Marine Biology 118, 593–600 (1994)

Marine Biology
International Journal on Life in Oceans and Coastal Waters

Influence of temperature on larval development of four co-occurring species of the brachyuran genus *Cancer*

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Received: 20 October 1993 / Accepted: 23 October 1993

Abstract. Effects of temperature on zoeal development of *Cancer productus, C. oregonensis*, and *C. gracilis* collected from Puget Sound, Washington, USA, were determined and compared with published data on *C. magister*. Survival through zoeal development, mortality per individual zoeal instar, instar duration, and megalopa weight were determined for zoeae of each species raised in the laboratory at 10, 15, and 20 °C. In contrast to larvae of *C. magister*, the larvae of both *C. productus* and *C. gracilis* survived to the megalopa at 20 °C. Larvae of *C. oregonensis*, however, died by Zoeal Stage 3 at 20 °C. Individual instar mortality rates varied as a function of temperature among species, reflecting different patterns of thermal tolerance through ontogeny. Zoeal duration varied inversely with temperature, although differences between 10 and 15 °C were far greater than those between 15 and 20 °C in each species. Duration of individual zoeal instars varied as a function of temperature and species. Megalopa weight was significantly reduced at 20 °C in *C. productus* and *C. gracilis*, although no differences were measured between 10 and 15 °C in any of the four species. Although literature reports indicate that reproductive output varies directly with adult size in these *Cancer* species, the larval traits measured here varied independent of body size.

Introduction

Reproducing populations of four species of the brachyuran Genus *Cancer* are present in the inland marine waters of the Puget Sound basin in the State of Washington, USA (Kozloff 1974, Nations 1975). Ovigerous females of *C. magister*, *C. productus*, *C. oregonensis*, and *C. gracilis* can be collected from these waters in late winter and early spring (Orensanz and Gallucci 1988). Zoeal development of all four species occurs in this region from January through May, a period of seasonal transition in water temperature. Post-larval development and settlement typically occur in summer months, when water temperatures are comparatively warm and stable (Orensanz and Gallucci 1988). The effect of temperature during the course of zoeal development has been reported only for *C. magister* (Poole 1966, Lough 1976, Sulkin and McKeen 1989). Optimal survival occurred at 10 °C, the lowest temperature tested, with development to the megalopa not possible at a temperature as high as 20 °C (Sulkin and McKeen 1989).

Hines (1991) has reported that, in *Cancer* species, female body size is a major determinant of such traits as reproductive output and fecundity. Possible relationships between adult body size and larval traits have not been examined, however. The group of four *Cancer* congeners that occur together in the Puget Sound region offers an excellent opportunity to investigate relationships between body size and larval traits. Female size at maturity ranges from 8 mm carapace width in *C. oregonensis* to 170 mm carapace width in *C. magister* (Hines 1991). Furthermore, because reproduction and larval development occur in the same region and at the same time in these four species, confounding effects of exposure of different species to different environmental conditions are eliminated.

In the present study, the effect of temperature on zoeal development is determined for *Cancer productus*, *C. oregonensis*, and *C. gracilis*, using the identical procedures used previously by Sulkin and McKeen (1989) for *C. magister*. Results are compared among the four species to determine whether differences occur in response to temperature and whether there is a relationship between such response and female body size.

Materials and methods

Experimental design

Sulkin and McKeen (1989) showed that survival and instar duration in *Cancer magister* was virtually the same when larvae were raised individually or in groups of ten larvae each.

To determine larval survival and instar duration through zoeal development, larvae of *Cancer productus*, *C. oregonensis*, and *C.*

gracilis were raised in groups from hatching up to molt to the megalopa at 10, 15 or 20 °C. The lower two temperatures typify the range to which larvae may be exposed during the period of their maximum abundance in the inland waters north of the Puget Sound in the State of Washington, USA. The 20 °C temperature treatment was employed here to introduce thermal stress, useful in comparing responses among species.

Experimental protocol

The same general protocol was followed for laboratory culture of all three species. Ovigerous females were collected from waters near the Shannon Point Marine Center (located on Guemes Channel near Anacortes, Washington, USA) in late winter and held in the laboratory with egg masses intact until larvae hatched. Ambient water temperature at the time of collection was 8 °C; salinity was 30‰.

