



Effects of temperature and food availability on adult body length in natural and laboratory populations of *Paracerceis sculpta* (Holmes), a Gulf of California isopod

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Received 25 August 1997; received in revised form 2 July 1998; accepted 28 July 1998

Abstract

In the Gulf of California, *Paracerceis sculpta* (Holmes), a sphaeromatid isopod, feeds on coralline algae and breeds in the spongocoels of calcareous sponges (*Leucetta losangelensis* de Laubenfels). Near Puerto Peñasco, Sonora, sea surface temperature and algal abundance fluctuate throughout the year. To investigate how these factors influence isopod growth, we plotted the body lengths of field-collected isopods against monthly sea surface temperatures, as well as against the relative abundance of coralline algae (*Corallina: Amphiroa*), over a 26-month period (1983–1985). We found that average body lengths of the four adult morphs in this species (α -, β -, γ -males and females), were larger in cool months and smaller in warm months. Our records of female reproductive condition at capture allowed identification of the approximate dates on which females matured, thus the effect of temperature on growth was most clearly seen in females. Monthly average body lengths correlated negatively with temperature for all adult morphotypes, with different slopes and intercepts; morphotypes undergoing more molts had steeper slopes. Coralline algae abundance showed no seasonal patterns, and we found no significant relationships between relative algal abundance and isopod body length for any adult morph. In the laboratory, animals reared at lower temperature (21°C) matured at larger body lengths than individuals reared at higher temperatures (27–30°C). However, well-fed individuals grew no more rapidly than poorly-fed individuals. Thus, variation in food availability had no recognizable effect on isopod growth in either the laboratory or in the field, whereas variation in temperature significantly influenced growth in both locations, with effects proportional to the number of pre-adult molts. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Crustacea; Isopoda; *Paracerceis*; Growth; Temperature; Food

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1. Introduction

Intra-specific patterns of growth and development are among the most meticulously documented aspects of crustacean biology. In an extensive review, Hartnoll (1982) introduced the concept of a crustacean growth format, a scheme which classifies species by their tendency to exhibit: (1) determinate or indeterminate growth, (2) fixed or variable molt numbers, and (3) sexual maturation before or after a terminal molt. Hartnoll (1982) discussed internal and external factors likely to influence growth format expression, and concluded that for most species, the effects of temperature and nutrient availability are most obvious, since these factors directly affect the ability of crustaceans to increase in size during their intermolt period. In most species, intermolt size increases appear to be proportional to nutrient intake, yet inversely proportional to temperature since cooler temperatures prolong intermolt duration and thus allow greater accumulation of biomass between molts. Hartnoll (1982) concluded that in species with determinate growth, increased body size results from increased food availability or exposure to cool temperatures during intermolt periods. Atkinson (1994) reached a similar general conclusion for crustaceans in a comprehensive review of the effects of temperature on growth in poikilothermic species, albeit from the perspective that increased temperature causes decreased size at a given stage of development.

Most recent field studies of crustacean growth sample all life stages from a particular environment, and make inferences about the effects of ambient conditions on development from morphological patterns observed among the collected animals (Holdich, 1976; Henmi, 1989; Wilkens et al., 1990; Sastre, 1991; Briones-Fourzán and Lozano-Alvarez, 1991; Hamano and Morrissy, 1992; Huntley and Lopez, 1992; Hartnoll et al., 1993; Hoenig et al., 1994; Soong and Mok, 1994). Since population samples of this kind may be expensive to collect and/or tedious to examine, conclusions tend to be drawn from a limited number of such population sections per year. Many crustacean species reproduce in thermally stable environments (Hughes and Matthiessen, 1962; Shuster, 1981; Boucher et al., 1984; Briones-Fourzán and Lozano-Alvarez, 1991; Soong and Mok, 1994) or during particular seasons (Runge et al., 1985; Caldwell, 1986; Paul et al., 1990; Morgan and Christy, 1994). Thus, the effects of environmental variation on particular life stages are difficult to identify in the field because seasonal changes in water temperature or nutrient availability either do not exist, or are visited on entire cohorts of individuals simultaneously.

When possible, laboratory studies are undertaken to determine whether variation observed in the field can be simulated, or simply to explore the possible effects of environmental manipulations (Hartnoll and Mohamedeen, 1987; Kuris et al., 1987; MacKenzie, 1988; West and Costlow, 1988; Ra'anan et al., 1991; Kondzela and Shirley, 1993; Schultze and Anger, 1997). However, in most crustacean species, individuals within each sex undergo similar numbers of molts to reach sexual maturity (above references; Aoki, 1997; see also Kuris et al., 1987; Ra'anan et al., 1991 for exceptions). Thus, in most species, the influence of environmental conditions on different molt numbers requires inter-specific rather than intra-specific comparisons.

In this paper, we examine the effects of water temperature and food availability on patterns of molting and growth in *Paracerceis sculpta* (Holmes), a sphaeromatid isopod

inhabiting a marine environment in which physical and biotic conditions vary widely throughout the year (Thomson and Lehner, 1976). Males in *P. sculpta* exhibit a genetically-based size polymorphism which causes individuals to mature at one of three different ages (Shuster and Wade, 1991; Shuster and Sassaman, 1997). Moreover, females in this species undergo marked changes in physical condition associated with their semelparous life history (Shuster, 1991a). These life history and environmental characteristics provide an opportunity to specifically test the hypotheses by Hartnoll (1982) regarding the effects of temperature and nutrient availability on crustacean growth in the field, in the laboratory, and within a single species.

1.1. The northern Gulf of California

Physical conditions in the intertidal zone of the northern Gulf of California are highly variable (Thomson and Lehner, 1976; Brusca, 1980; Shuster, 1991b). Mixed semidiurnal tides regularly expose an extensive coquina-limestone reef, seasonal fluctuations in temperature may exceed 20°C (Thomson and Lehner, 1976), and unpredictable storms (*chubascos*; Brusca, 1980) scour rocks and reef surfaces in intertidal areas, removing attached invertebrates as well as algal turf on which certain organisms (including isopods) may feed (Shuster, 1991b). The combined effect of these environmental factors create conditions which, while predictably variable over annual time scales, are also highly unpredictable over brief spatial and temporal scales. The Gulf thus provides an ideal natural environment in which to examine the effects of physical factors on crustacean growth over short and long durations.

