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Author(s): William D. P. Duguid and Louise R. Page

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Biennial reproduction with embryonic diapause in *Lopholithodes foraminatus* (Anomura: Lithodidae) from British Columbia waters

William D. P. Duguid[a] and Louise R. Page

Department of Biology, University of Victoria, Victoria, British Columbia V8W 3N5, Canada

Abstract. A paucity of data on the reproductive cycle of crabs in the family Lithodidae inhibits both the development of management strategies and the formulation of hypotheses regarding the evolution of lithodid life histories. Life-history parameters of *Lopholithodes foraminatus* from British Columbia, Canada, were investigated based on 26 females maintained in the laboratory and supplementary observations on other living and preserved animals. The rate of embryonic development was determined by measuring the percentage area occupied by yolk in lateral views of eggs removed from brooding females throughout development. Females of *L. foraminatus* exhibited biennial reproduction including an 18-month brooding period. Females molted, mated, and extruded eggs in mid-summer, and did not release larvae until late winter or early spring of the second year after fertilization. Embryogenesis included a 12-month diapause at the gastrula stage. Females released larvae over a mean interval of 69 d, the longest reported for any lithodid. While the development stage of embryos was observed to be heterogeneous within a brood, no spatial gradient in development rate was observed, calling into question the oxygen limitation hypothesis of extended hatching. Biennial reproduction of individuals of *L. foraminatus* may be a consequence of a relatively low-quality habitat. Relative to annual reproduction, biennial reproduction halves the potential rate of increase of a population and increases vulnerability to overharvesting, suggesting that *L. foraminatus* is not a good candidate for commercial exploitation. The adaptive value of embryonic diapause is uncertain and warrants further research.

Additional key words: embryogenesis, brooding, extended hatching, king crab

Knowledge of life-history parameters is critical to the development of management strategies for commercially harvested marine organisms. Species with slow growth, late first reproduction, and a low potential rate of population increase may be more vulnerable to overfishing than those with rapid growth, early first reproduction, and a high potential rate of population increase (Adams 1980). Commercially exploited representatives of the family Lithodidae (king crabs) have a history of stock collapse. Populations of red king crabs (*Paralithodes camtschaticus* (Tilesius 1815)) (Orensanz et al. 1998), blue king crabs (*Paralithodes platypus* Brandt 1850) (Stevens 2006a), and southern king crabs (*Lithodes santolla* (Molina 1782)) (Lovrich & Vinuesa 1999) have all experienced dramatic fishing-related declines. In addition to directed fisheries, by-catch can also have devastating impacts on lithodid populations. The decimation of the female broodstock of the Bristol Bay population of *P. camtschaticus* by groundfish trawling (Dew & McConnaughey 2005) illustrates the danger of fisheries policy that is not predicated on adequate life-history data.

Lithodid crabs exhibit a number of life-history traits that distinguish them from the morphologically similar but phylogenetically distant true crabs (infraorder Brachyura). Unlike brachyurans, female lithodids are incapable of sperm storage and must molt, mate, and extrude eggs almost simultaneously. As in other non-brachyuran decapods, the male transfers spermatophores to the female, and eggs are fertilized externally (Subramoniam 1993). The inability to store sperm can result in females missing a reproductive cycle if the supply of males is disrupted during the breeding period (Sato et al. 2005). As in other decapods (with the exception of penaeid shrimp), fertilized eggs are attached to the pleopods of the female and are brooded for the duration of

[a] Author for correspondence.
E-mail: willduguid@hotmail.com

embryogenesis. Lithodids generally have lower fecundity and larger eggs than sympatric true crabs of similar size; for example, 50,000–300,000 eggs, each 1.0–1.2 mm in diameter, in *P. platypus* (Somerton & MacIntosh 1985), compared with 938,000 eggs, each 0.44 mm in diameter, in *Cancer magister* Dana 1852 (Hines 1991). Where data are available, lithodids also appear to mature later and live longer than sympatric brachyurans (Gulf of Alaska commercial species reviewed in table 2 of Orensanz et al. 1998). Relative to other decapods, some lithodid crabs exhibit a very extended duration of larval release, often 30 d or more (Paul & Paul 2001; Thatje et al. 2003; Stevens 2006b; Stevens & Swiney 2007). Brachyuran crabs generally release larvae over a much shorter period, measured in hours or days rather than weeks or months (discussed by Stevens & Swiney 2007). Some authors have suggested that extended hatching could be an adaptive strategy to ensure that at least some larvae emerge at the right time to exploit the spring plankton bloom (Stevens 2006b; Stevens & Swiney 2007). Others have proposed that it may be a consequence of differential development rates resulting from an oxygen gradient within the egg mass (Thatje et al. 2003; Thatje 2004; Reid et al. 2007; Romero et al. 2010).

