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The effect of temperature on brood duration in three *Halicarcinus* species (Crustacea: Brachyura: Hymenosomatidae)

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The effect of temperature on brood development was investigated for three intertidal hymenosomatid crabs: Halicarcinus cookii, H. varius *and* H. innominatus *in Kaikoura, New Zealand. The duration of brood incubation decreased as temperature increased, as did the interbrood period. The duration of each stage of brood development also decreased with increased temperature, but the proportion of total incubation time for each stage remained relatively similar at different temperatures. Hymenosomatid crabs have determinate growth, but moult to maturity at different sizes, thereafter devoting most of their energy to reproduction. The number of broods a female could carry in her lifetime was estimated for each species.* Halicarcinus cookii *was estimated to be able to produce eight complete broods of 1146 eggs per lifetime,* H. varius *was estimated to be able to produce seven complete broods of 1051 eggs per lifetime and* H. innominatus *was estimated to be able to produce six complete broods of 1081 eggs per life time. With the predicted global temperature rise of 2°C in the next 50 years, the authors estimate that, for all three species, a female could produce one extra brood per lifetime (a 10–15% increase in fecundity depending on species), even more if crabs reach maturity faster, potentially leading to a significant population increase.*

Keywords: incubation duration, egg development, temperature effect, brood stage, fecundity, determinate growth, Hymenosomatidae, *Halicarcinus*, interbrood, climate change, Kaikoura, New Zealand

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INTRODUCTION

Growth and reproduction can be considered competing processes in terms of the allocation of energy. If less energy is allocated to growth, more energy can be invested into greater reproductive output (Hines, 1982; Hartnoll, 1985). Reproductive output is determined by the number of offspring produced over a lifetime (Shields, 1991). Hymenosomatid crabs of the genus *Halicarcinus* have a reproductive strategy involving a terminal, pubertal moult where reproduction begins only when growth has ceased (Melrose, 1975; McLay & Van den Brink, 2009). The terminal moult in *Halicarcinus* species allows females to maximize their reproductive output during a comparatively short (approximately six month) adult life span by producing broods continuously and successively, without the need for the female to suspend reproduction for moulting (Van den Brink & McLay, 2009, 2010). However, as body size is the primary determinant of brood size, and a terminal moult prevents further growth, the number of eggs per brood remains small (Hartnoll, 1969; Van den Brink, 2006). Due to their small size, hymenosomatids have some of the lowest fecundity levels among the Brachyura (Lucas, 1980; McLay & Van den Brink, 2009).

A female's reproductive output is influenced by the number of eggs per brood, the number of broods produced, the eggs' incubation time and survival rates. Being ovigerous throughout the year exposes *Halicarcinus* females and their externally carried eggs to various environmental factors that can affect their reproductive output. During different seasons, the growing embryos in the eggs are exposed to a range of temperatures that may affect their incubation time or survival that a discrete breeding season would avoid (Jansen, 1971). If different temperatures cause significant differences in incubation time then it is reasonable to assume that temperature can determine the number of broods produced in a lifetime and has the potential to influence local recruitment and population dynamics.

In this study the effect of temperature change on brood duration, comparing three species of hymenosomatid crabs, *Halicarcinus cookii*, *Halicarcinus varius* and *Halicarcinus innominatus*, living in the same intertidal habitat were measured.

MATERIALS AND METHODS

Crabs were collected from locations around the Kaikoura Peninsula in New Zealand (see Dunnington, 1999; Hosie, 2004; Van den Brink, 2006). Three temperatures that encompassed the annual mean seawater temperature of 12.9°C were chosen. It would have been useful to include a temperature the same as the mean, but facilities did not allow this. However, our intermediate temperature of ~15°C was close to the mean. For each temperature, 25 females for *Halicarcinus*

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cookii and *H. varius*, and 30 for *H. innominatus*, each marked with a commercial bee tag bearing a different number, were placed in a 50 × 20 × 5 cm tray with 3 l water and an air pump. For *H. cookii* and *H. varius*, temperature control rooms were set up but for *H. innominatus*, females were monitored in holding tanks during different seasons and ambient water temperatures were recorded (Dunnington, 1999; Hosie, 2004; Van den Brink, 2006). The mean temperatures for *H. cookii* were 10.31°C ± 0.21°C, 15.35°C ± 0.17°C and 20.28°C ± 0.096°C respectively, while for *H. varius* the mean temperatures were 10.04 ± 0.67°C, 14.35 ± 0.19°C and 20.73 ± 0.23°C. For *H. innominatus*, summer (December–February) temperatures averaged 18.7°C, winter (June–August) temperatures averaged 10.45°C and autumn (March–May) and spring (September–November) temperatures averaged 14.8°C and 14.2°C respectively. For ease of comparison between species, the temperatures are rounded and referred to as 10°C (winter), 15°C (autumn/spring) and 20°C (summer). Note that the latter two temperatures were higher than the annual mean of 12.9°C.