1.2. Male polymorphism in *P. sculpta*

P. sculpta (Holmes) is a sexually dimorphic, sphaeromatid isopod crustacean inhabiting the northern Gulf of California (Brusca, 1980; Shuster, 1987). In this species, males coexist as three genetically distinct adult morphs which differ in reproductive behavior and in external morphology (Shuster and Wade, 1991; Shuster and Sassaman, 1997). α -Males are larger than females and possess elongated, pointed uropods, which are used in courtship and in aggressive interactions with other males at breeding sites (the spongocoels of intertidal sponges, *Leucetta losangelensis* de Laubenfels, Shuster, 1990, 1991b, 1992). β -Males are smaller than α -males, resemble females in size and in uropod characteristics, and invade harems by mimicking female courtship behavior. γ -Males are smaller than β -males, are capable of rapid swimming and crawling movements, and invade harems by outmaneuvering resident α -males (Shuster, 1992).

In the laboratory, the three male morphs undergo different numbers of molts and mature at different rates; γ -males mature most rapidly (mean \pm 95% confidence intervals: N molts = 3.04 ± 0.45 , $N = 23$; days to maturity = 33.21 ± 6.45 , $N = 19$), β -males mature at an intermediate rate (N molts = 5.10 ± 0.19 , $N = 145$; days to maturity = 55.87 ± 2.45 , $N = 132$), α -males mature most slowly (N molts = 6.56 ± 0.49 , $N = 25$; days to maturity = 71.30 ± 5.80 , $N = 23$; Baitoo et al., 1988). Thus, in *P. sculpta*, three distinct, determinate growth formats are represented among males in a single species.

1.3. Female semelparity in *P. sculpta*

Females do not exhibit morphological polymorphism in *P. sculpta*. (Shuster, 1987). In general, female molting and maturation schedules are intermediate between those of α - and β -males (N molts = 5.85 ± 0.19 , $N = 219$; days to maturity = 66.43 ± 14.05 , $N = 197$; Baitoo et al., 1988). However, like certain other dynamenine sphaeromatids, females in this species are semelparous and undergo marked changes in morphology while brooding progeny (Harrison, 1984). Mature females enter spongocoels, undergo a sexual molt, mate, brood their progeny, release juveniles (mancas) and die, all within approximately five weeks (Shuster, 1989, 1991a).

Shuster (1991a) identified eight distinct stages in gestating *P. sculpta* females based on the physical condition of females' bodies and on the relative development of embryos during gestation. These stages, for the purpose of this study, can be condensed into three summary categories as follows: (1) "newly adult females (S_1 – S_3)," whose unmolted or newly molted condition indicate that they arrived at spongocoels less than 72 h prior to collection; (2) "gravid females (S_{4p-e} – S_5)," which possess brood pouches filled with developing embryos, indicating they arrived at spongocoels four days to four weeks before collection; (3) "spent females (S_6 – S_7)," which are in the process of releasing or have just released mancas, indicating they arrived at spongocoels three to six weeks before collection (Shuster, 1991a, 1995).

Since females breed throughout the year in the northern Gulf of California, newly adult females (S_1) continually arrive at sponges after leaving feeding sites in coralline algae. Thus, at any given time of the year, the sizes of females in a particular reproductive stage represent the size distribution of females that reached sexual maturity and entered spongocoels at approximately the same time (Harrison, 1984; Shuster, 1989, 1991a). Moreover, since each cohort of females presumably experiences similar environmental conditions while maturing, the body lengths (as well as other dimensions) of these individuals are expected to reflect environmental influences on their pre-adult growth.

1.4. Male polymorphism, female semelparity and isopod growth

The existence of three male morphs with distinct molting and growth schedules, as well as semelparous females with clearly distinguishable stages of reproductive condition, allowed us to make the following predictions about the influences of temperature and food availability on patterns of molting and growth in this species. Since increasing temperature appears to decrease intermolt duration (Hartnoll, 1982; Atkinson, 1994), we predicted that temperature should affect individuals in proportion to the number of pre-adult molts they undergo before reaching maturity. Thus, we expected α -males to be disproportionately smaller with increasing temperature, and disproportionately larger in cooler temperatures, than individuals undergoing fewer pre-adult molts (β -males, females and γ -males). Similarly, since nutrient availability appears to limit growth during the intermolt period (Hartnoll, 1982), we predicted that the effects of food surpluses should be most easily observed in α -males, who undergo more molts before reaching maturity than females, β -males or γ -males.

2. Methods

2.1. Measurement of sea surface temperature and coralline algae abundance

Daily water temperatures were measured to the nearest degree ($^{\circ}\text{C}$) by personnel at el Centro Intercultural de Estudios de Desiertos y Océanos (CEDO) between June 1982 and December 1986. Censuses of coralline algae reflect the overall abundance of two genera (*Corallina*; *Amphiroa*) in the entire intertidal zone, determined by the sum of all counts of individual thalli within 100 cm^2 plots, examined every 10 m along two linear 110 m transects, each separated by approximately 100 m and oriented perpendicular to shore at lowest low tide (details in Shuster, 1991b). To identify seasonal patterns in sea surface temperature, we plotted monthly averages in temperature ($\pm 95\%$ C.I.) for the duration of the study. To identify seasonal patterns in coralline algae abundance, we plotted total coralline algae abundance by month between June 1982 and September 1986, and we examined the relationship between sea surface temperature and coralline algae abundance over this duration using Spearman's rank correlation procedure (Siegel and Castellan, Jr., 1988).

2.2. Collection and identification of adult isopods

Every four to five days between the months of October of 1983 and November of 1985, isopods were collected from intertidal *L. losangelensis* sponges at Station Beach, approximately 3 km southeast of Puerto Peñasco, Sonora, Mexico ($\text{N}31^{\circ}.33$, $\text{W}113^{\circ}.58$), as described in Shuster (1991b; Table 1). All isopods were immediately transported to CEDO where each individual was identified by sex and reproductive condition (males by the presence of penes and appendices masculinae [Shuster, 1987]; females by the presence of mature ovaries visible through the ventral cuticle or by the condition of the marsupium, and if present, the embryos developing within [Shuster, 1991a]). All individual body lengths were measured to the nearest 0.15 mm using ocular micrometer and stereomicroscope. Individuals not used in other experiments (reviews in Shuster, 1995; Shuster and Sassaman, 1997) were returned to their approximate sites of collection.

