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Changes in Embryonic Development and Hatching in *Chionoecetes opilio* (Snow Crab) With Variation in Incubation Temperature

JOEL B. WEBB*, GINNY L. ECKERT, THOMAS C. SHIRLEY†, AND SHERRY L. TAMONE

University of Alaska Fairbanks, School of Fisheries and Ocean Sciences, 11120 Glacier Highway, Juneau, Alaska 99801

Abstract. Water temperature affects the distribution, movement, and reproductive potential of female snow crab, *Chionoecetes opilio.* Ovigerous females of *C. opilio* from the eastern Bering Sea were held at five temperatures (−1, 0, 1, 3, and 6 °C) in the laboratory while their embryos developed from gastrula to hatching. The duration of incubation increased by 105 d (30%) with decreasing temperature; however, a switch to a 2-year duration of embryo incubation was not observed. For females held at 6, 3, and 1 °C, their embryos underwent a short period of diapause late in development; no diapause was observed for embryos of females held at 0 or −1 °C. Successful extrusion of a subsequent clutch and hatch timing comparable with that observed in the eastern Bering Sea indicated that temperatures of 0 to 3 °C may be optimal for multiparous female reproduction. We demonstrated that a switch from 1-year to 2-year reproduction cannot be triggered by changing the thermal regime after several months of embryonic development. The timing of female movement from colder to warmer waters may be important for maintaining population reproductive potential during the recent phase of warming and contraction of cold-water biomes in the Bering Sea.

Introduction

Chionoecetes opilio (J. C. Fabricius, 1788) (Brachyura: Oregoniidae), commonly known as snow crab, is found in cold-water continental shelf environments at high latitudes throughout much of the northern hemisphere, with commercial fisheries occurring in the Northwest Atlantic, Sea of Japan, and eastern Bering Sea (EBS). Catch, catch per unit effort, and value of the eastern Bering Sea fishery peaked during the early and late 1990s, but declined dramatically in 2000 and have continued at low levels since (Rugolo *et al.,* 2006). The EBS *C. opilio* population was listed as "overfished" under the Magnuson-Stevens Fisheries Conservation and Management Act in 1999 (National Marine Fisheries Service, 1999).

Warmer-than-average water temperatures have predominated in the Bering Sea since 1977 when a regime shift from colder to warmer ocean conditions occurred (Hunt *et al.,* 2002). Temperatures in the EBS increased as much as 2 °C in the past decade, with warm temperature anomalies arriving earlier in the spring and persisting longer into the fall than in past years (Overland and Stabeno, 2004). Changes in EBS water temperature and ice cover have altered the ecosystem structure, biogeographical distribution, and life histories of organisms in the region (Hunt *et al.,* 2002; Overland and Stabeno, 2004; Overland *et al.,* 2005). Increased water and air temperatures and reductions in seasonal ice cover in the northern Bering Sea have coincided with decreased benthic productivity (Grebmeier *et al.,* 2006), and the northward shift and contraction of cold-water biomes is likely to continue in the near future (Overland *et al.,* 2005). Warming may also affect the timing of the spring phytoplankton bloom in the EBS. If sea-ice retreat occurs in mid-March or later, a cold-water (≤0 °C), ice-edge-associated bloom is likely in early spring. During warmer conditions, sea-ice retreat before mid-March will result in the primary spring bloom occurring in warmer (≥3°), open water, in May or June (Hunt and Stabeno, 2002).

The movement, physiology, early life history, and repro-

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* To whom correspondence should be addressed, at Alaska Department of Fish and Game, Commercial Fisheries Research, PO Box 115526, Juneau, AK 99811-5526. E-mail: joel_webb@fishgame.state.ak.us

† Current address: Harte Research Institute, Texas A&M University–Corpus Christi, 6300 Ocean Drive, Unit 5869, Corpus Christi, TX 78412.

ductive potential of females of *C. opilio* are all affected by temperature. Changes in distribution and abundance of this species in the EBS have been observed over the last several decades, when the centers of distribution of both mature male and female *C. opilio* shifted from southwest to northeast in the EBS from the late 1970s to the late 1990s (Zheng *et al.,* 2001; Orensanz *et al.,* 2004; Ernst *et al.,* 2005). This shift in distribution may have been associated with the regime shift in the EBS from colder to warmer conditions starting in 1976–1977 (Zheng *et al.,* 2001). After a lag time of 6 years, the northward displacement of the southern boundary of the EBS cold pool (<2 °C) was followed by a northward shift in the distribution of mature females (Orensanz *et al.,* 2004). Movements of the mature females may also be influenced by temperature. Females are hypothesized to follow gradients in near-bottom temperature or depth from colder to warmer areas, undergoing an offshore ontogenetic migration oriented from northeast to southwest (Ernst *et al.,* 2005). Among other factors, the subsequent southward range expansion of *C. opilio* may be limited by the southern extent of the cold pool, patterns of larval advection, and predation on juveniles by Pacific cod (*Gadus macrocephalus*) (Orensanz *et al.,* 2004). Pacific cod prey heavily on early benthic instars of *C. opilio* (Livingston, 1989) and are likely to increase in abundance and expand northward with warmer seawater temperatures in the EBS (Hunt *et al.,* 2002).