The following general protocol was used for all three species. Within several hours after hatching occurred, several thousand larvae were collected by skimming the surface of the seawater table with a small mesh net. Larvae were placed in a glass bowl (110 mm diam) and immediately fed freshly-hatched nauplii of the brine shrimp *Artemia* sp. Individual larvae were selected from this large group and placed in 80 mm-diam glass stacking-bowls each containing 50 ml of filtered seawater (30‰ S). Ten larvae were placed into each bowl. For each brood, 10 bowls were then assigned randomly to each of three experimental temperatures (10, 15 and 20 °C). Larvae were obtained in this fashion from one *Cancer productus* brood, one *C. gracilis* brood, and two *C. oregonensis* broods. Thus, for each temperature, totals of 100 larvae in 10 batches (bowls) were set up for *C. productus* and *C. gracilis* and a total of 200 larvae in 20 batches for *C. oregonensis*. Freshly-hatched *Artemia* sp. nauplii were placed in each bowl. The antibiotic chloramphenicol (5 mg/l) was added daily and the fungizone amphitericin-B (2.5 mg/l) was added every third day. Culture bowls were maintained in temperature–light controlled incubators, with the photoperiod set at 14 h light : 10 h dark and temperature set at 10, 15 or 20 °C (±0.5 C°). Cultures were examined daily for evidence of dead larvae and presence of exuviae. Live larvae were transferred to clean bowls of seawater and fed. Data were collected on numbers of larvae alive and dead and numbers of molts.

Data analysis

Data from the three *Cancer* species were treated identically. For each temperature, the percentage of larvae surviving each successive zoeal stage was calculated for each bowl of larvae. Mean percent survival through successive zoeal stages was then calculated for each temperature. Conditional mortality was calculated for each zoeal stage by subtracting the cumulative percentage survival through that stage from the survival through the preceding stage and dividing the result by the percentage that had survived the preceding stage. These data were subjected to arcsine transformation, followed by either a Student's *t*-test or one-way analysis of variance (ANOVA), as appropriate, to compare stage mortality as a function of temperature.

Zoeal duration through successive zoeal stages was determined by calculating a mean day of molt, based on all molts occurring in all culture bowls assigned to a particular temperature. Mean days of succeeding molts were then calculated for each temperature. Duration of each individual zoeal stage was calculated. Data were tested for homogeneity of variance and appropriate statistical tests were applied accordingly, as described in the "Results" section.

Megalopa weights

The same procedure for determining megalopa weight was used for all three species. When a megalopa was obtained from the culture, it was rinsed with a drop of freshwater, blotted dry, and placed in a pre-weighed aluminum boat. The megalopa was placed in a drying oven (100 °C) overnight and weighed on a balance to the nearest 0.1 mg. Data for each temperature were pooled for calculation of mean values for each species. In all cases, variances were found to be homogeneous (*F*-max, $P > 0.05$) and means were compared by appropriate statistical tests as described in the "Results" section.

Results

Cancer productus

Survival. Cancer productus larvae survived to the megalopa in all three temperature treatments (Table 1). Percent mortalities during each zoeal stage were calculated as described in "Materials and methods" and are shown in Fig. 1. Arcsine-transformed data were subjected to analysis of variance (ANOVA) comparing stage mortality as a function of temperature treatment at each zoeal stage. Only Zoeal Stage 5 showed a significant difference among temperatures ($P < 0.001$). The data were subjected to a Tukey's pairwise multiple-comparison (PMC) test (Zar 1984). The Tukey's PMC test ($P = 0.05$) indicated that during Zoeal Stage 5 mortality was significantly higher at 20 °C than at 10 or 15 °C. There was no significant difference between mortality at 10 and 15 °C.

Table 1. *Cancer* spp. Percent survival through zoeal development; 1 standard deviation is shown in parentheses. Data are shown for each of the three temperatures tested along with results of analysis of variance on arcsine-transformed data and Tukey's pairwise multiple-comparison test (PMC) when appropriate. Data for *C. oregonensis* at 20 °C not included in initial analysis

Species	Test temperature			ANOVA/ Student's *t*-test (*P*)	Tukey's test
	10 °C	15 °C	20 °C		
C. productus	48 (4)	58(14)	17(11)	<0.001	10=15>20
C. oregonensis	33(21)	21(14)	–	>0.05	–
C. gracilis	10(11)	67(15)	10 (8)	<0.001	15>10=20

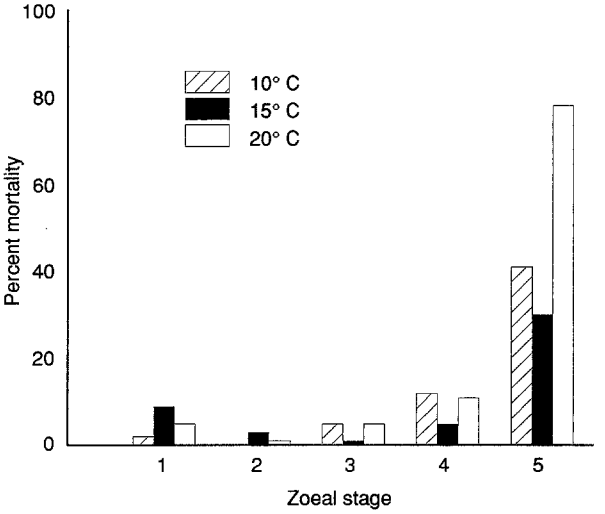

Fig. 1. *Cancer productus*. Percent mortality during each zoeal stage at 10, 15 and 20 °C

