Effects of water temperature and thermoclines on larval behaviour and development in the giant crab *Pseudocarcinus gigas* (Lamarck)

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*Pseudocarcinus gigas* is a deep-water commercial species. To date, only three larvae have been collected, despite extensive sampling. Therefore, to assist the targeting of field sampling of larvae, laboratory-based research was undertaken to identify temperature preferences. Two approaches were taken. The first investigated the behavioural responses of *P. gigas* larvae to temperature. Experimental columns with discontinuous temperature gradients were used to test the ability of *P. gigas* larvae to penetrate thermoclines vertically. Each trial also presented the larvae with a choice of two temperature options so results were used to infer preferred temperature ranges. In the second approach, we measured instar duration, somatic growth and survival of larvae reared at 12 temperatures between 10.5 and 21.1°C.

Behavioural experiments indicated that zoeas I and II could readily penetrate experimental thermoclines of ~2, 5 and 10°C. Upward swimming was induced in water temperatures ≤12.7°C and downward swimming or passive sinking induced by temperatures ≥16.2°C. Intermoult duration decreased with increasing temperature, although more rapid development was at the expense of somatic growth. Apparent temperature preferences of larvae from behavioural trials were also optimal for survival and growth. No larvae survived to megalopa in those treatments below the threshold temperature where upward swimming was induced in behaviour trials. Many megalopae died shortly after moulting from zoea V, particularly in treatments with rapid development (>16.8°C) and above those temperatures where downward migration of zoas was induced. Highest abundance of *P. gigas* larvae in the field is predicted to be in water of 13–16°C.

**INTRODUCTION**

The giant crab *Pseudocarcinus gigas* (Lamarck, 1818) is a large commercial species fished in deeper water (120–270 m) off southern Australia (Levings *et al*., 1996). Little is known of the recruitment of this species beyond a description of the five zoeal stages and the megalopa (Gardner and Quintana, 1998), laboratory-estimated larval duration (Gardner and Northam, 1997), and observations that juveniles tend to occur in deeper water than adults (Levings *et al*., 1996) in association with sponges (McNeill, 1920). Extensive plankton sampling in oceanic water at presumed appropriate times and areas has been of limited value with only three specimens obtained (Gardner, 1998a). The research presented here was intended to assist targeting of field sampling of *P. gigas* larvae and also expand on the general biological information on this species.

Temperature profoundly influences development of decapod larvae and numerous studies have demonstrated effects on instar duration, morphology, feeding rate, size, incidence of deformity and survival (Johns, 1981; Shirley *et al*., 1987). Crustacean larvae do not usually experience temperature passively, but regulate their vertical migration behaviour, and thus depth, in response to both absolute temperature and rates of temperature.
change (Forward, 1990). Sulkin reviewed the effect of temperature on vertical migration and noted that in most cases there is a direct relationship with swimming speed (Sulkin, 1984). The orientation of swimming responses may also be affected so that the geotaxis response is reversed (Forward, 1990). Forward considered that the larval response to temperature constituted a negative feedback system so that depth was regulated relative to temperature (Forward, 1990). These effects of temperature on development and behaviour may lead to crustacean larvae becoming restricted to water ranging over only a few degrees in temperature (Bruce et al., 2000).

In nature, the distribution of plankton in relation to temperature is strongly influenced by thermoclines, which thereby largely control vertical distribution (Harder, 1968). Evidence from laboratory studies with crab larvae indicate that thermoclines generally do not have an inhibitory effect on vertical migration, although only a few species have been examined, specifically: Geryon quinquedens (Kelly et al., 1982), Eurypanopeus depressus (Sulkin et al., 1983) and Callinectes sapidus (McConnaughey and Sulkin, 1984).

METHOD

We conducted a series of laboratory experiments to investigate the effect of temperature on swimming behaviour and development. Swimming behavioural responses were monitored for the first two zoeal stages, while larvae in development trials were reared through all five zoeal stages to the megalopa stage.

Source of larvae

Ovigerous females for all trials were collected from depths of 300–380 m off the east coast of Tasmania, Australia (41°17’S; 148°40’E) in June 1995 (development trials) and July 1996 (behavioural trials). Females ranged in size from 2.2 to 4.5 kg and were held communally in 4 m³ tanks with flow-through, unfiltered, sea water. Temperature in the broodstock tanks ranged from 8 to 14°C and the lighting regime was ~10 h light per day.