2.3. The effect of temperature on pre-adult growth

To examine the effect of sea surface temperature on pre-adult growth, the body lengths of all individuals were coded by adult morphology (α -, β -, γ -male; female), as well as by collection month, and were compared using analysis of covariance (ANCOVA), with monthly average sea surface temperature as the covariate. Since S_{1-3} females ("newly adult females") had most recently undergone their final molts and were thus most directly influenced by temperature in the current month, only these females were used in this analysis. Males can be aged by their relative degree of cuticular pigmentation, and among α -males, by the amount of algae they have accumulated on their pleotelsons (Shuster, 1986). However, this method is less accurate than that used to age females and was not used here. Thus, we expected to have greater precision in

Table 1
Aggregate monthly samples of *Paracerceis sculpta* adults 1983–1985

Date	α -Males	β -Males	γ -Males	Females	<i>N</i>
Oct 1983	120	14	10	346	490
Nov	124	18	15	377	534
Dec	38	6	5	115	164
Feb 1984	155	8	8	312	483
Mar	179	3	18	517	717
Apr	134	6	36	471	647
May	308	14	87	842	1251
Jun	59	1	16	146	222
Jul	236	9	68	772	1085
Sep	93	7	14	235	349
Oct	55	6	9	175	245
Nov	96	6	12	245	359
Dec	70	3	11	172	256
Jan 1985	252	14	18	409	693
Feb	196	2	12	316	526
Mar	187	7	14	440	648
Apr	180	12	29	497	718
May	24	0	1	27	52
Jun	12	0	2	28	42
Jul	75	2	15	220	312
Aug	152	7	43	443	645
Sep	88	10	31	224	353
Oct	86	7	25	289	407
Nov	106	12	5	297	420
Total	3025	174	504	7915	11 618

identifying the relationship between temperature and adult body size among females than among males.

To examine the effects of ambient temperature on isopod growth in a laboratory environment, we compared the adult body lengths of α - ($N = 17$), β - ($N = 138$), γ -males ($N = 24$) and females ($N = 203$) reared at 21°C (Baitoo et al., 1988), with the adult body lengths of α - ($N = 38$), γ -males ($N = 8$) and females ($N = 40$) reared at 27–30°C. In both experiments, newly released manca were separated into individual petri dishes and were reared to maturity under natural daylight (13L:11D). Isopods were fed bits of coralline algae supplemented with brine shrimp flakes and with bits of chalk as a calcium carbonate source (coralline algae were not provided to isopods reported in Baitoo et al., 1988). Seawater in all petri dishes was changed twice weekly. At maturity, each individual was sexed and measured as described above.

Since no β -males were present in the 27–30°C treatment, we first compared the body lengths of the adult morphs within each temperature treatment using single-factor analysis of variance (ANOVA). We next excluded the measurements of β -males from the 21°C treatment and compared the influences of adult morph and rearing temperature on adult body size between the two treatments using two-factor ANOVA.

Table 2
Effects of food availability on isopod growth: numbers of manca per female in treatments 1–3 (T1–3)

Female	T1	T2	T3	N
1	24	24	19	67
2	10	5	5	20
3	15	15	15	45
4	14	15	5	34
5	10	15	20	45
Total	73	74	64	211

2.4. The effect of nutrient availability on pre-adult growth

We collected five females at stage S_3 from natural spongocoels, each containing a female and one α -male. This procedure insured that all families used in this experiment were sired by α -males, and standardized maturation schedules among laboratory-reared individuals (Shuster and Wade, 1991; Shuster and Sassaman, 1997). Our use of α -sired progeny in this experiment, moreover, enhanced our opportunity to identify differences among feeding treatments since these individuals were most likely to be affected by differences in nutrient availability as described above. To control within-family sire- and dam-effects on individual life history, each family was divided into high, intermediate and low food treatment groups of approximately equal size (T1–3; Table 2). Individuals in T1 were provided food with every water change, individuals in T2 were provided food with every other water change, and individuals in T3 were provided food with every third water change. All individuals were measured after each molt as described above. Since this experiment was terminated after individuals reached their fifth molts, no individuals were identified by sex.

3. Results

3.1. Seasonal fluctuations in temperature and algae abundance

Sea surface temperatures showed regular seasonal fluctuations with extremes ranging from 32°C in August 1984 to 14°C in January 1985 (Fig. 1). Similar fluctuations were reported in Hendrickson (1973). Coralline algae abundance censused between 1982 and 1986 showed no seasonal patterns (Fig. 2), and we found no relationship between sea surface temperature and coralline algae abundance between 1982 and 1986 ($r_s = 0.098$; $P = 0.77$, $N = 10$). Thus, sea temperature in the northern Gulf of California showed considerable seasonal fluctuation, whereas seasonal fluctuations in coralline algae abundance were not identifiable.

3.2. Seasonal fluctuations in male and female body length

Average body length ($\pm 95\%$ C.I.) among the three male morphs as well as among