Temperature affects individuals of *C. opilio* physiologically throughout their life history. Mature males are energetically confined to waters below 7 °C, with peak activity occurring at 0 °C (Foyle *et al.,* 1989). Thermal tolerance also varies with body size. When held at −1 °C, male and female *C. opilio* weighing less than 200 g were in energetic deficit, while larger crab were not (Thompson and Hawryluk, 1990). For early benthic instars, temperature rather than substrate determines distribution, and instars segregate among discrete temperature strata (Dionne *et al.,* 2003). The duration of embryonic incubation in *C. opilio* can be extended by small changes in temperature. Primiparous and multiparous females in the Gulf of St. Lawrence, Canada (GSL), have reproductive cycles of 18 and 12 months, respectively, in warmer (3 to 5 °C) water and 27 and 24 months at colder (−1 to +1 °C) temperatures (Watson, 1970; Mallet *et al.,* 1993; Sainte-Marie, 1993; Moriyasu and Lanteigne, 1998; Comeau *et al.,* 1999). Recent field studies have confirmed the presence of a 2-year cycle of embryonic development for both primiparous and multiparous *C. opilio* in the EBS at temperatures below 1 °C in the northern portions of their range (Rugolo *et al.,* 2005). The potential range of temperatures experienced by mature female *C. opilio* in the EBS is about 1 to 3 °C (Luchin *et al.,* 1999; Zheng *et al.,* 2001), with females in the northern portion of the range more likely to experience colder temperatures for longer periods of time, because temperature generally increases with decreasing latitude in the EBS (Luchin *et al.,* 2002).

The presence of a substantial proportion of the mature female population on a 2-year reproductive cycle instead of a 1-year cycle could limit the reproductive potential of *C. opilio* on variable spatiotemporal scales in both the EBS and GSL. In the GSL, female *C. opilio* undergo a terminal molt to reproductive maturity at 5.5 to 6.5 years of age (Alunno-Bruscia and Sainte-Marie, 1998) and have a post-terminal molt survival of 5 to 6 years (Sainte-Marie, 1993), which on a 2-year cycle may produce only two clutches during a lifetime. In the EBS, post-terminal molt survival for female *C. opilio* has been estimated at 6 to 7 years on the basis of radiometric and instar analysis (Ernst *et al.,* 2005) and at 2 to 4 years on the basis of lipofuscin accumulation (Bluhm and Shirley, 2005); as a result, female *C. opilio* in the EBS are likely to produce only one to three clutches in a lifetime on a biennial reproductive cycle.

The effect of temperature on the duration of embryonic development has been well described for *C. opilio* from the northwestern Atlantic (Mallet *et al.,* 1993; Sainte-Marie, 1993; Moriyasu and Lanteigne, 1998; Comeau *et al.,* 1999). However, little is known about the effects of temperature on the duration of embryonic incubation, patterns of embryo development, or hatching of *C. opilio* from the EBS. Substantial decreases in the rate of embryo development in decapod crustaceans, including *C. opilio,* are due to periods of diapause, or suspension of growth (Wear, 1974; Moriyasu and Lanteigne, 1998). On a 2-year reproductive cycle, *C. opilio* has two distinct periods of diapause during embryonic development in the GSL. The first diapause period occurs at the gastrula stage and lasts for 6 months, and the second occurs at the stage of eye-pigment formation and lasts for 3 to 4 months (Moriyasu and Lanteigne, 1998). The presence or length of diapause periods in the embryo development of *C. opilio* in the EBS is unknown.

Temperature may also affect the survival and growth of larval *C. opilio* by altering the timing of larval release in relation to seasonal primary production. Peak abundance of stage-one zoeae of the species in the southern Bering Sea occurs in April (Incze and Armstrong, 1987) during the ice-edge-associated bloom. During warm years in the Bering Sea when ice-edge retreat occurs prior to mid-March, the timing of the spring phytoplankton bloom may be delayed by several months, from March to May or June (Hunt and Stabeno, 2002). Synchronization of larval release with periods of primary production may affect larval survival for *C. opilio* in the EBS (Somerton, 1982). Diapause periods may prolong embryonic development, delaying larval release into periods of increased primary production for some high-latitude cold-water decapods (Shirley *et al.,* 1990, Petersen and Anger, 1997), but mechanisms other than increased temperature (Mallet *et al.,* 1993) to reduce the duration of incubation and advance the timing of larval

release have not been proposed. Variability in the timing of larval release with incubation temperature has not been previously determined for *C. opilio* from the EBS.