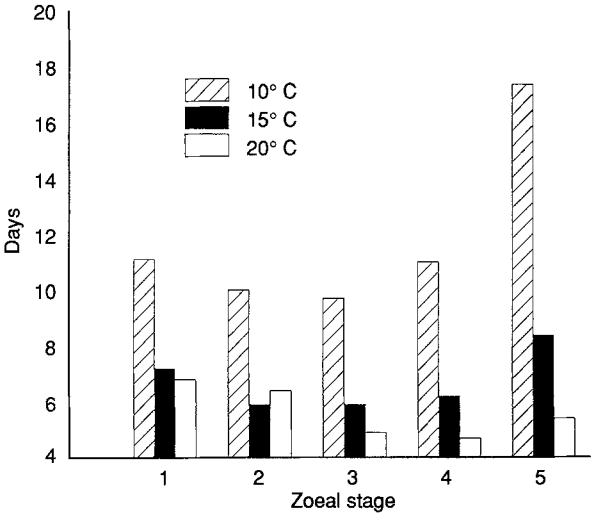

Fig. 2. *Cancer productus.* Mean duration of each zoeal stage at 10, 15 and 20 °C

Table 2. *Cancer* spp. Mean day of molt to megalopa (zoeal stage duration). Data are for larvae exposed to each of three temperature treatments except for *C. oregonensis*, which did not survive to the megalopa at 20 °C. Also shown are range, sample size (*n*) and results of Tukey's non-parametric PMC test comparing sample distributions among temperatures. Shared letters indicate no significant differences ($P<0.05$). Results for *C. oregonensis* were tested by Mann-Whitney *U*-test ($P<0.05$)

T (°C)	Day of molt		*n*	Tukey's test
	mean	(range)		
Cancer productus				
10	59.2	(55–68)	48	a
15	33.6	(30–39)	58	b
20	28.2	(26–32)	17	c
Cancer oregonensis				
10	71.7	(64–83)	65	a
15	34.8	(32–40)	42	b
Cancer gracilis				
10	67.0	(64–71)	10	a
15	34.2	(32–40)	66	b
20	23.4	(21–26)	10	b

Cumulative percent survival through zoeal development is shown in Table 1. *Cancer productus* larvae survived to the megalopa stage in all three temperatures. After arcsine transformation, cumulative percent survival through the fifth (terminal) zoeal stage was compared among the three temperatures by ANOVA (Table 1). A significant difference was found and the data were subjected to the Tukey's PMC test. Survival was significantly lower at 20 °C than at 10 or 15 °C and no significant differences in cumulative survival were found between the latter two temperatures.

Duration of zoeal-development. Mean values for individual stage durations as a function of temperature are shown in Fig. 2 for each of the five zoeal stages of *Cancer productus*. A series of *F*-max tests, conducted for each stage, indicated that variances were non-homogeneous ($P<0.05$), necessitating use of the non-parametric Kruskal-Wallis ANOVA to determine whether differences in sample distribution among temperature treatments were significant. Results of the analysis indicated a significant difference among temperatures at each molt stage ($P<0.001$). A Tukey's non-parametric PMC test (Zar 1984) then was used to further analyze data for each stage. The analyses indicated that, for each zoeal stage, duration was always longer at 10 °C than at 15 °C, while development at 15 °C exceeded that at 20 °C only during Zoeal Stages 3 and 4.

The total time of zoeal development is shown in Table 2 as the mean day of molt to the megalopa for larvae raised at each of the three temperatures. As temperature increased, zoeal duration decreased, although the difference between 10 and 15 °C was greater than that between 15 and 20 °C. Sample distributions among the three temperature treatments were tested by the non-parametric Kruskal-Wallis ANOVA and Tukey's non-parametric PMC test. Results indicated significant differences among temperatures, with differences present between each pair of treatments (Table 2).

Megalopa weight. A total of 41 D-1 laboratory-raised megalopae were dried and weighed. The mean values (sample size in parentheses) for megalopae raised through zoeal development at each temperature are as follows: 10 °C, 0.65 mg (20); 15 °C, 0.56 mg (14); 20 °C, 0.39 mg (7). Data were tested by one-way ANOVA which revealed significant differences among the means ($P<0.01$). A Tukey's PMC test for unequal sample sizes indicated significant differences only between 10 and 20 °C.