For development trials, larvae were collected from two tanks to ensure that they were not from a single parent; further mixing of genetic source probably occurred as several females were releasing larvae in each tank. For behaviour trials, eight females were separated into four tanks before larval release so that larvae could be collected separately. Each of these tanks yielded a replicate group of larvae, which were reared in 200 L upwelling cultures at 14°C (range ±0.3°C) for 18 days, through to the second zoeal stage. The cultures were maintained in a reverse circadian cycle with 12 h light (i.e. light phase from 19.00 h to 07.00 h) as experimentation was conducted in darkness. Water for these 200 L cultures was recirculated through a shared sump and biofilter to minimize variation from tank effects. Zoea larvae for both trials were fed a mix of Protein Selco® enriched rotifers (Brachionus plicatilis) maintained at ~10 mL⁻¹ and enriched Artemia instar II nauplii for the first two zoeal stages maintained at ~3 mL⁻¹ (after which behavioural trials were terminated) and enriched Artemia only thereafter (for development trials). Prey items were replenished twice daily to maintain high density and also to reduce the likelihood of zoas encountering prey items with depleted levels of enriching formula.

System design and protocol for swimming behaviour experiments

Experiments to measure both the response of P. gigas larvae to thermoclines and also their selected temperature range used an experimental system modified from McConnaughey and Sulkin (McConnaughey and Sulkin, 1984) to produce thermoclines in vertical columns (Figures 1 and 2). Testing columns (450 mm) were surrounded by heated or chilled, upper and lower water baths, separated by a 10 mm insulated layer. Water in the lower bath was recirculated through a sump with a heat/chill unit, while water in the upper baths was heated with aquarium heaters and circulated by aeration. The temperature of the upper water bath was increased relative to the lower water bath to produce thermoclines in the testing columns of ~10, 5 and ~3°C.
Trials to assess the preferred temperature range of stage I and II zoeas were conducted with five different temperatures in the lower water bath which were intended to differ in 2°C steps (actual values 11, 12.7, 14.5, 16.0 and 18.4°C), although there was slight variation between tests on stage I and stage II zoeas (precise values in Figures 3, 4 and 5). In control chambers, the regime was the same in both the upper and lower water baths so that no thermocline was generated.

Between 20 and 35 larvae were introduced to each of four replicate testing columns by syringe after acclimatizing to the experimental temperature for 5 min. Trials were run in darkness for 15 min and columns were then illuminated, to record the position of larvae in four divisions, two upper and two lower, using red light of 617 nm wavelength (Kodak™ gelatine filter #25) at 10 lux, which does not induce phototaxis (Forward, 1990; Gardner, 1996). Light was directed perpendicular to the testing chambers so any phototaxis of larvae would not result in vertical movement along the column. No trials were run with simulated natural lighting due to the difficulty of avoiding laboratory artefacts (Haney, 1988). Larvae were never reused.

**Behavioural response to thermoclines**

The ability of larvae to penetrate thermoclines was analysed by comparing the larval distribution following introduction through either the top or the bottom of the testing chamber; a difference in distribution between these two protocols after 15 min was taken to indicate an effect of the thermocline on movement within the testing chamber. Larvae were introduced to the chamber with a syringe and this was attached to a ball valve to enable them to be introduced at the base. Experiments to test response to thermoclines were conducted with the coldest lower bath temperature configuration (11.1 and 10.8°C for Z1 and Z2 larvae, respectively) as this induced upward swimming. The proportion of larvae in the upper and lower halves of the testing column was compared between treatments where larvae were introduced either at the top or at the base; a significant difference between these treatments was taken to indicate an effect of the thermocline.
thermocline on larval movement. As each of the four replicates of each treatment consisted of larvae of different maternal origin, there was potential for heterogeneity in behavioural responses. Consequently, replicates were tested for heterogeneity by G-statistic. The effect of treatment was then tested with a replicated goodness of fit test (G-statistic) to retain information obtained through replication (Sokal and Rohlf, 1981).