Females were monitored through one complete brood cycle. The five stages of brood development were: stage 1 eggs have 100% bright yolk (orange in *H. cookii*, olive green/yellowish in *H. varius* and olive green in *H. innominatus*) with little or no embryo cleavage; stage 2 eggs show 75% orange yolk and obvious embryo cleavage; stage 3 eggs show 50% yolk, more cleavage and the development of chromatophores; stage 4 eggs have chromatophores, 25% yolk and an embryo with developing eyespots; and stage 5 eggs have less than 10% yolk, prominent eyespots on a fully developed zoea ready to hatch. The interbrood period was the time between a brood hatching and the oviposition of a new brood (Dunnington, 1999; Hosie, 2004; Van den Brink, 2006).

Records of the brood cycle began from the first change in brood stage observed and ended when that same stage was reached in the following brood to ensure an accurate record of the beginning of a stage. For example, if the female was initially observed to carry a brood at stage 2, the recorded brood cycle began only when the brood first developed into stage 3, and ended the day before the first observation of stage 3 of the following brood. In this way we ensured that the entire duration of each stage for each species was measured and so we did not have to make any assumptions about how much of a stage might already have been completed when the crab was added to the experiment, and also allowed time for acclimatization to the temperature. The mean duration of each brood stage at each temperature was compared using one-way analysis of variance (ANOVA). The interbrood period was also recorded and compared between temperatures to investigate the influence of temperature on the time it takes for a female to lay a new brood (Dunnington, 1999; Hosie, 2004; Van den Brink, 2006). This is a reflection of the effects of temperature on the duration of the ovarian cycle.

RESULTS

Brood cycle

Incubation time for all three species was negatively correlated with temperature (Figure 1). Mean incubation period for all species ranged from 43.8–56.8 days at 10°C, 22.8–32.4 days at 15°C and 14.7–18.9 days at 20°C. The mean incubation period for *Halicarcinus cookii* at 10°C was 43.8 days, at 15°C: 22.8 days ± 1.0 days and at 20°C: 14.7 days ± 1.2 days. For *H. varius* the incubation duration at 10°C was 53.3 days, at 15°C: 25.7 ± 0.7 days and at 20°C: 16.9 ± 0.4 days. For *H. innominatus* the mean incubation duration at 10°C was 56.8 ± 0.5 days, at 15°C: 32.4 ± 0.3 days and at 20°C: 18.9 ± 0.5 days (Figure 1). There was a significant difference in total incubation duration according to temperature between 15°C and 20°C for *H. cookii* and *H. varius* (as 10°C had no variation) (ANOVA: *H. cookii*: $F_{1,14} = 51.04$, $P < 0.0001$; *H. varius*: $F_{1,21} = 99.38$, $P < 0.001$) and for all temperatures for *H. innominatus* ($F_{3,116} = 1575.60$, $P < 0.001$).

Mortality was high during the experiment at 20°C. Therefore sample sizes for *H. cookii* and *H. varius* were smaller (N = 7 and 8 in 20°C respectively) compared with the other temperatures where sample size remained at 25 for *H. cookii* and *H. varius*, and 30 for *H. innominatus* due to negligible mortality or successful replacement of females. Although additional females were added to compensate for the loss, this proved unsuccessful due to high mortality of 76% for *H. cookii* and 73% for *H. varius*. Females entering the experiment with broods at stages 4 or 5 tended to lay another brood successfully, but females entering the experiment carrying broods at stages 1 or 2 often died before laying their next brood, or simply failed to lay a second brood. As no females of either *H. cookii* or *H. varius* completed an entire brood cycle in 10°C, the total brood duration was calculated as the sum of the average duration for each individual brood stage, and therefore shows no overall estimate of variation.