Cancer oregonensis

Survival. Cancer oregonensis larvae survived to the megalopa only at 10 and 15 °C (Table 1). Percent mortality during each zoeal stage is shown in Fig. 3. Arcsine-transformed data were subjected to ANOVA comparing stage mortality as a function of temperature treatment at Zoeal Stages 1, 2 and 3. Significant differences were present in each case ($P<0.001$). Tukey's PMC tests indicated that, for each stage, mortality at 20 °C exceeded that at 10 and 15 °C and that there was no difference in percent mortality between the latter two temperatures ($P=0.05$). Thus, significantly increased mortality was seen at 20 °C as early as Zoeal Stage 1, with 100% mortality occurring during the third stage (Fig. 3). A Student's *t*-test was conducted on the remaining two temperature treatments used during Zoeal Stages 4 and 5. There was no significant difference during Stage 4 ($P>0.05$), while during Stage 5 percent mortality was significantly higher at 15 °C ($P<0.05$).

Cumulative percent survival through zoeal development is shown in Table 1. *Cancer oregonensis* zoeae survived to the megalopa only at 10 and 15 °C. After arcsine transformation, the cumulative survival values for 10 and 15 °C were subjected to a Student's *t*-test and found not

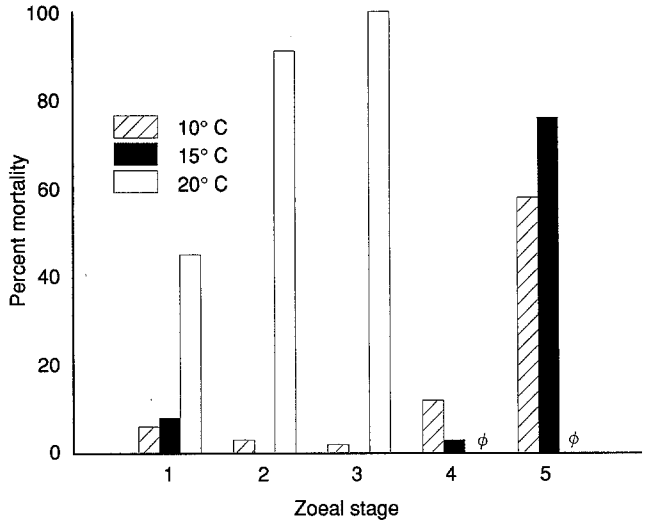

Fig. 3. *Cancer oregonensis.* Percent mortality during each zoeal stage at 10, 15 and 20 °C. ϕ: no data

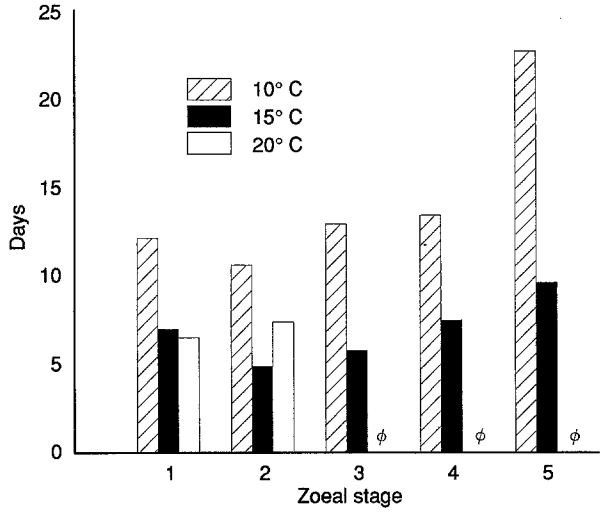

Fig. 4. *Cancer oregonensis.* Mean duration of each zoeal stage at 10, 15 and 20 °C. ϕ: no data

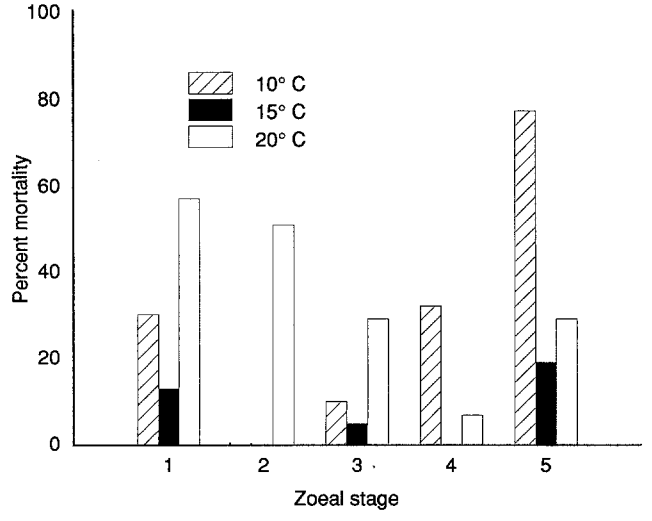

Fig. 5. *Cancer gracilis.* Percent mortality during each zoeal stage at 10, 15 and 20 °C

to be significant. Survival to the megalopa was the same at 10 as at 15 °C in *C. oregonensis* (Table 1).