The purpose of this study was to examine the effect of a range of environmentally relevant incubation temperatures on the duration and rate of embryonic development, the duration and timing of hatching, and the extrusion of a subsequent clutch after larval release for multiparous female *C. opilio* from the EBS.

Materials and Methods

Ovigerous females were collected by bottom trawl on 5 July 2002 south of St. Matthew Island (60°N,172°W) (Fig. 1) in the Eastern Bering Sea (EBS) at a depth of 117 m with a bottom temperature of 3.02 °C. Crabs were maintained on board ship in circulating ambient seawater, estimated to be 3–6 °C from average seasonal sea-surface temperatures (Luchin *et al.,* 1999), and transported by air in coolers lined with burlap and chilled by ice packs to Juneau, Alaska, on 10 July 2002. On arrival, crabs were maintained in 700-l flow-through seawater tanks cooled by chillers (Frigid Units Inc. model D1-33) to a constant temperature of 3 °C. On 14 July 2002, 25 females classified as multiparous, old shell (Jadamec *et al.,* 1999) were assigned to treatments of −1, 0, 1, 3 and 6 °C in a random stratified design based on carapace width such that no significant differences in crab sizes existed among treatments. Seawater temperatures in each tank were monitored using Stowaway Tidbit temperature loggers at 15-m intervals and when averaged (±1 SD) daily over the duration of the study for the 6, 3, 1, 0 and −1 °C treatments were 6.32 (±0.36), 3.24 (±0.18), 1.37 (±1.03), 0.12 (±0.94), and −0.89 °C (±0.59 °C), respectively. Females that were classified as primiparous or very old shell multiparous on the basis of shell condition, had low scores for clutch fullness, or had two or more missing or damaged limbs were excluded from the study.

Embryonic incubation and development

Starting on 2 September 2002, at 4-week intervals, about 50 embryos were collected from each of 15 females per tank and preserved in Bouin's solution. Embryos were consistently collected from an area near the center of the clutch to control for potential variation in developmental stage within the clutch. Within a few days of collection, the developmental stage of 10 preserved embryos per female was determined using criteria established for the embryonic de-

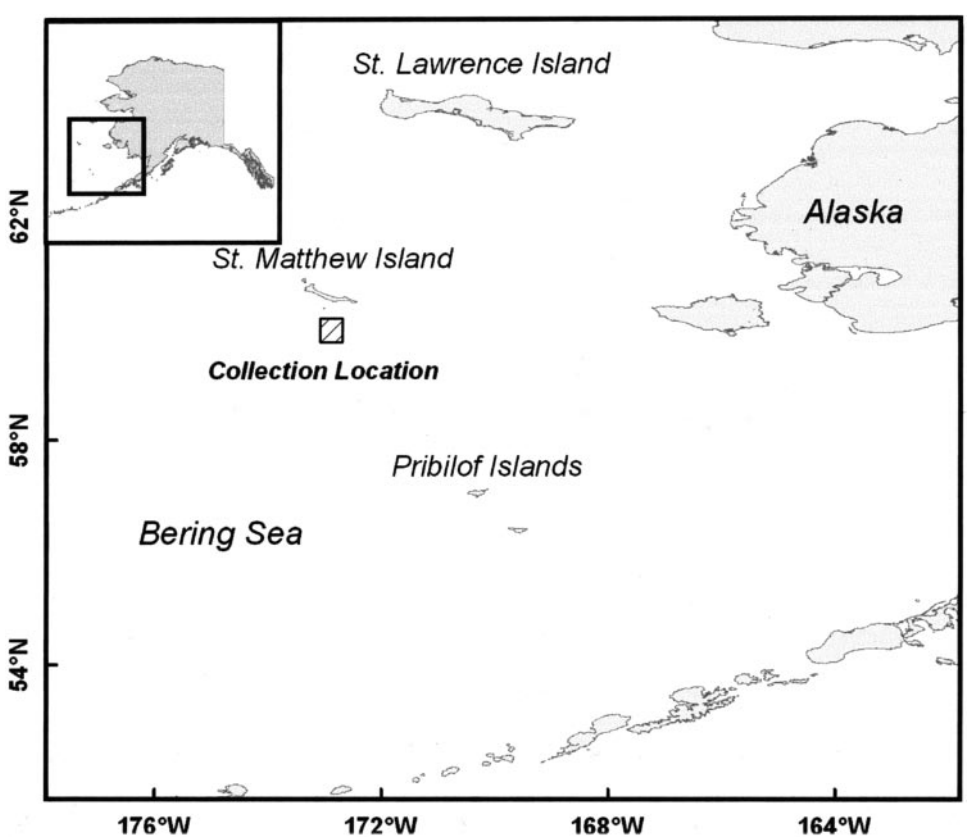

Figure 1. Locations at which multiparous female *Chionoecetes opilio* were collected by bottom trawl on 5 July 2002 south of St. Matthew Island in the eastern Bering Sea.