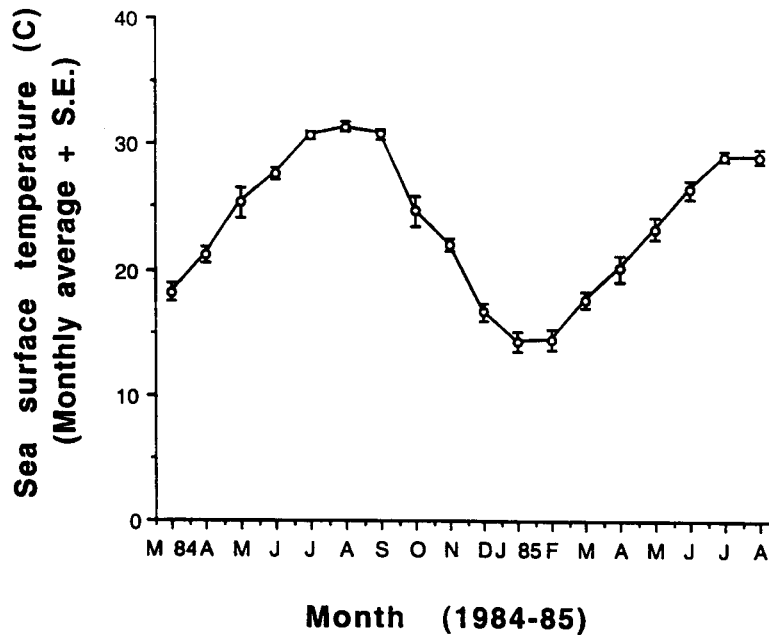


Fig. 1. Variation in sea surface temperature between October 1983 and November 1985 in the northern Gulf of California, recorded near Puerto Peñasco, Sonora, México: squares represent monthly averages \pm 95% C.I.

females of different reproductive condition showed considerable seasonal variation (Figs. 3 and 4, Table 1). In most cases, the size distributions of individuals within each male type, as well as within each female reproductive condition, did not overlap significantly among monthly aggregate samples. Among males, the amplitude of body size fluctuations within each year varied among morphotype, such that α -males showed wider fluctuations in body size than γ -males, as we predicted from Hartnoll (1982). Specifically, the ratio of the smallest average body length to the largest average body length within each morph, within each year, was 0.82 for α -males vs. 0.80 for γ -males in 1984, and 0.79 vs. 0.77 in 1985. This pattern was less apparent among β -males because sample sizes for these individuals were usually small (Fig. 3, Table 1).

Among females, the body lengths of all individuals, regardless of reproductive condition were approximately the same in late winter and late summer (Fig. 4). However, between March and August, S_{5-7} females were significantly larger than S_{1-3} females (indicated by non-overlap of 95% C.I.), whereas between September and February, S_{1-3} females were significantly larger than S_{5-7} females. Throughout the year, S_4 females were of intermediate body length between S_{1-3} and S_{5-7} females. As expected since there were no seasonal patterns in coralline algae abundance (see above), there were no significant relationships between coralline algae abundance and body length for any of the adult morphs between 1983–1985 ($r_s = -0.51$; $P > 0.50$; $N = 5$ for all morphs).

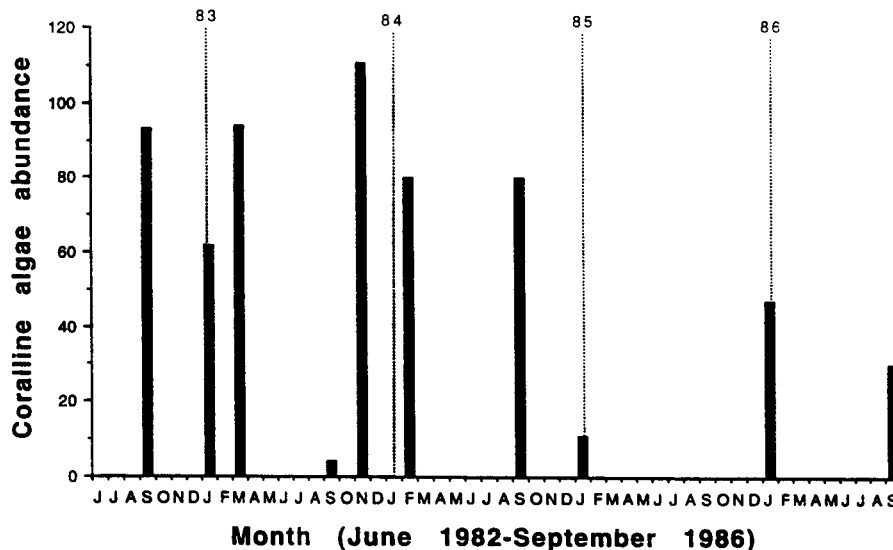


Fig. 2. Coralline algae abundance between June 1982 and September 1986, recorded in the intertidal zone near Puerto Peñasco, Sonora, México; abundances represent the sum of counts of all individual *Corallina* and *Amphiroa* thalli within 100 cm² plots, examined every 10 m along two linear 110-m transects, oriented perpendicular to shore at lowest low tide (details in Shuster, 1991b).

3.3. The relationships between sea surface temperature and body length among adult morphotypes

The body lengths of the four adult morphs, pooled across all monthly aggregate samples from 1983 to 1985, differed significantly ($F_{[3,6725]} = 4928.76$, $P < 0.0001$), as has been shown elsewhere (Shuster, 1987). However, separate regressions of adult body length on sea surface temperature were significant for all adult morphs (α -males: $F_{[1,3015]} = 1824.80$, $P < 0.0001$; β -males: $F_{[1,172]} = 61.68$, $P < 0.0001$; γ -males: $F_{[1,502]} = 264.74$, $P < 0.0001$; females: $F_{[1,3032]} = 3791.50$, $P < 0.0001$), indicating that adult body length correlates negatively with increasing sea temperature for all morphs, and thus that pooling of samples can obscure seasonal differences in body size among morphs.

Analysis of adult body length among the four adult morphs, using sea surface temperature as the covariate, showed significant interaction among the individual regression slopes ($F_{[3,6725]} = 53.41$, $P < 0.0001$), indicating that sea temperature differentially influences adult body length among the four morphs. In particular, as we predicted from Hartnoll's hypothesis, the degree to which sea temperature affected the body length of each morph differed among adult morphs, such that morphs undergoing more molts before sexual maturity were more strongly influenced by temperature (i.e., had steeper negative slopes) than morphs undergoing fewer molts before reaching maturity (Fig. 5).