Duration of zoeal development. Mean values for individual stage durations as a function of temperature are shown in Fig. 4 for each of the five zoeal stages of *Cancer oregonensis*. Because the variances were not homogeneous (F-max test, $P<0.05$), a non-parametric Kruskal-Wallis ANOVA followed by a Tukey's non-parametric PMC test ($P=0.05$) were used to compare sample distributions among the three temperatures for Zoeal Stages 1 and 2. Significant differences were found among sample distributions for each of the zoeal stages ($P<0.001$). During Zoeal Stage 1, there was a significant reduction in time to molt at 15 °C compared to 10 °C, with a further significant reduction at 20 °C compared to 15 °C. During Zoeal Stage 2, however, duration at 10 and 20 °C was the same, with both significantly longer than at 15 °C. This may reflect the effects of temperature stress at 20 °C. A Mann-Whitney U-test compared sample distributions between 10 and 15 °C in Zoeal Stages 3, 4, and 5. A significant difference was present in each case ($P<0.001$), with duration at 10 °C exceeding that at 15 °C.

The total time of zoeal duration for *Cancer oregonensis* is shown in Table 2 as the mean day of molt to the megalopa for larvae initially raised in 10 and 15 °C; larvae did not survive to the megalopa at 20 °C. The results for the Mann-Whitney U-test on sample distributions at 10 and 15 °C indicated that development was significantly delayed at 10 °C ($P<0.05$).

Megalopa weight. A total of 25 Day-1 laboratory-raised megalopae were dried and weighed for groups raised at 10 and 15 °C. Mean values (sample sizes in parentheses) are as follows: 10 °C, 0.46 mg (10); 15 °C, 0.48 mg (15). There was no significant difference between the means (Student's t-test $P>0.05$).

Cancer gracilis

Survival. Cancer gracilis larvae survived to the megalopa in all three temperature treatments (Table 1). Percent mortality during each zoeal stage is shown in Fig. 5. Arcsine-transformed data were subjected to ANOVA comparing stage mortality as a function of temperature treatment at each zoeal stage. Results are summarized in Table 3. Significant differences among temperatures were measured in each stage except Zoeal Stage 3. Relationships among temperatures varied according to zoeal stage, but, in general, mortality was higher at 20 °C early in development while higher mortality occurred at 10 °C during later zoeal stages.

Cumulative percent survival through zoeal development is shown in Table 1. *Cancer gracilis* larvae survived to the megalopa stage in all three temperatures. After arcsine transformation, cumulative percent survival was compared among the three temperature treatments by ANOVA (Table 1). Significant differences were found and the data were subjected to the Tukey's PMC test. Survival was higher at 15 °C than at 10 or 20 °C, but there was no difference between 10 and 20 °C.

Table 3. *Cancer gracilis.* Results of ANOVA on arcsine-transformed data comparing mortality among temperatures for each zoeal stage (Fig. 5). Also shown are results of Tukey's PMC test ($P<0.05$) where ANOVA was significant

Zoeal stage	ANOVA (P)	Tukey's test
1	<0.001	20>10>15
2	<0.001	20>10=15
3	0.46	NS
4	0.003	10>15; 10=20; 15=20
5	<0.001	10>20=15

Table 4. *Cancer gracilis.* Results of Tukey's PMC non-parametric test ($P=0.05$) on sample distribution of zoeal duration as a function of temperature for each zoeal stage. Kruskal-Wallis analysis of variance indicated significant difference among temperatures in each case ($P<0.001$)

Zoeal stage	Tukey's test
1	10>15>20
2	10>15=20
3	10>15=20
4	10>15=20
5	10>20; 10=15; 15=20

Table 5. *Cancer* spp. Mean body size, egg diameter, brood weight and fecundity. Data from Hines (1991, his Table 3)

Species	Body size (mm)	Egg diam (mm)	Brood weight (g)	Fecundity (no. eggs/brood)
C. magister	155	442	22.20	938 300
C. productus	116	367	12.70	877 300
C. gracilis	68	329	2.36	453 700
C. oregonensis	23	383	0.21	18 200