Interbrood period

The interval between the hatching and oviposition of a new brood was generally shorter at higher temperatures for all three species (Figure 2). Note that in Figure 2 the minimum interbrood period is shown as one day; although results for *Halicarcinus cookii* and *H. varius* include proportions of a single day where a brood was laid within one day, *H. innominatus* was recorded with a minimum one day interbrood period. Therefore 1 was added to the results for *H. cookii* and *H. varius* in Figure 2 for ease of comparison (for *H.*

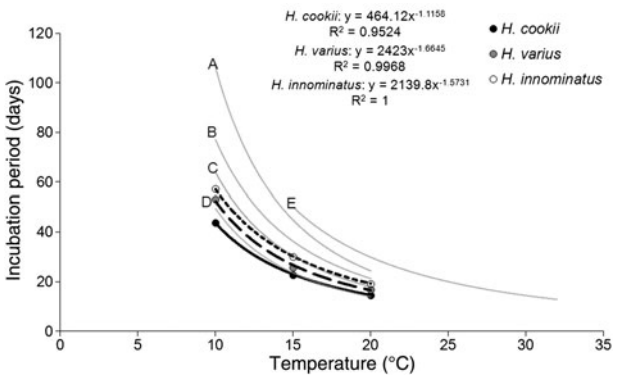

Fig. 1. Mean incubation time (days) according to temperature for *Halicarcinus cookii*, *Halicarcinus varius* and *Halicarcinus innominatus* (black lines). Symbols represent experimental results. Regression equations and R^2 values are also shown. Grey lines indicate incubation time for other crab species: A, *Palaemon serratus*; B, *Carcinus maenas*; C, *Inachus dorsettensis*; D, *Macropipus depurator*; E, *Elamenopsis kempi* (from Ali *et al.*, 1995).

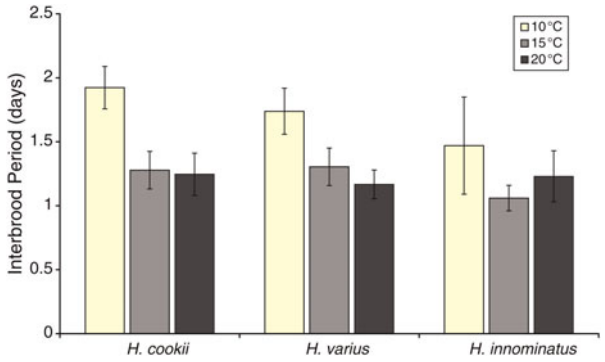

Fig. 2. Mean duration (days) of the interbrood period between larval release and oviposition of the following brood (stage 5 to stage 1) at temperatures of 10, 15 and 20°C for *Halicarcinus cookii* (N = 13, 19 and 13 respectively), *Halicarcinus varius* (N = 17, 15 and 8 respectively) and *Halicarcinus innominatus* (N = 30 for all temperatures). Error bars are ± 1 SE.

cookii actual average interbrood periods in days were: 10°C = 0.92, 15°C = 0.28, 20°C = 0.25; and for *H. varius*: 10°C = 0.74, 15°C = 0.30, 20°C = 0.17).

For *H. cookii*, there was a significant difference in interbrood duration between temperatures ($F_{3,34} = 9.45$, $P < 0.001$) (ANOVA) and interbrood durations were significantly longer in 10°C than both 15°C and 20°C ($P < 0.05$ in all cases) while interbrood periods at 15°C and 20°C were not significantly different ($P = 0.894$) (Tukey's honestly significant difference test). Similarly, for *H. varius* the interbrood period was significantly longer at 10°C than in 15°C and 20°C ($F_{2,55}$:3.687, $P < 0.05$), but there was no significant difference between 15°C and 20°C ($P > 0.05$). For *H. innominatus*, there was no significant difference between interbrood periods at different temperatures ($F_{3,116} = 3.23$, $P > 0.01$, higher P value used because variances were heterogeneous).

Brood stages

There were significant differences in incubation period at different temperatures for all stages for all three species (Table 1). The mean percentage of total incubation time for each brood stage was calculated for all three species (Figure 3). The proportions of incubation time for each stage were relatively similar between species. For the three species at all three temperatures, stage 1 was the longest in duration of all brood stages while stages 3 and 5 were the shortest brood stages (Figure 3).

Table 1. Results of the analysis of variance for the duration of each brood stage at different temperatures.