**Temperature selection trials**

Additional experiments were conducted to determine the temperature range selected by larvae as indicated by vertical distribution. These trials used the same apparatus as described for testing the response to thermoclines, with larvae offered two temperature choices to select (or avoid). These experiments differed from those for testing the response to thermoclines as larvae were only introduced at the top of the column and a range of lower water-bath temperatures was tested. The distribution of larvae within the testing chamber was used to estimate the temperature range selected by *P. gigas* zoeas. Note that several studies have demonstrated that decapod larvae will passively sink to avoid temperatures above a preferred range (Ott and Forward, 1976; Yule, 1984). This implies that the accumulation of larvae in the lower half of the testing chamber indicates that the temperature above the thermocline is above the preferred range. Additional information was obtained by comparing the distribution within each of the four divisions of the testing column. For instance, a higher frequency of larvae in the divisions immediately above and
below the thermocline suggests both downward movement induced by the upper temperature and upward movement induced by the lower temperature.

The null hypothesis that larvae were randomly distributed in the column was tested by comparing the observed distribution in each of the four divisions against a predicted distribution of a 1:1:1:1 ratio. As with the thermocline experiments, these frequency data were tested with a replicated goodness of fit test (G-statistic) after testing for homogeneity.

System design and protocol for development experiments

The effect of temperature on larval development was tested by culturing larvae in 12 temperature regimes separated by ~1°C increments (10.5, 11.7, 12.8, 13.8, 14.8, 15.8, 16.8, 17.8, 18.6, 19.4, 20.2 and 21.1°C). The 12 temperature treatments were created with an aluminium temperature gradient plate constructed from a large aluminium block (300 x 400 x 50 mm) with channels at each end for circulating heated or chilled water (Edwards and Van Baalen, 1970). This created an even temperature gradient along the aluminium block and 50 mL culture vessels were placed into 12 rows of holes bored into the block. Six vessels were maintained at each temperature: three replicate larval cultures (n = 10 per replicate) and three vessels for preheating water prior to daily transfer of larvae into new water (0.2 μm filtered sea water).

Larval development in each of the 12 temperature treatments was monitored by recording the number and stage of dead larvae and exuviae. Many larvae moulted through to megalopa but died shortly afterwards. Those larvae that survived 24 h after moulting to megalopa were scored as viable. All megalopas were sacrificed at this stage, then rinsed with distilled water and dried at 80°C for 24 h to determine dry weight.

Statistical analysis of development data

The effect of temperature on the timing of mouls was tested by one-way ANOVA at each zoal stage using log-transformed time (Hayes, 1949). Changes in survival due to temperature were tested by Kaplan–Meier survival analysis (Miller, 1981) to overcome the non-linear pattern in mortality and to enable censoring of viable megalopas in each treatment was assessed with a Kolmogorov–Smirnov test (Sokal and Rohlf, 1981) by comparing the observed number of viable megalopas against the predicted number of viable megalopas if there was no temperature effect [i.e. predicted frequency = initial number of megalopas in treatment x (total viable megalopas/total initial number of megalopas)].

RESULTS

Response of larvae to thermoclines

The distribution of larvae within the testing columns after introduction either below or above the thermocline indicated that there was no inhibition of larval movement (Figure 3). The ratios of larval numbers in the upper half to those in the lower half of the testing column appeared homogeneous between replicates within each treatment (P > 0.05). A significant difference between the distribution of zoas after introduction above or below the thermocline was observed in two experiments (P < 0.05; treatments 19.6°C/11.1°C with stage I zoas and 15.1°C/10.8°C with stage II zoas; Figure 3). These results were caused by a greater than predicted proportion of zoas swimming up through the thermocline when introduced from below. That is, the trend was opposite to that which would occur if the thermocline had inhibited larval movement.

Temperature selection trials

The ratios of larvae within divisions of the testing column appeared homogeneous between replicates for most treatments, although heterogeneity was detected in five cases (P > 0.05; Figures 4 and 5). While deviation from homogeneity in some cases is not surprising, given the large number of separate tests (37), this result suggests that some replicates may have behaved differently from others, possibly due to their different genetic origin. The implication from this result is that significant tests of the effect of treatment in these tests may be false, although trends between treatments appear robust, as replicates were generally homogeneous.