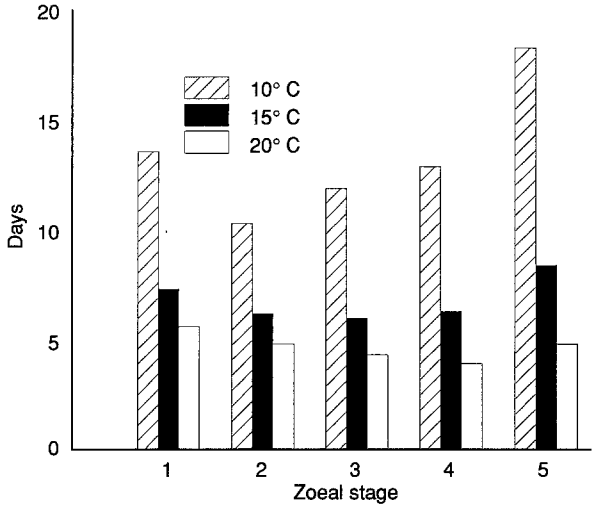

Fig. 6. *Cancer gracilis.* Mean duration of each zoeal stage at 10, 15 and 20 °C

Duration of zoeal development. Mean values for individual stage duration are shown in Fig. 6 for each of the five zoeal stages. Because variances were not homogeneous (F-max, $P<0.05$), the non-parametric Kruskal-Wallis ANOVA compared sample distributions among temperatures at each stage, with a significant difference being found in all cases ($P<0.001$). Results of the Tukey's non-parametric PMC test are shown in Table 4 ($P=0.05$). In general, duration of 10 °C exceeded that at 20 °C in all zoeal stages and at 15 °C during the first four zoeal stages. Duration at 15 °C exceeded that at 20 °C only during Zoeal Stage 1.

The total time of zoeal development is shown in Table 2 as the mean day of molt to the megalopa for larvae raised in each of the three temperature treatments. There is an inverse relationship between temperature and zoeal duration. Results of a non-parametric Kruskal-Wallis ANOVA and the Tukey's non-parametric PMC indicated that significant differences were present between each pair of treatments (Table 2).

Megalopa weight. A total of 82 Day-1, laboratory-raised megalopae was dried and weighed. The mean values (sample size in parentheses) for megalopae raised through zoeal development at each temperature are as follows: 10 °C, 0.26 mg (8); 15 °C, 0.24 mg (65); 20 °C, 0.14 mg (9). A one-way ANOVA revealed a significant difference among the means ($P<0.001$). A Tukey's PMC test ($P=0.05$) indicated that there was no difference between 10 and 15 °C, with mean weights at both 10 and 15 °C significantly higher than at 20 °C (10 °C=15 °C >20 °C).

Comparisons among species

Direct comparisons were made among *Cancer magister* (Sulkin and McKeen 1989), *C. productus*, *C. oregonensis* and *C. gracilis* for three selected responses to temperature in order to facilitate analysis of relationships between female body size and zoeal response. Table 5 provides data extracted from Hines (1991) for the four *Cancer* species analyzed in this study. Note that as female body size increases, so does average brood weight and fecundity (no. eggs/brood). Cumulative fecundity (over the life of the crab) shows a similar relationship to body size (Hines 1991).

Survival to megalopa

Table 6 shows the mean values of percent survival to the megalopa for each of the four species at 10, 15 and 20 °C. Analysis of variance on arcsine-transformed data revealed significant differences among species at each temperature ($P<0.001$). The Tukey's PMC test indicated that at 10 °C survival was significantly lower in *Cancer gracilis* than in the other three species. At 15 °C, however, *C. productus* and *C. gracilis* showed significantly higher survival than did the other two species, while at 20 °C neither *C. magister* nor *C. oregonensis* survived to the megalopa.

Table 6. *Cancer* spp. Mean percent survival to megalopa at 10, 15 and 20 °C. Also shown are results of Tukey's PMC tests. Shared letters indicate no significant difference between species ($P=0.05$). Species arranged in order of descending female size at maturity. Data for *C. magister* from Sulkin and McKeen (1989)

Species	10 °C		15 °C		20 °C	
	% Survival	Tukey's test	% Survival	Tukey's test	% Survival	Tukey's test
C. magister	41	a	31	a	0	a
C. productus	48	a	58	b	17	b
C. gracilis	10	b	67	b	10	b
C. oregonensis	33	a	21	a	0	a