velopment of *Chionoecetes opilio* by Moriyasu and Lanteigne (1998) (Table 1). Embryonic development is a continuous process, but staging of embryos is based on static morphology of the embryo when certain physiological and morphological features are observable through the course of development (Moriyasu and Lanteigne, 1998). The developmental stage of the clutch was assigned for each female at each sampling date, using the mean developmental stage observed among the 10 embryos. Little variation in stage was observed among sampled embryos from the same clutch for a given sampling date. Embryo development data from females that died prior to larval release were excluded from analysis.

Hatching

When embryos neared the final developmental stage, tanks were monitored daily for the presence of larvae by placing filters on tank outflows. When hatching commenced, 7 females from the 15 females monitored for embryo development with a representative range of carapace widths from each treatment were placed in plastic boxes (33 × 18 × 10 cm) with sides replaced by 500 μm (47% open) Nitex mesh to allow adequate seawater circulation while retaining larvae hatched by the female. All zoeae were removed from the container at 24-h intervals, and the number of zoeae hatched was estimated on an order-of-magnitude scale (0–10, 10–100, 100–1000, 1000+). An estimate of the daily minimum larval release was calculated for each treatment as the mean of the lower bounds of each order of magnitude category for all females in the treatment. This value was a consistent index of daily hatching activity but was not an estimate of hatching success because females hatched more than 1000 larvae in a 24-h period. Duration of incubation at each temperature was calculated as the number of days from collection to first hatching of 10 or more zoeae in a 24-h period among females monitored for hatching. Duration of hatching was measured from the first release of 10 or more zoeae in a 24-h period to the final release of 10 or more zoeae in 24 h. Females were kept in enclosures until they spawned a new clutch or for at least 2 weeks after the conclusion of hatching. Differences in time from collection to hatch, in hatching duration, and in minimum daily larval release among temperature treatments were examined using one-way ANOVA with Tukey-Kramer multiple comparisons tests. Daily tidal range data from 1 February 2003 to 30 September 2003 were obtained for Juneau tide station (#9452210) from the NOAA Center for Operational Oceanographic Products and Services, Silver Spring, Maryland. Only females that extruded a clutch after hatching or survived 2 weeks post-hatch were included in hatching analyses. All statistical analyses were conducted using SAS release 8.02 (SAS Institute, Cary, NC). All averages are reported as mean ± SD.

Table 1

Embryo development stages for Chionoecetes opilio *from the Gulf of St. Lawrence, Canada (Moriyasu and Lanteigne, 1998)*

Stage #	Morphometric development stage
1	prefuniculus
2	funiculus
3	cleavage and blastula
4	gastrula
5	lateral ectodermal band
6	prenauplius
7	nauplius
8	maxilliped formation
9	metanauplius
10	late metanauplius
11	eye pigment formation
12	chromataphore formation
13	reduced yolk
14	prehatching

Results

Duration of embryonic incubation

The duration of embryonic incubation from field collection to initial larval release increased significantly with decreasing incubation temperature ($F_{4,28} = 167.25$, $P < 0.0001$), except for 0° and 1 °C, which were not significantly different from each other ($P > 0.05$). The mean incubation time from collection to first hatch (days ± SD) was 248 ± 6 d ($n = 7$) at 6 °C, 275 ± 8 d ($n = 7$) at 3 °C, 314 ± 8 d ($n = 3$) at 1 °C, 331 ± 11 d ($n = 7$) at 0 °C, and 353 ± 2 d ($n = 3$) at −1 °C. Mean incubation time decreased 105 d (30%) between −1 and 6 °C.

Embryonic development

The rate of embryonic development increased with increasing temperature (Fig. 2). The duration of embryonic development at 6 °C (6–8 months) was half that of embryos at −1 °C (13–14 months). Embryos at 6 °C reached the final stage of development between January and March 2003, whereas embryos from the 3, 1, 0, and −1 °C treatments reached the final stage in March, April, May, and August, respectively. Differences in rates of development were observed as early as 7 weeks after placement in treatments (2 September 2003), when embryos at 6 °C had progressed one to two egg stages further than those at −1 to 1 °C (Fig. 2). A 1-month diapause period, noted by a decrease in mean developmental rate, was evident at stages 12 or 13 in the 6, 3, and 1 °C treatments. A period of decreased developmental rate was also observed for 2 months in the −1 °C at egg stage 7. Developmental trajectories were largely linear (Fig.