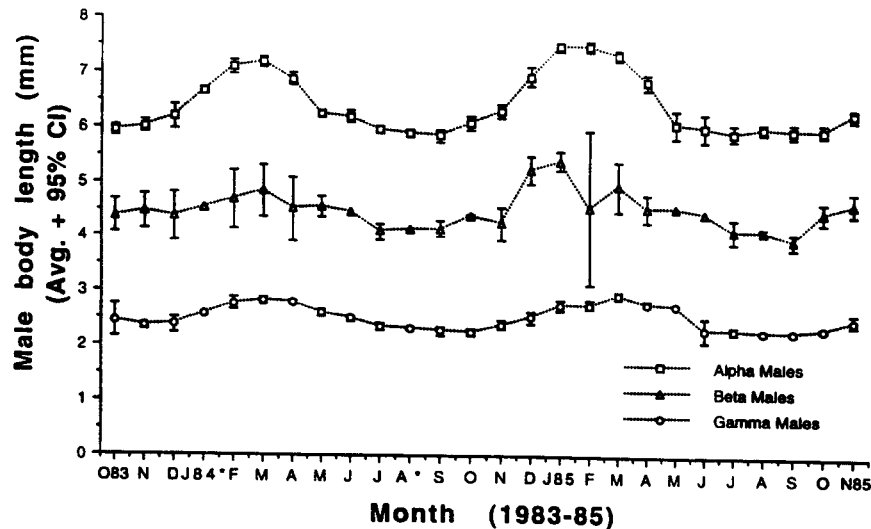


Fig. 3. Monthly average adult body lengths ($\text{mm} \pm 95\%$ C.I.) of the three male morphs in *P. sculpta* collected near Puerto Peñasco, Sonora, México between October 1983 and November 1985; asterisks (*) beside months indicate dates for which no sample was collected: the average body lengths for these points were extrapolated from average body lengths of the preceeding and following months; no C.I.s are provided for these estimates; a similar procedure was followed for β -males in May and June 1985 when no individuals appeared in samples (Table 1).

3.4. The effect of temperature on the body lengths of laboratory-reared individuals

α -, β -, γ -Males and females matured at significantly different body lengths when reared at 21°C ($F_{[3,378]} = 4.46$; $P < 0.001$). Similarly, α -, γ -males and females matured at significantly different body lengths when reared at 27 – 30°C , ($F_{[2,83]} = 5.48$; $P < 0.001$). Two-factor ANOVA of adult body length among laboratory-reared α -, γ -males and females showed significant effects of adult morph ($F_{[2,462]} = 68.18$, $P < 0.001$) and rearing temperature ($F_{[1,462]} = 96.68$; $P < 0.001$) on adult body size, but no significant interaction between these factors ($F_{[2,462]} = 0.71$, $P > 0.49$), indicating that in the laboratory, ambient temperature had no differential influence on adult body length (Fig. 6). The body lengths of field-collected α -males, γ -males and females collected during April and June 1984, when sea surface temperature averaged 21°C and 27°C respectively, were significantly different from the body lengths of α -males, γ -males and females reared at these temperatures in the laboratory (indicated by non-overlap of 95% C.I. in Figs. 3–6).

3.5. The effect of food availability on the body lengths of laboratory-reared individuals

We found no significant differences in the body lengths of individuals reared at high,

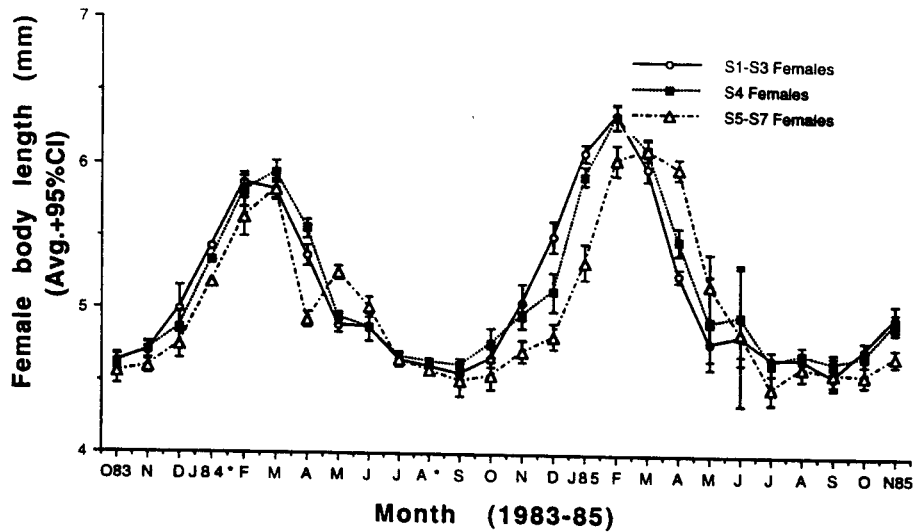


Fig. 4. Monthly average adult body lengths ($\text{mm} \pm 95\%$ C.I.) of *P. sculpta* females under three reproductive conditions (see Section 2.4 Section 3.2 for details) collected near Puerto Peñasco, Sonora, México between October 1983 and November 1985; as in Fig. 3, asterisks (*) beside months indicate dates for which no sample was collected; the average body length for these points were extrapolated from average body lengths of the preceding and following months; no C.I.s are provided for these estimates.

intermediate and low food availability (T1–3; Fig. 7). Food availability in T1 was equal to or greater than that made available to laboratory-reared individuals in experiments described above, yet high mortality was observed among all treatments in this experiment (Table 3) and thus prevented comparison of adult body lengths among individuals, as well as comparison of progeny growth trajectories among dams. Compared to temperature, the influence of varied food availability on isopod growth was undetectable.

4. Discussion

These results demonstrate the considerable effect of ambient temperature on pre-adult growth in *P. sculpta*. Not only were seasonal fluctuations in body length apparent among all adult morphs, but the relative effect of sea temperature on adult body size among males was proportional to individuals' numbers of pre-adult molts, as we predicted from Hartnoll (1982). Between 1983–1985, recently molted females were larger than spent females in winter, yet smaller than spent females in summer. This pattern is consistent with our predictions since S_{1-3} females reached sexual maturity within a few days of each collection, whereas S_{5-7} females, collected from spongocoels at the same time as S_{1-3} females, had matured several weeks earlier under a different thermal regime. The effect of temperature on male and female growth in this species was confirmed in the