Brood stage	*Halicarcinus cookii*	*Halicarcinus varius*	*Halicarcinus innominatus*
1	$F_{2,46} = 119.0$, $P < 0.001$	$F_{2,27} = 23.8$, $P < 0.001$	$F_{3,116} = 159.01$, $P < 0.001$
2	$F_{2,28} = 29.6$, $P < 0.001$	$F_{2,27} = 87.4$, $P < 0.001$	$F_{3,116} = 118.13$, $P < 0.001$
3	$F_{2,36} = 60.6$, $P < 0.001$	$F_{2,27} = 14.4$, $P < 0.001$	$F_{3,116} = 67.10$, $P < 0.001$
4	$F_{2,45} = 66.3$, $P < 0.001$	$F_{2,27} = 19.0$, $P < 0.001$	$F_{3,116} = 216.71$, $P < 0.001$
5	$F_{2,39} = 50.8$, $P < 0.001$	$F_{2,27} = 71.4$, $P < 0.001$	$F_{3,116} = 4.46$, $P < 0.01$

For *Halicarcinus cookii* data for duration of each stage and for each temperature were normalized with a square-root transformation (Cochran $P = 0.053$). For *H. varius* variances for brood stage duration at 15°C were heterogeneous (Cochran's test $P < 0.05$) and all attempts to make them homogeneous failed. The criteria for significance was then lowered to $P = 0.001$. For *H. innominatus* variances for the ANOVA were heterogeneous for all stages. Data were log-transformed for brood stages 1, 3 and 5 to stabilize the variances. For brood stages 2 and 4, all attempts to make the variances homogeneous failed and the significance levels for these two analyses were raised to <0.01.

DISCUSSION

Of the three species, *Halicarcinus cookii* has the shorter incubation time at any given temperature than *H. innominatus* and *H. varius*. While interbrood periods were similar, at a mean temperature of 15°C, *H. cookii* incubation took 22.8 days, whereas *H. varius* took 25.7 days (Hosie, 2004) and *H. innominatus* 30.2 days (Dunnington, 1999). At maximum mean temperatures of around 20°C *H. cookii* incubated their eggs in 14.67 days, while *H. varius* took 16.88 days (Hosie, 2004) and *H. innominatus* took 22.3 days (with a mean temperature of 18.7°C) (Dunnington, 1999). These are all relatively short incubation periods when compared with other hymenosomatid species at similar temperatures such as *H. ovatus* (29 days), *Amarinus paralacustris* (25.5 days) (Lucas, 1980) and *A. laevis* (29 days) (Lucas & Hodgkin, 1970). The three study species also have relatively short incubation periods when compared with various other crab species at a range of temperatures (Figure 1).

At temperatures around 15–20°C incubation in *Elamenopsis kempi* took 48 days (Ali *et al.*, 1995). However *E. kempi* occurs in sub-tropical waters and is the only hymenosomatid species, for which data are available, to incubate its eggs in a mean water temperature greater than 20°C (ranging from 25–32°C). At these temperatures incubation was completed in about 23 days, suggesting that relative to their respective temperature regimes, *E. kempi* has a faster incubation time. Similarly, brood incubation in the sub-Antarctic species *Halicarcinus planatus* took 60 days at 6–8°C at the Kerguelen Islands (Richer de Forges, 1977).

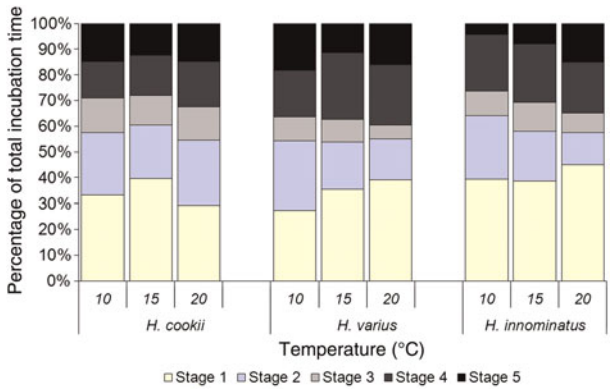

Fig. 3. Each brood stage as a percentage of the entire brood cycle for *Halicarcinus cookii*, *Halicarcinus varius* and *Halicarcinus innominatus* at different termperatures.

This may simply be an indication that temperature related differences in incubation rates between species are based on adaptations to their environments with their optimal incubation times in synchrony with the temperature regime they experience in the field.

Although there were significant differences in the duration of each individual brood stage, their proportions of the total incubation time were similar. These results are reflected in the field. As the three *Halicarcinus* species all live in similar habitats on the same rocky shore and cannot burrow or hide, any bias in sampling can be eliminated. As they can store sperm to reduce sperm limitation, they have consistent brood production, and as females appeared to be completely passive participants during mating and mate-guarding (Van den Brink, 2006), behavioural effects on selection can also be ruled out. Therefore, for a random sample of crabs from the shore, the proportion of females with eggs at different stages should be a reflection of the duration of each stage.