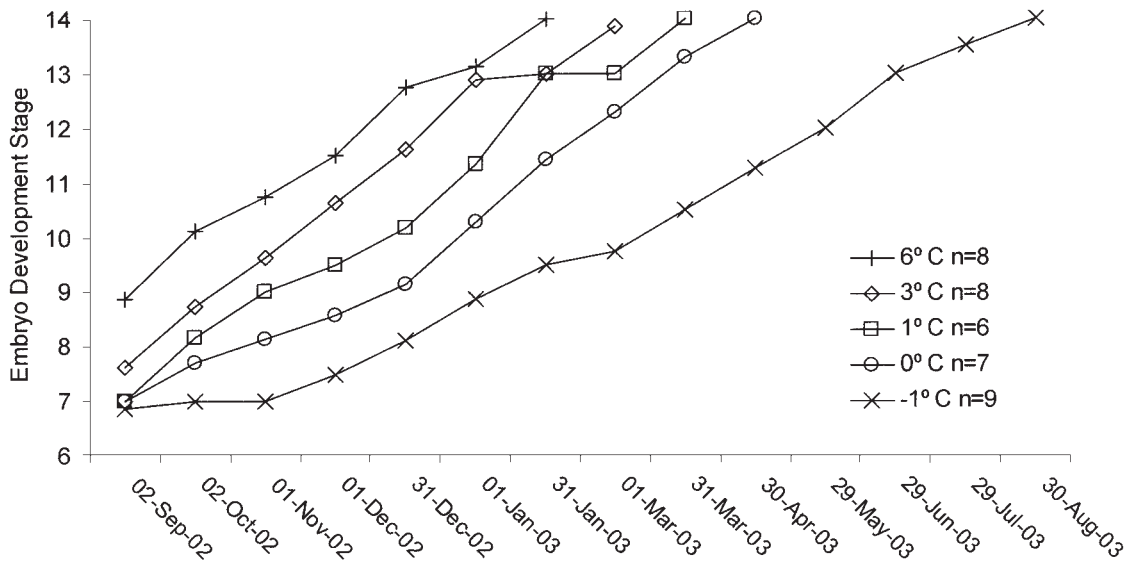

Figure 2. Mean stage of embryonic development by sampling date for multiparous *Chionoecetes opilio* from the eastern Bering Sea held at constant temperature from collection to hatch. Stages as in Table 1.

2), with a slope of 0.835 (r^2 = 0.99) at 6 °C, 0.90 (r^2 = 0.99) at 3 °C, 0.87 (r^2 = 0.98) at 1 °C, 0.80 (r^2 = 0.98) at 0 °C, and 0.594 (r^2 = 0.98) at −1° C. A 28.9% reduction in developmental rate (slope) with temperature between 6 and −1° C was observed.

Hatching and spawning

Hatching was first observed at 6, 3, 1, 0, and −1 °C on 8 March, 1 April, 10 May, 1 June, and 26 June, respectively (Fig. 3). The mean duration of hatching was 11 d for all females, with a minimum of 7 d and a maximum of 17 d to complete hatching. Significant differences in the mean duration of hatching ($F_{2,16}$ = 0.09, P < 0.91) were not observed among the 6, 3, and 0 °C treatments. The number of days of larval release per female for each minimum daily release category, 10–100 ($F_{4,20}$ = 0.60, P < 0.668), 100–1000 ($F_{4,20}$ = 0.60, P < 0.784), and >1000 ($F_{4,20}$ = 2.60, P < 0.067) did not vary significantly with incubation tem-