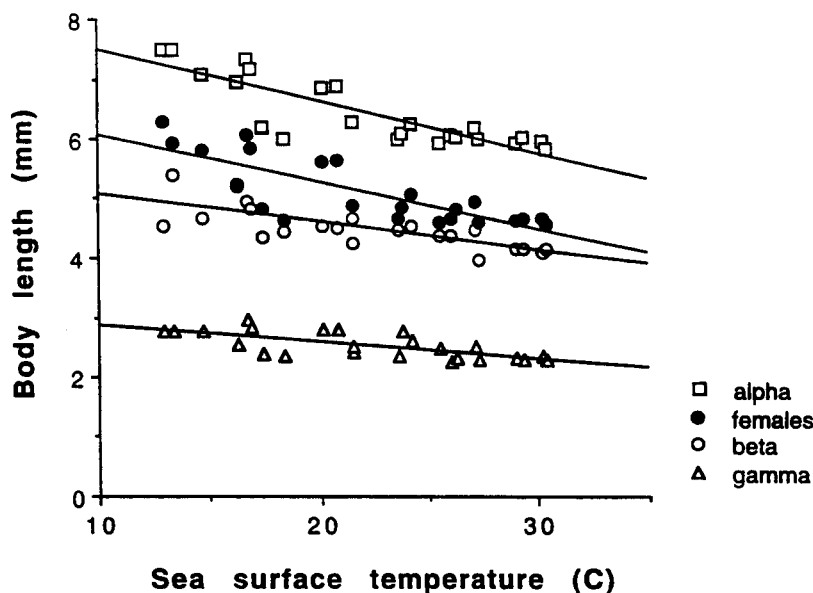


Fig. 5. The relationships between sea surface temperature and body length among field collected *P. sculpta* adults: α -males: $F_{[1,3015]} = 1824.80$, $P < 0.0001$; β -males: $F_{[1,172]} = 61.68$, $P < 0.0001$; γ -males: $F_{[1,502]} = 264.74$, $P < 0.0001$; females: $F_{[1,3032]} = 3791.50$, $P < 0.0001$; the slopes and y -intercepts of these relationships differ significantly ($F_{[3,6725]} = 53.41$, $P < 0.0001$; $F_{[3,6725]} = 7678.33$, $P < 0.0001$, respectively), indicating that the four adult morphs in *P. sculpta* respond differently to sea surface temperature; symbols represent monthly averages of adult body lengths calculated from individuals collected every four to five days.

laboratory, except for β -males, which were unavailable for rearing at 27–30°C. Although there was no interaction between rearing temperature and adult morph among laboratory-reared individuals, as was evident in field collected animals, this difference was probably due to the smaller temperature range provided under laboratory conditions than individuals experienced in nature.

Differences in the average body lengths of isopods which matured at 21°C and 27°C in the laboratory, compared to isopods which matured at these temperatures in the field, are at first puzzling, but may be explained by the fact that CEDO sea surface temperatures were recorded at the waters edge between 1983–1985. If the actual subtidal temperatures to which maturing isopods were exposed were lower than those recorded on shore, isopods collected at sea surface temperatures of 21°C and 27°C are expected to be slightly larger in size than isopods reared in the laboratory at these same recorded temperatures. This expectation is met in Figs. 3–6.

Adult body lengths among isopods showed clear seasonal fluctuations and correlated closely with fluctuations in sea surface temperature among all adult morphs (Fig. 5). Despite fewer recorded measurements of algae abundance (10 transect samples) than of sea surface temperature (24 monthly averages) between 1982–1986, seasonal fluctua-

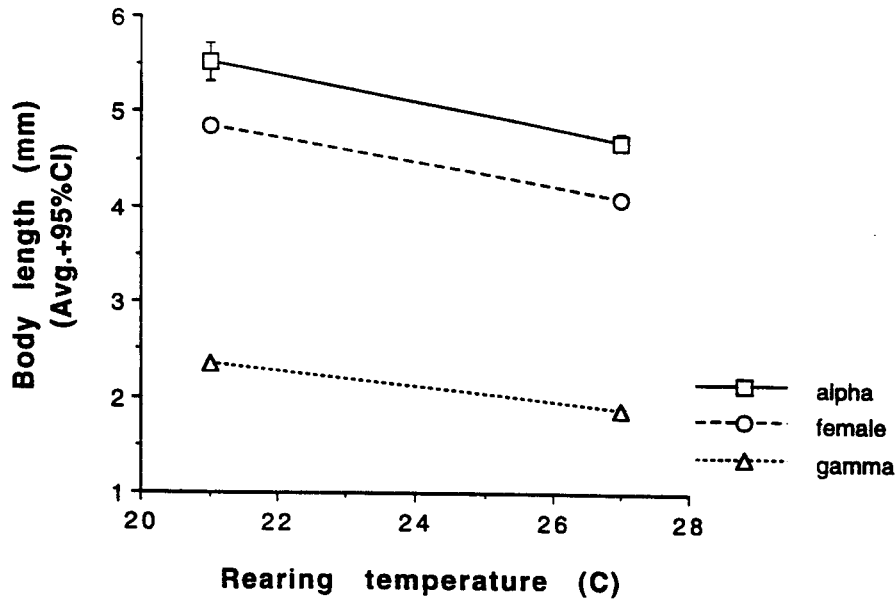


Fig. 6. The relationships between ambient temperature and adult body length for α -males, γ -males and females reared at 21°C and 27–30°C; there was no significant interaction among the individual regression slopes ($F_{12,4651} = 0.71$, $P > 0.49$), indicating that in the laboratory, ambient temperature had no differential influence on adult body length; γ -intercepts of adult body length adjusted for the effects of rearing temperature were heterogeneous ($F_{13,4641} = 572.17$, $P < 0.0001$).

tions in algae abundance do not appear to exist. Thus, variation in sea temperature is both necessary and sufficient to explain adult body size variation. In the laboratory, there was no clear effect of variable food availability on isopod growth, consistent with our results from the field.

Our results demonstrate that ambient temperature affects pre-adult growth in *P. sculpta*, as proposed by Hartnoll (1982), and according to our specific extensions of his hypotheses. Our results also suggest that the relative influence of temperature on pre-adult growth far exceeds that of food availability in this species, in the field as well as in the laboratory. Nutritional influences on adult size in *P. sculpta* remain somewhat uncertain, since our laboratory investigations focused mainly on individuals in early life stages. Food availability may more strongly affect adult size during later intermoult when energy requirements for gonadal and somatic maturation compete (Shuster, pers. obs.).