In addition to its management implications, knowledge of life-history data for the members of a clade allows for the formulation and testing of hypotheses regarding the evolution of life-history strategies within that group. There is considerable variability in reproductive traits within the Lithodidae. Dramatic differences exist even between congeners, and between morphologically or ecologically similar species. Some lithodids invest in few large eggs and produce lecithotrophic larvae, while others invest in many small eggs and produce planktotrophic larvae. For example, a female golden king crab (*Lithodes aequispinus* Benedict 1895) of 120 mm carapace length (CL) produces 11,330 eggs, each 2.2 mm in diameter (Otto & Cummiskey 1985), while a similar sized female of *P. camtschaticus* produces 150,000 eggs, each 1 mm in diameter (Haynes 1968). In addition, different lithodid species may spawn annually, biennially, or asynchronously (Lovrich & Vinuesa 1993), leading to differences in predicted lifetime fecundity. Differences occur even among species falling into each of these three categories. For species with biennial reproduction, embryogenesis may occupy 1 year of the 2-year cycle as in *P. platypus* (Jensen & Armstrong 1989), or as much as 18–22 months as in the false southern king crab, *Paralomis granulosa* (Hombron and Jacquinot 1846) (Lovrich & Vinuesa 1993). Even within a species, members of different age classes may exhibit different reproductive strategies. Small females of *P. platypus* may produce broods in consecutive years, while larger females reproduce biennially (Jensen et al. 1985). The variation in reproductive traits among lithodids makes this family a candidate for research into life-history evolution.

A major obstacle to the formulation of hypotheses regarding lithodid life-history evolution is the narrow taxonomic focus of research on the reproductive biology of this family. Essentially all published work focuses on members of the three most commercially important genera: *Lithodes, Paralomis,* and *Paralithodes*. Information on the reproduction of members of the other six genera in the subfamily Lithodinae, and on members of the five genera in the subfamily Hapalogastrinae, is mostly limited to anecdotal accounts of the timing of mating or hatching (see Zaklan 2002). Information on the reproductive biology of members of species in the genus *Lopholithodes* falls into this category despite their large size, coastal habitat, and commercial and recreational harvesting.

The brown box crab *Lopholithodes foraminatus* (Stimpson 1859) occurs in coastal waters on the West Coast of North America from Alaska to California. Members of this species may be $\leq$18.5 cm in carapace width (CW) (Jensen 1995), and have been the subject of experimental commercial fisheries in California, Oregon, and British Columbia (reviewed by Zhang et al. 1999). Recreational harvesters also take some individuals of *L. foraminatus* by trapping (pers. obs.), and they are caught as by-catch in groundfish and shrimp trawl fisheries (Kato 1992; Zhang et al. 1999). Despite this utilization, very little is known about box crab reproduction. Based on data from test fisheries in California, Oregon (Goddard 1997), and British Columbia, Zhang et al. (1999) concluded that females of *L. foraminatus* probably reach functional maturity at a CL of 78–83 mm and release larvae in the spring. The authors also speculated that embryogenesis probably requires 200–300 d. An April 2001 test fishery in BC confirmed that females achieve functional maturity at ~8 cm CL (Zhang 2001).

The present study combines field and laboratory observations to determine the reproductive cycle of females of *L. foraminatus* in British Columbia. The timing of molting, egg extrusion, brooding, and larval release by captive females is related to the reproductive status of females captured in the field and preserved specimens from the Royal B.C. Museum. Data on the reproductive timing of adult females are corroborated by qualitative and quantitative analysis of eggs sampled throughout the brooding period.

Detailed data are also presented on the duration and magnitude of larval release by females in the laboratory. Analysis of these data is a necessary first step toward the development of management strategies to prevent targeted or incidental depletion of box crab populations. These data also facilitate progress toward reconstructing the evolution of life-history strategies in the Lithodidae.