Larvae in control treatments without a temperature gradient tended to actively swim upwards at temperatures ≤12.6°C and ≤12.7°C, while sinking was induced at ≥16.2°C and ≥18.3°C for stage I and II zoas, respectively (Figures 4 and 5, upper row). The distributions were significantly different from random distribution along the testing column in all control treatments except 15.0 and 15.9°C for stage I and II zoas, respectively (P < 0.05). A similar pattern was detected in treatments where two alternative temperatures were separated by a thermocline. The response of stage II
zoeas to the 16.3°C/14.0°C treatment indicates that stage II zoeas will also descend at temperatures ≥16.3°C. Although a significantly higher proportion of zoea I larvae was found in the upper half of the 16.7°C/12.6°C treatment, this appeared to be due to larvae swimming upwards to avoid the lower temperature as most larvae were found immediately above the thermocline. Larvae placed in treatments where both the upper and lower temperature alternatives were outside the apparent preferred range tended to congregate around the thermocline (21.3°C/12.6°C in zoea I and 17.9°C/12.7°C in zoea II).

**Growth**

Intermoult duration decreased with increasing temperature at each instar (n = 3; P < 0.0001; Figure 6). Larvae reared at 10.5°C failed to develop past zoea II and the mean duration of the first zoeal stage was 32 days (± 0.33; n = 3). Most rapid development through to megalopa was 41 days (± 0.41; n = 3) at 20.2°C. The plot of log time to instar against temperature was not linear, which indicates that the decrease in intermoult duration with increased temperature is not simply exponential as occurs in chemical systems by van’t Hoff’s rule (Hayes, 1949; Garside, 1966). The more rapid development of larvae at higher temperature appeared to be at the expense of somatic growth as the dry weight of megalopas declined significantly with increasing temperature (slope of regression < 0, P < 0.01; Figure 7).

**Survival**

Survival increased with higher temperatures (P < 0.001) so that best survival was obtained with treatments 15.8–21.1°C, with most zoeas in these treatments reaching at least stage III (Figure 8). No larvae survived to megalopa in treatments <12.8°C. Most mortality occurred at zoea I and at megalopa (Figure 9). Although survival to megalopa was low (mean of all cultures = 23%), the proportion of viable megalopas (those alive after 24 h) was significantly affected by temperature (P < 0.05). The largest unsigned difference in the Kolmogorov–Smirnov test, which indicates greatest viability of megalopas, was at 15.8°C (Figure 10).

**DISCUSSION**

Consistent patterns were observed in the behavioural and physiological response of *P. gigas* larvae to temperature.
Vertical swimming behaviour was influenced by temperature and our results suggest that larvae in the field would attempt to vertically migrate to avoid temperatures outside the range of 13–16°C, when in the absence of light. Results from development trials also indicated that the ideal temperature for development lies within this range, based on poor survival and growth at lower temperatures and reduced viability of megalopa at higher temperatures.

Although several studies on brachyurans have demonstrated close relationships between laboratory results and observations from plankton sampling (Anger, 1983; Shirley et al., 1987), laboratory results can be misleading. For instance, the optimal temperature for growth and survival of *Jawus edwardsii* larvae in the laboratory was reported as 21–24°C by Tong et al. (Tong et al., 2000), yet Bruce et al. found that few animals were captured in plankton tows when the temperature exceeded 15°C (Bruce et al., 2000). Clearly, compounding factors in laboratory studies, such as egg incubation temperature, will influence results (Laughlin and French, 1989). Nonetheless, collection of *P. gigas* larvae from plankton tows has proved difficult (Gardner, 1998a), so information on probable distribution in relation to temperature is of value for providing a starting point for future surveys. At this stage, the only information available to link laboratory data with information from the field are three stage II zoeas captured in plankton tows off southern Tasmania (Gardner, 1998a). These were all in water of 12–12.5°C, which is within the range selected by stage II zoeas in laboratory behaviour trials, although survival was low at this temperature.