Consistent with evidence that adult male morphology in this species is controlled by genes of major effect (Shuster and Sassaman, 1997), we saw no evidence that temperature or food availability influences the expression of male morphotype or sex ratio in these experiments. Experiments to examine the specific effects of food availability on the expression of male morphotype in *P. sculpta* are currently underway.

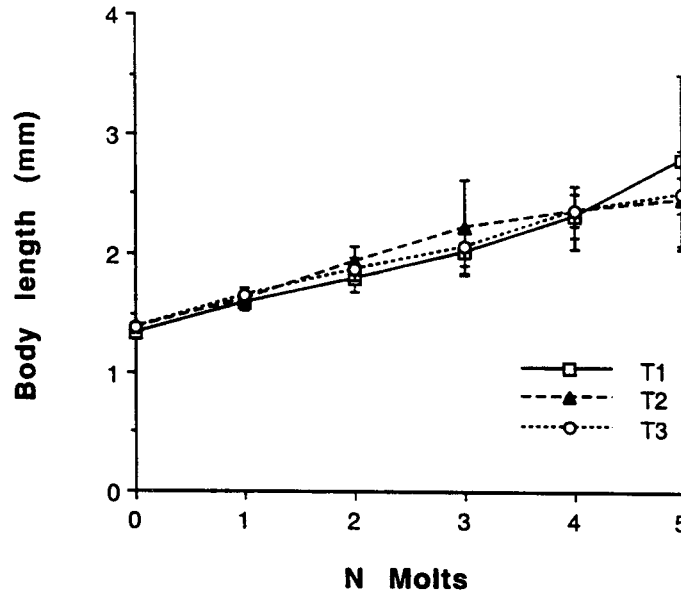


Fig. 7. Comparison of body lengths ($\text{mm} \pm 95\%$ C.I.) among α -sired progeny reared at 21°C under three feeding treatments; individuals in T1 were provided food with every water change, individuals in T2 were provided food with every other water change, and individuals in T3 were provided food with every third water change; overlapping 95% C.I.s indicate no significant differences in isopod body lengths among treatments.

Acknowledgements

Logistical support for this research was provided by el Centro Intercultural de Estudios de Desiertos y Océanos (CEDO) in Puerto Peñasco, Sonora, México. Permission to collect and study *P. sculpta* in México (Oficio No. A00702-06296 and DAN 02384) was authorized by el Instituto Nacional de Ecología, Dirección General de Aprovechamiento Ecológico de los Recursos Naturales, México, D.F., and was obtained with the assistance of A. Narvaez, Science Officer, US Embassy, Mexico, D.F.; assistance in maintaining laboratory animals was provided by H. Baitoo, S. Bhakta, K. Johnson, H. Wildey, R. Williams, P. Nelson and T. Wertz; K. Johnson, H. Wildey, P.A. Nelson, C. Sassaman and anonymous reviewer provided useful comments on the

Table 3
Effects of food availability on isopod growth: sample sizes for treatments 1–3

Treatment	Initial	Molt 1	Molt 2	Molt 3	Molt 4	Molt 5
T1	73	60	47	34	25	16
T2	74	62	47	32	9	6
T3	64	55	27	27	9	7

manuscript: financial assistance was provided by Organized Research grants from Northern Arizona University, and by NSF grants OCE-84-01067 and BSR-91-0644.

References

- Aoki, M., 1997. Comparative study of mother–young association in caprellid amphipods: is maternal care effective? *J. Crustacean Biol.* 17, 447–458.
- Atkinson, D., 1994. Temperature and organism size – a biological law for ectotherms? In: Begon, M., Fitter, A.H. (Eds.), *Advances in Ecological Research* 25. Academic Press, New York, pp. 1–54.
- Baitoo, H., Shuster, S.M., Sassaman, C., 1988. Polymorphic male molting and growth schedules in a marine isopod crustacean. *Am. Zool.* 28, 134A.
- Boucher, P., Blinn, D.W., Johnson, D.B., 1984. Phytoplankton ecology in an unusually stable environment (Montezuma Well, Arizona, USA). *Hydrobiologia* 119, 149–160.
- Briones-Fourzán, P., Lozano-Alvarez, E., 1991. Aspects of the biology of the giant isopod, *Bathynomus giganteus* A. Milne Edwards, 1879 (Flabellifera: Cirolanidae), off the Yucatan Peninsula. *J. Crustacean Biol.* 11, 375–385.
- Brusca, R.C., 1980. *Common Intertidal Invertebrates of the Gulf of California*, University of Arizona Press, Tucson, AZ, 2nd ed.
- Caldwell, R.L., 1986. Withholding information on sexual condition as a competitive mechanism. In: Drickamer, L.C. (Ed.), *Behavioral Ecology and Population Biology*, Privat. International Ethological Conference, Toulouse 1986, pp. 83–88.
- Hamano, T., Morrissy, N.M., 1992. Growth of *Oratosquilla oratoria* (De Haan, 1844) (Stomatopoda) in the Sea of Suo-Nada, Japan. *Crustaceana* 63, 263–269.
- Harrison, K., 1984. The morphology of the sphaeromatid brood pouch (Crustacea: Isopoda: Sphaeromatidae). *Zool. J. Linnean Soc.* 82, 363–407.
- Hartnoll, R.G., 1982. Growth. In: Abele, L.G. (Ed.), *The Biology of Crustacea*, Vol. 2, Academic Press, New York, pp. 111–196.
- Hartnoll, R.G., Bryant, A.D., Gould, P., 1993. Size distribution in spider crab populations – spatial and temporal variation. *J. Crustacean Biol.* 13, 647–655.
- Hartnoll, R.G., Mohamedeen, H., 1987. Laboratory growth of the larvae of six British crabs. *J. Exp. Mar. Biol. Ecol.* 107, 155–170.
- Hendrickson, J.R., 1973. Study of the marine environment of the northern Gulf of California. Final report. Goddard Space Flight Center, Maryland.
- Henmi, Y., 1989. Life-history patterns in two forms of *Macrophthalmus japonicus* (Crustacea: Brachyura). *Mar. Biol.* 101, 53–60.
- Holdich, D.M., 1976. A comparison of the ecology and life history of two species of littoral isopod. *J. Exp. Mar. Biol. Ecol.* 24, 133–149.
- Hoenig, J.M., Dawe, E.G., O'Keefe, P.G., 1994. Molt indicators and growth per molt for male snow crabs (*Chionoecetes opilio*). *J. Crustacean Biol.* 14, 273–279.
- Hughes, J.T., Matthiessen, G.C., 1962. Observations on the biology of the American lobster, *Homarus americanus*. *Limnol. Oceanogr.* 7, 414–421.
- Huntley, M.E., Lopez, M.D.G., 1992. Temperature-dependent production of marine copepods: a global synthesis. *Am. Nat.* 140, 201–242.
- Kondzela, C.M., Shirley, T.C., 1993. Survival, feeding and growth of juvenile Dungeness crabs from southeastern Alaska reared at different temperatures. *J. Crustacean Biol.* 13, 25–35.
- Kuris, A.M., Ra'anan, Z., Sagi, A., Cohen, D., 1987. Morphotypic differentiation of male Malaysian giant prawns, *Macrobrachium rosenbergii*. *J. Crustacean Biol.* 7, 219–237.
- MacKenzie, B.R., 1988. Assessment of temperature effects on inter-relationships between stage durations, mortality, and growth in laboratory reared *Homarus americanus* Milne Edwards larvae. *J. Exp. Mar. Biol. Ecol.* 116, 87–98.