Methods

Adult capture

Adult box crabs were captured in rectangular Dungeness crab traps at ~120 m depth west of Twin Islands in the Northern Strait of Georgia, British Columbia, Canada (50°01′12″N, 124°56′43″W) on March 12 and June 4, 2006, and on January 13 and March 4, 2007. Crabs were transported to the University of Victoria in insulated boxes of seawater. Additional crabs were captured by a Department of Fisheries and Oceans research vessel on March 8, 2008, north of Double Island at the entrance to Toba Inlet (~50°19′N, 124°47′W) at a depth of between 60–95 m. These crabs were held in the re-circulating seawater system at the Pacific Biological Station in Nanaimo until May 7, 2008, when they were transported to the University of Victoria. Living female crabs were assigned specimen numbers from 1 to 30 (supporting information, Table S1). The individuals assigned specimen numbers 2, 8, 13, and 9 correspond to females A, B, C, and D, respectively, in table 1 of Duguid & Page (2009) and Duguid (2010).

Female reproductive status in the field

The reproductive status of living females was scored as pre-reproductive, brooding uneyed eggs, brooding eyed eggs, or post-brooding. Post-brooding females could be distinguished from pre-reproductive females because the former had a dark "moss" of egg attachment filaments on the pleopods. Note was also made of the condition of the exoskeleton, including presence of staining and epizootic growth. CW was measured at the widest point of the carapace including spines. To facilitate comparison with other studies, mean CW was converted to CL using the formula $CL = (CW \times 0.703) + 1.3219$ (Zhang et al. 1999).

Reproductive status was also determined for 16 females from the Royal British Columbia Museum invertebrate collection (Table S2). These females were scored simply as pre-reproductive, post-brooding, or egg bearing, as it was not possible to determine the developmental state of preserved eggs. Preserved female crabs for which reproductive status was determined were assigned a number from 31 to 46. Date of capture was known for all but one of these specimens.

Female reproductive status in the laboratory

Twenty-six females of *Lopholithodes foraminatus* were maintained in the laboratory to determine the timing of key reproductive events. Crabs were held singly or in groups of up to eight individuals in 150–230 L tanks with sand substrate in the University of Victoria re-circulating seawater systems. Where possible, at least one male crab was present in each tank at all times. Crabs were fed twice a week with frozen krill (*Euphausia* sp.) supplemented occasionally with pieces of fish, cracked sea urchins (*Strongylocentrotus* spp.), and brittle stars (*Ophiopholis* sp.).

As it was not possible to maintain crabs in the same seawater system over the entire study period, there was some variation in temperature, light, and salinity regimes when individuals were switched between systems. However, all holding locations received at least some natural light from a window, and water temperatures were generally between 9°C and 10°C. During the study period the mean temperatures and salinities (±standard deviations [SD]) for the three re-circulating seawater systems were 10.3°C ± 0.4°C/29.3 ± 1.0‰; 9.7°C ± 0.5°C/30.1 ± 1.6‰; and 9.4°C ± 0.4°C/30.3 ± 2.0‰. Females 16–24 and 27–30 were maintained in the same re-circulating system under natural photoperiod illumination for their entire time in the laboratory; Fig. 1A illustrates the temperature regime experienced by these crabs. The temperature regime experienced by female 1 from June 21, 2006, to September 30, 2008, is presented in Fig. 1B.

Tanks were examined daily and molts and dead crabs were removed. In most cases, the exact date of molting was recorded; however, in 2006 and 2007 exuviae were occasionally mistaken for live crabs. When this occurred, the date of molting was taken to be the mid-point between confirmed observations. The greatest uncertainty in molting date occurred for female 2, which molted between July 31 and August 14, 2006. Uncertainty in molting date was 8 d or less for all other females.