**Behavioural responses to temperature**

Sulkin described the mechanism for vertical migration of brachyuran larvae as a combination between cues to orientate swimming and cues to influence locomotor responses, either through passive sinking or active swimming (Sulkin, 1984). The principal factor influencing locomotion and orientation during daylight hours is light, and there is potential for this to be important to *P. gigas* larvae even at the depth of hatching, around 300 m (Clarke, 1970; Levings et al., 1996). However, phototactic responses clearly do not account for larval migration patterns during the night. In an early paper, Sulkin proposed that decapod larvae regulate depth in the absence of light by a combination of responses to hydrostatic pressure and gravity (Sulkin, 1973). Since then, the response of larvae to temperature has been studied in greater detail and it appears that thermokinesis is also critical in maintaining depth (Ott and Forward, 1976; Kelly et al., 1982). *Pseudocarcinus gigas* zoeas do not appear to respond to change in hydrostatic pressure (Gardner, 1996), so the thermokinesis observed in these trials may be an alternative mechanism for regulating locomotion. Although we did not investigate the effect of temperature on the response of *P. gigas* larvae in the presence of light, the observed temperature response indicates that the vertical position of stage I and II zoeas at night would be maintained within water of 13 and 16°C.

These laboratory results are consistent with water temperatures expected around areas where the giant crab fishery operates during October–December when *P. gigas* larvae would be expected in the water column (Levings et al., 1996; Gardner and Quintana, 1998). Water temperature off eastern Tasmania in early summer...
(December) ranged from 17.5 to 14.5°C at the surface to 12.5°C at 80 m depth during 1989–1991 (Jordan et al., 1995). At Maria Island, which approximates the southern range of the fishery off eastern Tasmania, October–December temperatures at the surface and 50 m depth ranged from 12.5 to 15.5°C and from 12.5 to 14.0°C, respectively (Young et al., 1993).

**Behavioural responses to the thermocline**

Stage I and II *P. gigas* zoeas were not influenced by the experimental thermoclines produced in this trial, a finding that has also been reported for other brachyuran larvae including *G. quinquedens* (Kelly et al., 1982) and *E. depressus* (Sulkin et al., 1983). This apparent absence of an inhibitory effect of thermoclines on zoal movement suggests that there is no physical barrier to restrict larval movement. Rather, *P. gigas* larvae appeared to vertically migrate in response to absolute temperature so that they accumulated either above or below the thermocline, regardless of which side of the thermocline they originated from. A similar response was observed with *C. sapidus*, where larvae failed to penetrate a thermocline only when the upper absolute temperature was extreme (McConnaughey and Sulkin, 1984). Our results indicate that *P. gigas* larvae in the field would not be expected to accumulate around thermoclines unless the temperature either side was outside their apparent selected range of ~13–16°C.

Although thermoclines appeared to have no effect on larval movement in this trial, the distribution of planktonic organisms in nature is often strongly influenced by the presence of thermoclines, with organisms restricted to one side, or found in greatest abundance around this layer (Keifer and Kremer, 1981; Harding et al., 1987). Various mechanisms have been proposed for this phenomenon, including aggregation around areas of greatest prey density associated with the nitrite maxima at the thermocline (Keifer and Kremer, 1981), an inability to penetrate density gradients (Harder, 1968) and a negative feedback system of depth regulation based on rates of temperature change (Forward, 1990). Note that the last of these proposed mechanisms, response to rates of temperature change, involves larvae detecting changes in temperature in relation to time, rather than responses to absolute temperatures. Our experimental system was more suited to testing the proposed mechanism of inability to penetrate density gradients, rather than rates of temperature change, as the gradient was sharper than typically occurs in nature.

Most of the giant crab fishery off the coast of eastern Australia lies between 40 and 43°S (Gardner, 1998b). When present, thermoclines in this region during the months following larval release (late spring/early summer) typically span ~17–13°C over distances of at least 10 m (Young et al., 1993; Jordan et al., 1995). This gradient is far more gradual than examined in our laboratory study and would appear unlikely to provide a barrier to *P. gigas* zoeas. Grey (Grey, 1996) reported that thermoclines formed in waters at the northern end of the range of *P. gigas* in New South Wales (McNeill, 1920) did not appear to influence the broad-scale distribution of larval fishes. We predict similar results with *P. gigas*, although absolute temperature ranges appear to be critical for influencing larval distribution. While the well-defined results from our laboratory study of the response of *P. gigas* to thermoclines provide a useful starting point for future field surveys, it must be acknowledged that a number of variables, which could result in different patterns in the field, remain untested here.