- Morgan, S.G., Christy, J.H., 1994. Plasticity, constraint and optimality in reproductive timing. *Ecology* 75, 2185–2203.
- Paul, A.J., Coyle, K.O., Ziemann, D.A., 1990. Timing of spawning of *Thysanoessa raschii* (Euphausiacea) and occurrence of their feeding-stage larvae in an Alaskan bay. *J. Crustacean Biol.* 10, 69–78.
- Ra'anan, Z.A., Wax, Y., Karplus, I., Hulata, G., Kuris, A., 1991. Growth, size, rank and maturation of the freshwater prawn, *Macrobrachium rosenbergii*: analysis of marked prawns in an experimental population. *Biol. Bull.* 181, 379–386.
- Runge, J.A., McLaren, I.A., Corkett, C.J., Bohrer, R.N., Koslow, J.A., 1985. Molting rates and cohort development of *Calanus finmarchicus* and *C. glacialis* in the sea off southwest Nova Scotia. *Mar. Biol.* 86, 241–246.
- Sastre, M.P., 1991. Sex-specific growth and survival in the mole crab *Emerita portoricensis* (Schmitt). *J. Crustacean Biol.* 11, 103–112.
- Schultze, K., Anger, K., 1997. Larval growth patterns in the Aesop shrimp, *Pandalus montagui*. *J. Crustacean Biol.* 17, 472–489.
- Shuster, S.M., 1981. Life history characteristics of *Thermosphaeroma thermophilum*, the Socorro Isopod (Crustacea: Peracarida). *Biol. Bull.* 161, 291–302.
- Shuster, S.M., 1986. The reproductive biology of *Paracerceis sculpta* (Crustacea: Isopoda). Ph.D. dissertation, University of California, Berkeley, CA.
- Shuster, S.M., 1987. Alternative reproductive behaviors: three discrete male morphs in *Paracerceis sculpta*, and intertidal isopod from the northern Gulf of California. *J. Crustacean Biol.* 7, 318–327.
- Shuster, S.M., 1989. Female sexual receptivity associated with molting and differences in copulatory behavior among the three male morphs in *Paracerceis sculpta* (Crustacea: Isopoda). *Biol. Bull.* 177, 331–337.
- Shuster, S.M., 1990. Courtship and female mate selection in a semelparous isopod crustacean (*Paracerceis sculpta*). *Anim. Behav.* 40, 390–399.
- Shuster, S.M., 1991. Changes in female anatomy associated with the reproductive molt in *Paracerceis sculpta* (Holmes), a semelparous isopod crustacean. *J. Zool. (London)* 225, 365–379.
- Shuster, S.M., 1991. The ecology of breeding females and the evolution of polygyny in *Paracerceis sculpta*, a marine isopod crustacean. In: Bauer, R., Martin, J. (Eds.), *Crustacean Sexual Biology*, Columbia University Press, pp. 91–110.
- Shuster, S.M., 1992. The reproductive behaviour of α -, β - and γ -males in *Paracerceis sculpta*, a marine isopod crustacean. *Behaviour* 121, 231–258.
- Shuster, S.M., 1995. Female reproductive success in artificial cavities in *Paracerceis sculpta* (Crustacea: Isopoda). *J. Exp. Mar. Biol. Ecol.* 191, 19–27.
- Shuster, S.M., Sassaman, C., 1997. Genetic interactions between male mating strategy and sex ratio in a marine isopod. *Nature* 388, 373–376.
- Shuster, S.M., Wade, M.J., 1991. Equal mating success among male reproductive strategies in a marine isopod. *Nature* 350, 606–610.
- Siegel, S., Castellan, Jr., N.J., 1988. *Nonparametric Statistics for the Behavioral Sciences*, McGraw-Hill, New York, 2nd ed.
- Soong, K., Mok, H.-K., 1994. Size and maturity stage observations of the deep-sea isopod, *Bathynomus doederleini* Ortmann, 1894 (Flabellifera: Cirolanidae) in eastern Taiwan. *J. Crustacean Biol.* 14, 72–79.
- Thomson, D.A., Lehner, C., 1976. Resilience of a rocky intertidal fish community in a physically unstable environment. *J. Exp. Mar. Biol. Ecol.* 22, 1–29.
- West, T.L., Costlow, J.D., 1988. Determinants of the larval molting pattern of the crustacean *Balanus eburneus* Gould (Cirripedia: Thoracica). *J. Exp. Zool.* 48, 33–44.
- Wilkins, H., Parzefall, J., Ribowski, A., 1990. Population biology and larvae of the anchialine crab *Munidopsis polymorpha* (Galatheidae) from Lanzarote (Canary Islands). *J. Crustacean Biol.* 10, 667–675.