Van den Brink & McLay (2010) found that in the population of *H. cookii* sampled from the field, most ovigerous females were found carrying stage 1 eggs and fewest carrying stage 4 eggs; they estimated that the brood stage of longest duration was likely to be stage 1, followed by stages 2, 5, 3 and the shortest, stage 4. The present results differ slightly from those estimates, but follow a similar trend for all three species (see Table 2).

Once mature, *Halicarcinus* species can mate at any time, and with short interbrood intervals, have the potential to have a high reproductive output and produce recruits year-round (Van den Brink & McLay, 2010). This is in contrast with species such as *Hemigrapsus sexdentatus* from the same habitat, which have a very restricted breeding season and only produce one brood per year (Brockerhoff & McLay, 2005). With this continuous brood production regardless of season, water temperature directly affects the duration of brood incubation with incubation time decreasing in increasing temperatures. Temperature therefore influences the number of broods a female can produce per lifetime.

The mean annual seawater temperature in Kaikoura from December 2003 through to November 2005 was 12.9°C ranging from 8.77°C (August) to 17.86°C (February). Over the summer months from November to April (peak breeding period, due to the increased numbers of adult females and therefore more net reproduction in the population; see Van den Brink & McLay, 2010) the mean temperature was 15.36°C, while over the winter months from May to October the mean temperature was 10.5°C. Assuming an adult life span of about six months then during the peak breeding period an *H. cookii* female could produce a maximum of approximately eight broods in a lifetime, *H. varius* about seven broods, and *H. innominatus*, about six broods. Given the mean fecundities of eight complete broods of 1146 eggs for *H. cookii* (Van den Brink, 2006), seven complete broods of 1051 eggs for *H. varius* (Hosie, 2004), and six complete broods of 1081 eggs per brood for *H. innominatus* (Dunnington, 1999), an average sized female *H. cookii* could be expected to produce 9168 larvae in a lifetime, *H. varius* 7357 and *H. innominatus* 6486 offspring in a lifetime (Table 3).

Table 2. Comparisons of the proportion (%) of each brood stage during brood development in the laboratory (Lab) and observed in the field.

Brood stage	*Halicarcinus cookii*		*Halicarcinus varius*		*Halicarcinus innominatus*	
	Field	Lab	Field	Lab	Field	Lab
1	44	34	36	34	39	41
2	16	22	18	20	20	19
3	12	13	11	8	9	9
4	10	17	20	23	24	22
5	18	14	15	15	8	9

In the temperature regime experienced by these three *Halicarcinus* species in the field, successive brood production over a female's adult life exposes broods to a range of temperatures according to different seasonal changes in climate. Incubation times of decapod eggs are closely linked to the temperature of the water they are incubated in (Wear, 1974). At Kaikoura the water temperature varies throughout the year due to seasonal changes, and as the three *Halicarcinus* species produce eggs for most of the year, not just in optimal conditions, their eggs experience a range of temperatures. The incubation times of the study species were typical of decapods in that incubation time decreased as temperature increased, probably due to an increase in the speed of metabolic processes with increased temperature (Leffler, 1972). However, in the 20°C temperature control room *Halicarcinus cookii* and *H. varius* did not survive. At this temperature it is possible that heart failure, which affects oxygen uptake, oxygen delivery and oxygen utilization, caused the observed high mortalities (Stillman, 2002). Stillman (2002) reported that at the thermal limits of *Petrolisthes* species, heart function was damaged irrecoverably. This was due to either the molecular properties of the heart muscle being damaged, or that the nerves innervating the heart were damaged. The high mortality may also have been a result of oxygen depletion. Walther *et al.* (2010) suggested that mortality at higher temperatures in the spider crab, *Hyas araneus* could be explained from the principles of oxygen- and capacity-limited thermal tolerance; that the brooding of the crustacean eggs enhances the oxygen demand of the female at constant oxygen supply capacity and, thereby, exacerbates any oxygen limitation. Despite the presence of an air pump during the experiment, the oxygen levels were likely to be lower at 20°C than at the other temperatures, and may, therefore, have been below the tolerance level of the crabs.