**Comparison between the effect of temperature on development and behaviour**

Our observations of a retarding effect of lower temperature and an accelerating effect of higher temperature on intermoult duration were the same as those reported for numerous other decapod larvae (Sulkin and McKeen, 1994; Goncalves et al., 1995). The relationship between log(time) and larval instar was not linear, so van’t Hoff’s rule for chemical reactions was not met (Johansen and Krough, 1914; Garside, 1966), and larval development almost ceased in the 10.5°C treatment with no larvae surviving beyond zoea II. This indicates that the thermal requirements for growth of *P. gigas* larvae have an optimal range and are not simply cumulative (degree days), but involve some component of threshold phenomena (Waddy and Aiken, 1996).

Behavioural and development trials also gave similar results in relation to the upper temperature range. Downward vertical migration of stage I and II zoeas was initiated at 16.2 and 16.3°C, respectively. Although overall survival (cumulative for all zoea instars) was relatively high in treatments warmer than these thresholds, the viability of megalopas appeared reduced so that few survived this final instar in treatments warmer than 16.8°C. Larval response to temperature is known to change during development in other species (Forward, 1990), so the behavioural response of stage I and II larvae is not directly applicable to the final zoeal stage. Nonetheless, it is noteworthy that the optimal treatment for viability of stage V zoeas moulting to megalopa (15.8°C) was within the range that stage I and II larvae would migrate to in the absence of light. This 15.8°C treatment was the closest treatment in development trials to the control treatments in behavioural trials where larvae were distributed evenly throughout the testing chamber (15.0 and 15.9°C for stage I and II, respectively).

Sulkin and McKeen considered the final zoeal stage of *Cancer magister* to be the most sensitive to temperature
stress and *P. gigas* appears to be similar as mortality was highest at this stage (Sulkin and McKeen, 1989). The incidence of deformity increases at extreme high temperature in most organisms (Battle, 1930) and this appeared to contribute to the low survival of megalopa typical at high temperatures (Okamoto, 1993). Johns (Johns, 1981) noted that larval size of *Cancer irroratus* was greatest in the mid-range of thermal tolerance, although larval weight more typically declines with increased temperature (Shirley et al., 1987; Sulkin and McKeen, 1994), as was observed with *P. gigas*. Low weight of larvae reared at higher temperatures may be indicative of reduced energy stores (Minagawa, 1990), which may have contributed to the poor survival of *P. gigas* larvae to megalopa in treatments >16.8°C.

The remarkably similar range of unfavourable temperatures for development of *P. gigas* and temperatures that these larvae avoid by vertical migration suggests that the behavioural response is of metabolic advantage. Haney discussed a range of hypotheses to explain the adaptive advantage of diel migration of planktonic organisms and these include predator avoidance, avoidance of damaging solar radiation, tracking of prey items and metabolic advantages (Haney, 1988). Our results support the hypothesis of a metabolic function, although they do not negate other hypotheses proposed by Haney (Haney, 1988).

**Implications of temperature on distribution of *P. gigas***

Kinne (Kinne, 1963) considered that temperature was the principal abiotic factor influencing the distribution of species, and temperature can also moderate biotic factors, for example by increasing exposure to predation when instar duration is extended (Jamieson and Armstrong, 1991). Given the low survival of *P. gigas* larvae in treatments <14°C, it is likely that zoal larvae typically have a plankton period of <3 months and hence there may be little potential for long-distance dispersal (Thorson, 1961). *P. gigas* has not colonized nearby New Zealand (McLay, 1988), while *J. edwardsii* (McLay, 1988), which has a 12–24 month larval duration (Phillips and Sastry, 1980), is found in both locations. The distribution of *P. gigas* within waters around Tasmania may also reflect temperature tolerances of larvae. Relatively few giant crabs are harvested south of 43°S (Gardner, 1998b), and sea surface temperature in these areas ranged between 10 and 14°C in the months of October and November for 8 of the 10 years from 1988 through to 1997 (Bruce et al., 2000). Our development results suggest low survival at these temperatures. Likewise, poor survival to megalopa in treatments >16.8°C may limit the northern range of the species and explain the rarity of specimens from the state of New South Wales (McNeill, 1920), where temperature at 34°S regularly exceeds 16°C in the upper 70 m during September (Grey, 1996).

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