Table 7. *Cancer* spp. Total zoeal duration at 10, 15 and 20 °C. Also shown are results of Tukey's non-parametric PMC tests at 10 and 15 °C, in which sample distributions were shown to differ significantly by Kruskal-Wallis ANOVA ($P<0.001$). Results for 20 °C are based on significant two-sample *t*-test ($P<0.001$). Shared letters indicate no significant difference between species ($P=0.05$). Species arranged in order of descending female size at maturity. Data for *C. magister* from Sulkin and McKeen (1989). –: no data

Species	10 °C		15 °C		20 °C	
	Mean duration (d)	Tukey's	Mean duration (d)	Tukey's	Mean duration (d)	Tukey's
C. magister	68.9	a	38.5	a	–	
C. productus	59.2	b	33.6	c	28.2	a
C. gracilis	67.0	a	34.2	c	23.6	b
C. oregonensis	71.7	a	34.8	b	–	

Table 8. *Cancer* spp. Megalopa weight (mg) at 10, 15 and 20 °C. Also shown are results of Tukey's non-parametric PMC tests at 10 and 15 °C, in which sample distributions were shown to differ significantly by Kruskal-Wallis ANOVA ($P<0.001$). Results for 20 °C are based on Mann-Whitney *U*-test ($P<0.001$). Shared letters indicate no significant difference between species ($P=0.05$). Species arranged in order of descending female size at maturity. *C. magister* data from Sulkin and McKeen (1989). –: no data

Species	10 °C		15 °C		20 °C	
	Mean wt (mg)	Tukey's	Mean wt (mg)	Tukey's	Mean wt (mg)	Tukey's
C. magister	1.30	a	1.20	a	–	
C. productus	0.65	b	0.56	b	0.39	a
C. gracilis	0.26	c	0.24	c	0.14	b
C. oregonensis	0.46	bc	0.48	b	–	

Total zoeal duration

Table 7 shows the mean values for total zoeal duration for each of the four *Cancer* species at 10, 15 and 20 °C. A Kruskal-Wallis ANOVA revealed significant differences among the four species at 10 and 15 °C. The Tukey's non-parametric PMC test showed that at 10 °C zoeal duration of *C. productus* was significantly shorter than that for the other three species. At 15 °C, zoeal duration of *C. magister* was significantly longer than for the other three species, while in *C. oregonensis* total zoeal duration was significantly shorter than among the other three species. At 20 °C, a two-sample *t*-test for samples with equal variances indicated that *C. gracilis* showed a significantly faster development time than did *C. productus*.

Megalopa weight

Table 8 shows the mean value of megalopa weight for each of the four species at 10, 15 and 20 °C. A Kruskal-Wallis ANOVA revealed significant differences among species at 10 and 15 °C ($P<0.001$). The Tukey's non-parametric PMC test ($P=0.05$) indicated that, at 10 °C, *Cancer magister* megalopae were significantly larger than those of all other species and that *C. productus* were larger than *C. gracilis*. The test failed to determine whether *C. oregonensis* megalopae differed from either *C. productus* or *C. gracilis*. At 15 °C, the relationships were similar, although *C. oregonensis* was significantly larger than *C. gracilis*. At 20 °C, results of a Mann-Whitney *U*-test indicated that *C. productus* megalopae were significantly larger than *C. gracilis* megalopae.

Discussion

Mortality rates as a function of temperature

The three *Cancer* species tested here showed different patterns of mortality as a response to temperature during the course of zoeal development. In *C. productus*, there was no differential mortality in response to temperature through the first four zoeal stages, although a significant increase in mortality did occur in the last zoeal stage at 20 °C. By contrast, significantly increased mortality occurred at 20 °C in *C. oregonensis* as early as the first zoeal stage, a pattern that persisted through the second and third zoeal stages until all larvae maintained at 20 °C had died. Yet another pattern of response occurred in *C. gracilis*, with higher mortality occurring in the first two zoeal stages at 20 °C, the third zoeal stage showing no differential mortality as a function of temperature, and the fourth and fifth stages showing higher mortality at 10 °C. Sulkin and McKeen (1989) reported that *C. magister* showed a pattern similar to that of *C. productus*, with increased mortality at 20 °C present only in the fifth (terminal) zoeal stage.

Thus the four *Cancer* species show different tolerances to high temperature stress at different stages of zoeal development. Although this pattern of response could produce different natural mortality rates among species at different zoeal stages, significant thermal stress occurred in this study primarily at 20 °C, a temperature higher than that which these species normally encounter in nature. The exception is *C. gracilis*, in which survival during the first zoeal stage was actually higher at 15 °C than at 10 °C. This is remarkable considering that hatching larvae of *C. gracilis* are likely to be exposed to temperatures below 10 °C in the Puget Sound region.