In contrast, *H. innominatus*, kept in ambient temperatures where the highest mean temperature was 18.9°C, suffered negligible mortality. As ambient temperature fluctuates, *H. innominatus* was not exposed to the consistently high temperatures experienced by the other two species in the temperature control rooms, and therefore experienced less physiological stress. The ambient temperature experienced by *H. innominatus* is obviously more accurate to the natural habitat as temperatures fluctuate daily, whereas the temperature control rooms were kept relatively constant. When considering the observed incubation times and potential levels of mortality observed in *H. cookii* and *H. varius* in the temperature control rooms, it can be assumed that an optimal consistent temperature for these species to incubate eggs is about, and perhaps slightly less than, 15°C.

Sea temperatures from December 2003 through to November 2005 in Kaikoura ranged from 8.77°C to 17.86°C, reaching over 15°C in only 8 of the 24 months

Table 3. Estimated number of broods produced by *Halicarcinus cookii*, *Halicarcinus varius* and *Halicarcinus innominatus* per month during November 2004–April 2005 and the same months in approximately 2050 after a 2°C sea temperature rise using regression equations (Figure 1). This period is both peak breeding season and an average female adult life span. Incubation period includes interbrood interval.

Month	Average temperature		Days per month	Estimated broods per month					
				H. cookii		*H. varius*		*H. innominatus*	
	2005	2050		2005	2050	2005	2050	2005	2050
November 2004	13.8	15.8	30	1.2	1.4	1	1.2	0.9	1.1
December 2004	14.1	16.1	31	1.3	1.5	1	1.3	0.9	1.1
January 2005	16.11	18.11	31	1.5	1.7	1.3	1.6	1.1	1.4
February 2005	17.86	19.86	28	1.5	1.7	1.4	1.7	1.2	1.4
March 2005	16.21	18.21	31	1.5	1.7	1.3	1.6	1.2	1.4
April 2005	14.11	16.11	30	1.2	1.4	1	1.3	0.9	1.1
Total broods per lifetime				8.2	9.4	7.1	8.7	6.2	7.5
Complete broods per lifetime				8	9	7	8	6	7

recorded (one-third of the year) with an average of 15.36°C in the summer months and 10.5°C in the winter months. The mean seawater temperature during this time was 12.9°C, suggesting that these *Halicarcinus* species are well adapted to the temperature of their environment.

However, a change in water temperature may affect the generation time of the species and therefore impact the population. Global temperatures are predicted to rise by at least 2°C in the next 50 years (Hoegh-Guldberg *et al.*, 2007). Such a change may result in sea temperatures in Kaikoura reaching over 15°C for half or more of the year. Although at higher temperatures there is the possibility of increased mortality in the three *Halicarcinus* species (in cases of prolonged periods with water temperatures over 20°C where mortalities above 70% were observed), the fact that the natural environment fluctuates in temperature rather than remains at a consistent temperature suggests that it is more likely that broods would develop faster, allowing each female to produce more offspring per lifetime and resulting in possible population increase and a change in geographical boundary limits.

If temperatures rise 2°C as predicted, each of the three species could produce one extra brood per female lifetime (Table 3). This would result in the production of over 1000 extra larvae per female resulting in a 10–15% increase in fecundity. Assuming a larval survival rate of about 1–5%, a 2°C sea temperature rise could result in a single female producing 10–50 extra surviving offspring per lifetime.

Additionally, an increase in temperature is also likely to increase larval growth rates and therefore generation time, adding to the potential population growth. Larval development in crabs is temperature related, with an increase in temperature resulting in shorter development times (Nakanishi, 1981; Vinuesa *et al.*, 1985; Anger, 1993; Okamoto, 1993; Anger *et al.*, 2003; Walther *et al.*, 2010). Less time spent in the plankton as vulnerable larvae may also increase survival rates to final instars and eventually adults, thus potentially increasing the size of the population.

Furthermore, the current six month peak breeding season in the three *Halicarcinus* species may increase as temperatures rise. Walther *et al.* (2010) found the larval release of the spider crab *Hyas araneus* occurred almost a month earlier than it did 30 years ago, correlating with a recorded increase in water temperature of 1.1°C. An increased temperature and extension of the peak breeding time in Kaikoura may allow the three *Halicarcinus* crabs more time to carry eggs and therefore produce even more offspring per lifetime (provided they live long enough).

Although the exact geographical ranges of these three *Halicarcinus* species is not known, an increase in temperature may shift or extend their natural distributional boundaries that are currently limited by temperature. Walther *et al.* (2010) suggested that with a 1.1°C temperature rise since 1969, the southernmost limit of the geographical range of *H. araneus* may have moved north from the English Channel, and that continual rise in water temperature may result in further northward shift of the geographical range.

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