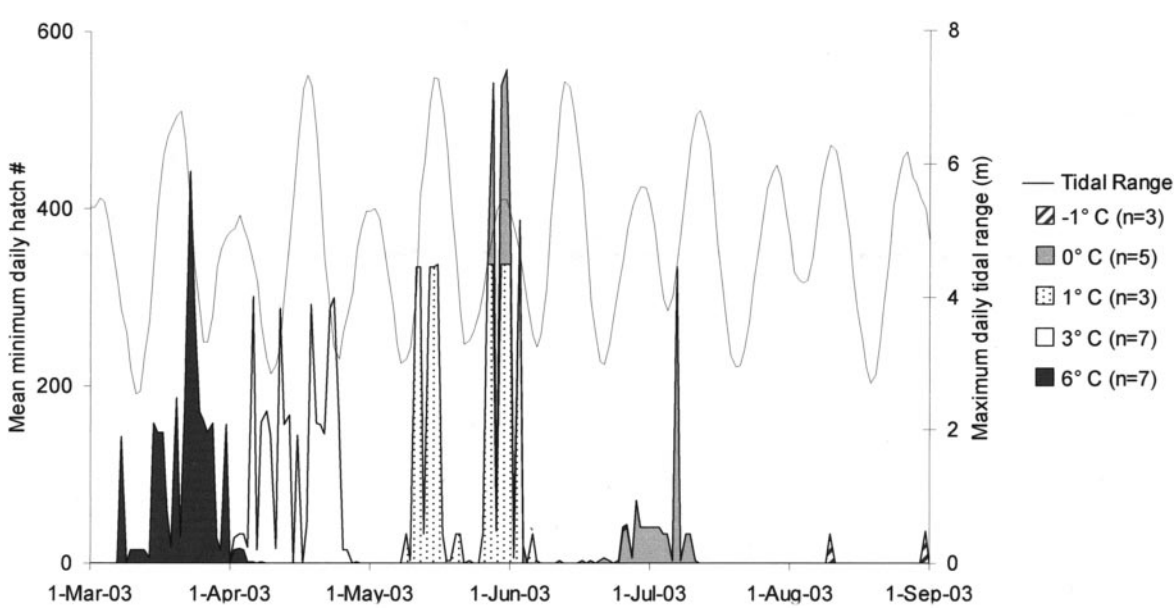

Figure 3. Maximum daily tidal range observed at Juneau, Alaska, and pooled minimum number of zoeae hatched per day by temperature from multiparous female *Chionoecetes opilio* held at constant temperature from collection to hatching.

perature. Linear regression indicated that pooled minimum daily larval release was not associated with maximum daily tidal range ($r^2 = 0.01$, $P < 0.1809$). Hatching data from the 1 °C and −1 °C treatments were not included in duration of hatch analyses or minimum larval release analyses due to asynchronous hatching patterns, low hatching success, and maternal mortality rates of 57% and 86%, respectively, during the hatching period.

The number of females that extruded a new clutch subsequent to completion of hatching varied among temperatures. Zero (0%) of seven females that completed larval release (eclosion) at 6 °C spawned a new clutch within 2 weeks. Six (86%) of seven females at 3 °C and all (100%) five females that completed larval release at 0 °C spawned a new clutch. Comparisons with 1° and −1 °C treatments were limited by high maternal mortality prior to eclosion at those temperatures.

Discussion

The length of embryonic incubation increased with decreasing temperature for *Chionoecetes opilio.* We found an increase in embryonic incubation of 17 days per 1 °C for multiparous females from the Eastern Bering Sea (EBS) at temperatures of 3, 1, and 0 °C. Our result is similar to an increase of 21.4 days per 1 °C in the total duration of incubation for embryos of primiparous *C. opilio* from the Gulf of St. Lawrence (GSL) (Moriyasu and Lanteigne, 1998). Differences in these values are likely a result of longer overall incubation periods for primiparous *versus* multiparous females (Sainte-Marie, 1993), but direct comparisons were not possible because data on changes in development time with temperature were not available for multiparous females from the GSL nor for primiparous females from the EBS. A further difference confounding comparison was that females from the GSL were held at constant temperature for the duration of embryonic development in the laboratory (Moriyasu and Lanteigne, 1998), whereas, judging from the results of Rugolo *et al.* (2005), females in our study likely extruded eggs about 2 to 4 months prior to their collection (March to May), and were exposed to an unknown temperature regime *in situ* before their introduction to constant temperature regimes in the laboratory.

A 2-year cycle of embryonic development was not observed in our study. On the basis of temperature records from annual summer trawl surveys and the temperature recorded at collection, the previous thermal history of our females was probably about 2–3 °C, which is warmer than the temperature (<1 °C) at which *C. opilio* both in the EBS (Rugolo *et al.,* 2005) and the GSL (Moriyasu and Lanteigne, 1998) switch to a 2-year cycle of embryo incubation. Our results indicate that changing temperature later in development (2 to 3 months post-extrusion) does not induce a 2-year incubation period. This result is comparable to observations of embryonic development for the high-latitude majid *Hyas araneus* from the North Sea, in which switching from an annual to a biennial reproductive cycle occurs between 6 and 12 °C, but for which a biennial cycle was not observed in the laboratory for females held at 6 °C from the gastrula embryo stage onward (Petersen, 1995). Thermal exposure soon after extrusion, during embryo cleavage, was postulated to determine whether the reproductive cycle would be annual or biennial (Petersen, 1995). In our laboratory study, embryos sampled in early September were at the prenauplius/nauplius stage (stage 6 to 7) at −1 °C and at the metanauplius stage (stage 9) at 6 °C. According to Moriyasu and Lanteigne (1998), the clutches of females on a 2-year reproductive cycle from the GSL would be at the blastula or gastrula stage (stages 3–4) in the early fall, having arrested development for 6 months at stage 4. It is likely that the embryos of our females skipped this first diapause period as a result of warmer temperatures experienced earlier in development. Patterns of embryonic development from extrusion to the first sampling date were similar to those observed for multiparous females on an annual cycle from the GSL (Moriyasu and Lanteigne, 1998). Female *C. opilio* in the EBS follow gradients of near-bottom temperature from colder (~0 °C but interannually variable, Luchin *et al.,* 1999) to warmer waters (~2–3 °C) as they migrate offshore in a southwesterly direction during the year following the primiparous molt (Ernst *et al.,* 2005). This migration of females from colder to warmer waters in the EBS before extrusion of the multiparous clutch could increase the reproductive potential of the population by increasing the proportion of the population on a 1- *versus* a 2-year reproductive cycle, if females are in waters warmer than 1 °C during the first several months post-extrusion.