The differences in survival among species in response to temperature cannot be explained readily by differences in either seasonal occurrences or latitudinal ranges. Larvae of all four species are generally in the water column at the same time and are thus exposed to similar natural temperature regimes. All four species have a broad distribution along the west coast of North America, from Alaska to at least southern California, USA (Hart 1982). *Cancer magister* and *C. gracilis* have been reported farther south along the coast of Mexico than the other two species (Hart 1982); however, the former cannot develop to the megalopa at 20 °C while the latter can. Thus, while clear differences in temperature tolerance exist among species, it is not clear that such differences have an ecological significance.

Development rates as a function of temperature

The effect of temperature on zoeal duration can have important consequences to recruitment success. The length of zoeal duration can affect dispersal, as well as total survival to settlement based on the length of time zoeae are subjected to predation. There could also be effects on survival and growth based upon prey availability and energetics.

The expected inverse relationship between temperature and zoeal duration occurred for each of the three species tested here (Table 2). The magnitude of differences between 10 and 15 °C always exceeded those measured between 15 and 20 °C, however. Indeed, if one examines the data for individual zoeal stages (Figs. 2, 4, 6), exceptions to the inverse relationship between temperatures and instar duration are frequent. For example, *Cancer productus* zoeal duration at 15 °C exceeded that at 20 °C only in Zoeal Stages 3 and 4 (Fig. 2). In *C. oregonensis*, duration of Stage 2 at 20 °C actually exceeded that measured at 15 °C, a result presumably of the temperature stress being experienced by this species at 20 °C as early as Stage 1 (Figs. 3, 4). In *C. gracilis*, zoeal duration at 15 °C exceeded that at 20 °C only in the first zoeal stage (Fig. 6, Table 4).

In spite of these exceptions, response within the temperature ranges normally experienced by larvae in nature will result in reduced zoeal duration with increasing temperature. The complex patterns of temperature to which larvae of *Cancer* species may be exposed during ontogeny will determine the duration of zoeal instars. Duration of early zoeal stages that hatch in outer coastal waters at the southern end of the geographic range is likely to be shorter than that of zoeae that hatch in the relatively cold waters of the Puget Sound basin. The total length of zoeal duration will be dependent upon the temperature exposures that characterize ontogenies and may differ geographically and seasonally within *Cancer* species. As a consequence, estimates of the dispersion ranges of larvae and of mortality due to predation also will be influenced by the pattern of temperatures to which larvae are exposed through the course of zoeal development.

Megalopa weight as a function of temperature

In the two species in which development at 20 °C was possible (*Cancer productus* and *C. gracilis*), megalopae were smaller at 20 °C than at 10 °C. However, in no species were there significant differences between megalopae produced at 10 and 15 °C. This absence of size difference occurred in spite of a substantial and statistically significant difference in zoeal duration between the two temperatures. *Cancer* larvae are planktotrophic and the results suggest an energetic balance between metabolic rate and feeding, at least in the 10 to 15 °C range. Because neither weights of individual zoeal stages nor stage-dependent metabolic efficiencies were measured as a function of temperature in the present study, further speculation on this point is not warranted.

Female body size and larval traits

Hines (1982, 1986) applied life-history data from $\simeq 200$ species of brachyuran crabs from seven different families to a consideration of reproductive strategies in the group. He concluded that female body size is the principal determinant of reproductive output, an apparent function of limitation imposed by volume of the body cavity, the site

of oogenesis. Hines (1991) confirmed this same relationship within the genus *Cancer*, reporting that female body size and egg size are the major variables that predict fecundity.

The significance of the relationship between female body size and apparent fecundity may be modified, however, by differences among species in the success of the free-living zoeal stage in reaching settlement. Differential zoeal mortality, development, or growth rates among species could alter predictions of reproductive output based on body size/fecundity relationships. The comparisons of survival, zoeal duration, and megalopa weight among species in Tables 6, 7, and 8, respectively, fail to reveal systematic differences among species that are related to body size. In general, the highest mortality was seen in the largest and smallest species (Table 6), and no clear pattern emerges from the data on zoeal duration (Table 7). In the case of megalopa weight, the mean values follow egg diameter although the non-parametric pairwise comparison test fails to distinguish differences in sample distributions that would confirm this relationship.

It would thus appear that while reproductive output is related to female body size in these *Cancer* spp., as reported by Hines (1991), factors that influence settlement success such as larval survival, development rate, and growth vary independently from the body size of the parent female.

Acknowledgement. This research was supported in part by a grant from the Washington Sea Grant Program (Project No. R/F-73 pd).

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Communicated by M. G. Hadfield, Honolulu