J. Mar. Fresh. Res.*, 30: 1187-1199.

Johnston, D., R. Melville-Smith, B. Hendriks and B. Phillips. 2008. Growth rates and survival of western rock lobster (*Panulirus cygnus*) at two temperatures (ambient and 23°C) and two feeding frequencies. *Aquaculture*, 279: 77-84.

Maxwell, K. E., T. R. Matthews, R. D. Bertelsen and C. D. Derby. 2009. Using age to evaluate reproduction in Carribean spiny lobster, *Panulirus argus*, in the Florida Keys and Dry Tortugas, United States. *N. Z. J. Mar. Freshwat. Res.,* 43: 139-149.

Melville-Smith, R. and S. de Lestang. 2005. Visual assessment of the reproductive condition of female western rock lobsters (*Panulirus cygnus*). *N. Z. J. Mar. Freshwat. Res.,* 39: 557-562.

Melville-Smith, R., J. B. Jones and R. S. Brown. 1997. Biological tags as moult indicators in *Panulirus cygnus* (George). *Aust. J. Mar. Fresh. Res.*, 48: 959-965.

Pearce, A. and M. Feng. 2007. Evidence for global warming on the Western Australian continental shelf. *Mar. Freshwat. Res.*, 58: 914-920.

Pollock, D. E. 1987. Simulation models of rock lobster populations from areas of widely divergent yields on the Cape west coast. *S. Afr. J. Mar. Sci.*, 5: 531-545.

Pollock, D. E. 1991. Spiny lobsters at Tristan da Cunha, South Atlantic: inter-island variations in growth and population structure. *S. Afr. J. Mar. Sci.*, 10: 1-12.

Poloczanska, E. S., R. C. Babcock, A. Butler, A. J. Hobday, O. Hoegh-Guldberg, T. J. Kunz, R. Matear, D. Milton, T. A. Okey and A. J. Richardson. 2007. Climate change and Australian marine life. *Oceanogr. Mar. Biol. Ann. Rev.*, 45: 409-480.

Ray, C. 1960. The application of Bergmann's and Allen's rules to the poikilotherms. *J. Morphol.*, 106: 85-108.

Sibly, R. M. and D. Atkinson. 1994. How rearing temperature affects optimal size in ectotherms. *Funct. Ecol.*, 8: 486-493.

Smith, D. M., K. C. Williams and S. J. Irvin. 2005. Response of the tropical spiny lobster *Panulirus ornatus* to protein content of pelleted feed and to a diet of mussel flesh. *Aquacult. Nutr.*, 11: 209-217.