The presence or absence of diapause, or resting periods, is the primary cause of variation in the length of the embryonic incubation cycle in crustaceans (Wear, 1974). Two periods of diapause occurred in the development of *C. opilio* embryos from the GSL held at 1.85° C on a 2-year reproductive cycle (Moriyasu and Lanteigne, 1998). The first diapause period occurred at the gastrula stage (stage 4) and lasted for 6 months, and the second occurred at the stage of eye-pigment formation (stage 11) and lasted for 3 to 4 months (Moriyasu and Lanteigne, 1998). We observed a 1-month period of diapause at the reduced yolk stage (stage 13) at 6, 3, and 1° C, but no diapause periods were evident late in embryo development at 0 or −1 °C. A period of slow development was also observed at −1 °C during the first three sampling dates at the nauplius stage (stage 7), but classification as diapause was limited by a lack of data prior to the initial sampling date. The extended duration of embryonic development in this study was primarily due to an overall decrease in developmental rate rather than to periods

of diapause (Fig. 2). Diapause patterns also varied with incubation temperature for red king crab, *Paralithodes camtschaticus,* from southeast Alaska. A 3-month period of diapause was observed just prior to hatching at warmer incubation temperatures (6 to 12 °C), but diapause was not observed at 0 or 3 °C (Shirley *et al.,* 1990). Wear (1974) noted that changing temperatures during diapause did not change the length of resting period, but rather the rate of development responded to increased temperature after the diapause period. Our results are comparable to those for *P. camtschaticus* and indicate that the presence or absence and timing of diapause periods late in embryonic development for multiparous *C. opilio* from the EBS may be influenced by the previous thermal history of the clutch during early development.

Diapause periods may affect larval survival by changing the timing of larval release in relation to periods of primary production. Diapause periods in the high-latitude majid *Hyas araneus* from the North Sea are hypothesized to time larval release with periods of primary production, which vary seasonally at high latitudes (Petersen, 1995; Petersen and Anger, 1997). Similar patterns of embryonic diapause, hypothesized to delay larval release into periods of primary production, occurred at warmer (6 to 12 °C) temperatures with red king crab, *P. camtschaticus* (Shirley *et al.,* 1990). In the EBS, larval survival and recruitment success of *C. opilio* may be higher in years with a strong ice-edge-associated bloom early in spring (Somerton, 1982). Periods of diapause observed in our study at 6, 3, and 1 °C, delayed larval release into March, April, and May, respectively; which could serve to postpone larval release into periods of increased primary productivity associated with ice-edge retreat. If females experienced incubation temperatures of ~3° throughout development, our results indicate that larval release would occur near the beginning of April. In warmer years with early ice-edge retreat, the spring bloom in the EBS takes place in open water in May or June (Hunt and Stabeno, 2002). A mismatch between *C. opilio* larval release and primary production, resulting in reduced larval survival, could occur if, during development, embryos experienced incubation temperatures ≥3 °C that caused larvae to be released in March or April, before the primary spring bloom in May or June.

Field observations indicate that significant hatching of *C. opilio* occurs in the EBS by mid-April (Incze *et al.,* 1984) and *C. opilio* zoeae are present in the water column into July (Somerton, 1982). Our study confirms these field observations, as the clutches of multiparous females from the EBS held at 6, 3, and 1°C hatched in March, April, and May. In the GSL, hatching was observed in April for multiparous females held at 1.85°C for the duration of embryonic development (Moriyasu and Lanteigne, 1998).

The timing of larval release in wild populations of *C. opilio* and *Chionoecetes bairdi,* a congener of *C. opilio,* may be associated with specific environmental cues (Starr *et al.,* 1994; Stevens, 2003). Hatching in *C. opilio* from the GSL was hypothesized to be linked with the presence of senescing phytoplankton following the spring bloom (Starr *et al.,* 1994). Peak larval release in female *C. bairdi* near Kodiak, Alaska, occurred during the first hours of darkness on high-amplitude spring tides in early May (Stevens, 2003). Females in our study were held in tanks with running seawater filtered by a sand filter and may have been exposed to similar tidal or phytoplankton signals; however, extended laboratory residence times in our study may have confounded potential relationships between environmental cues and hatching. Periods of larval release occurred for multiparous female *C. opilio* during both spring and neap tidal series at all incubation temperatures in our study (Fig. 3), but our study design did not include analysis of diel hatching patterns. With the exception of the 0 and −1 °C treatment, hatching was significantly delayed by decreasing incubation temperature and was consistently observed when embryos reached competency. Differences in the timing of larval release with varying incubation temperature were related to incubation-temperature-induced delay in embryos reaching competency rather than in response to environmental cues.

Hatching at −1 °C was characterized by sporadic, asynchronous patterns of larval release, lower magnitudes of daily larval release, and qualitatively low larval survival; two females with full clutches at the pre-hatching embryo stage died during monitoring with no hatching observed. Poor hatching success was likely due to low maternal fitness rather than to a lack of embryo competency. Thompson and Hawryluk (1990) found that small (<200 g) mature male and female *C. opilio* held at −1 °C were in energetic deficit. Females in our study had wet weights (mean ± SD) of 64.1 ± 17.6 g (J. Webb, unpubl. data). Poor physiological condition of females held at −1 °C may have reduced levels of active maternal care (*e.g.,* abdominal pumping) or disrupted endogenous or exogenous cues (Saigusa, 1992), decreasing hatching success in this treatment.

The duration of hatching observed for high-latitude cold-water decapods varies among taxa. The mean duration of hatching of 11 d observed for multiparous female *C. opilio* in our study was similar to the 9.4 d (Stevens, 2003) and 12 d (Swiney, NOAA, Kodiak Fisheries Research Center, Kodiak, AK; unpubl. data) found in laboratory studies for multiparous *C. bairdi* from Kodiak Island, Alaska. In contrast, the mean durations of hatching for two commercially important lithodids from the north Pacific, red king crab (*Paralithodes camtschaticus*) and blue king crab (*P. platypus*), were 32 d at an incubation temperature of 7.6 °C (Stevens and Swiney, 2007) and 29 d at 2, 3.5, and 4 °C (Stevens, 2006), respectively. For *P. platypus* (Stevens, 2006), as for *C. opilio* in our study, no significant differences were found in the duration of hatching with varying

incubation temperature. Peak periods of hatching in *C. bairdi* were associated with high-amplitude spring tidal series (Stevens, 2003), but periods of larval release for *C. opilio* in this study were not associated with maximum daily tidal range. The brief durations of hatching potentially associated with environmental cues (Starr *et al.,* 1994; Stevens, 2003) observed for *C. opilio* and *C. bairdi* contrast with the durations of nearly 1 month or more observed in high-latitude cold-water lithodids from the northern and southern hemispheres (Paul and Paul, 2001; Thatje *et al.,* 2003; Stevens, 2006). Differences in duration of hatching among *Chionoecetes* and lithodid crabs may be due to phylogenetic constraints or alternate strategies to increase larval survival in high-latitude environments (Thatje *et al.,* 2005; Stevens, 2006).

Successful extrusion of a new clutch within 2 weeks of the completion of larval release differed among temperature treatments in this study (0% at 6 °C, 86% at 3 °C, 100% at 0 °C, and 14% at −1 °C). Reduced spawning success at 6 °C may be due to differences in ovarian development rates. After seven (6 °C) to thirteen (−1 °C) months at temperatures near their limits of energetic tolerance (Foyle *et al.,* 1989; Thompson and Hawryluk, 1990), female *C. opilio* may have had fewer resources available for ovarian development, which either delayed or prevented development of the subsequent clutch. Higher extrusion rates were observed at temperatures (3° and 0 °C) similar to those likely to be experienced *in situ* by females in the EBS. These temperatures are likely within the range of energetic tolerance for female *C. opilio,* so ovarian maturation and extrusion of a new clutch occur soon after the completion of larval release.

Warming and concurrent shifts in the distribution of organisms and cold-water biomes in the Bering Sea have persisted since the mid-1970s and are likely to continue in the near future (Overland *et al.,* 2005; Grebmeier *et al.,* 2006). The distribution of female *C. opilio* contracted northward during the same period (Zheng *et al.,* 2001), and female abundance in the warmer southern EBS decreased (Orensanz *et al.,* 2004). Displacement of the distribution of female *C. opilio* from south to north may interannually increase the proportion of females on a biennial reproductive cycle if cold temperatures (<1 °C) persist in the northern EBS. In these circumstances the timing, relative to embryonic development, of female movement from colder to warmer water (Ernst *et al.,* 2005) may increase in importance as a factor affecting the proportion of females on an annual *versus* biennial reproductive cycle. Our findings indicate that switching from an annual to a biennial reproductive cycle is likely determined within the first few months post-extrusion. Improved understanding of the distribution and movement of ovigerous females in relation to bottom temperature during the first few months of embryonic development could provide fisheries managers with valuable insight into the effect of temperature on population reproductive potential.

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