Analysis of development

Eggs were removed from several females throughout development for qualitative observations of embryogenesis. Samples of eggs were obtained by gently prying the edge of the abdomen away from the

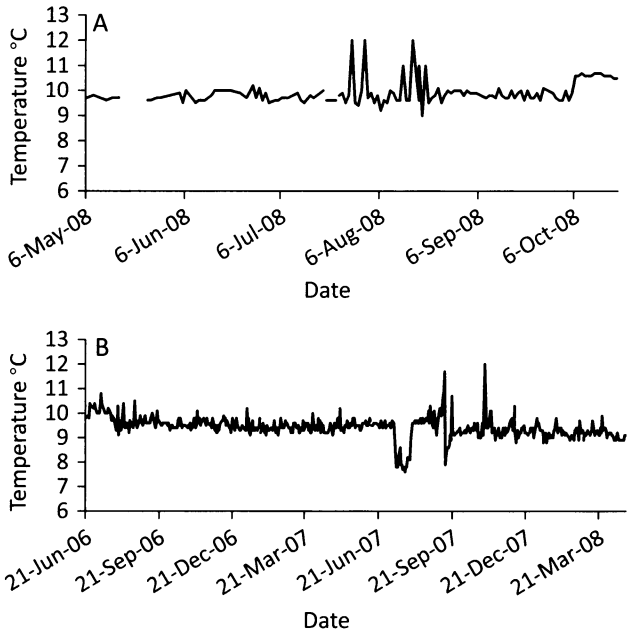


Fig. 1. Temperature regimes experienced by female *Lopholithodes foraminatus* maintained in the University of Victoria re-circulating seawater systems. **A.** Temperatures experienced by females 16–24 and 26–30. **B.** Temperatures experienced by female 1.

underside of the thorax and inserting the tips of a pair of forceps. The timing of this sampling is indicated in Fig. 2.

Quantitative analysis of development rate was primarily based on one individual (female 1) that was captured in a pre-reproductive state on March 12, 2006, and molted, extruded eggs, and mated in the lab in the last week of July 2006. A sample of at least ten eggs was removed from this female every 1–2 months beginning in March 2007. Photographs were taken of individual eggs in a drop of seawater on a glass slide at $\times 50$ magnification using a Sony PowerHAD digital video camera (Sony of Canada, Toronto, Ontario, Canada) mounted on an Olympus SZX9 dissecting microscope (Olympus Canada Inc., Markham, Ontario, Canada). Eggs were photographed in a lateral orientation under dark field illumination from a fiber optic source (Stevens 2006a).

Photographs were analyzed using Northern Eclipse (Empix Imaging, Inc., Mississauga, Ontario, Canada) or ImageJ (public domain, W. Rasband, Research Services Branch, National Institute of Mental Health, Bethesda, MD, USA) software calibrated with a slide micrometer. Egg area and yolk area were outlined manually using the polygon tool, and measured using the "area" function of the software. The "diameter" (Northern Eclipse) or "Feret's diameter" (ImageJ) functions were used to estimate the maximum egg diameter. Percentage yolk area in lateral view (PYA) was calculated as the ratio of yolk area to total egg area, and mean values ($\pm$95% confidence intervals) were calculated for samples of at least ten eggs. The green and red dashed lines in Fig. 3 illustrate the measurements of yolk area and egg area used to calculate PYA.

Decrease in PYA of embryos brooded by female 1 was related to days since extrusion and days before the mid-point of hatching (calculated as described below). Because qualitative observation did not show evidence of differentiating larval tissues until August 2007, no quantitative analysis was made of photographs taken before July 2007.

Supplementary mean PYA measurements were obtained in the same manner from three other female crabs (8, 9, and 14). As dates of egg extrusion were not known for these females, average PYA values were related to the number of days before the mid-point of hatching for each female. The timing of quantitative egg sampling for each female is indicated in Fig. 2.

For comparison, average PYA values were also determined on October 9, 2008, for samples of eggs removed from females 27 to 30. These females had been trapped brooding uneyed eggs on March 8, 2008.

Timing and magnitude of larval release

Female crabs were moved to individual flow-through containers before the anticipated start of hatching (assessed from developmental stage of embryos). Suspended zoeae released by female 2 in spring 2006 were collected from a 170-L tank with a screened outflow using either a 5 mm diameter pipette or a fine mesh net. All suspended larvae were counted daily. Zoeae on the bottom of the tank were siphoned out and discarded. In the subsequent two seasons, females releasing zoeae were maintained in partially covered 20-L plastic tubs supplied with a constant flow of seawater. Larvae passed through a 90° overflow pipe that ended in a T at the bottom of a 750-mL plastic container with a 400-μm Nitex® mesh bottom (Sefar BDH Inc., Chicoutimi, Quebec, Canada). This container was seated in a 1-L glass beaker. Healthy zoeae were collected from the 750-mL containers each morning and counted. Virtually all zoeae remaining on the bottom of the plastic tubs in the morning had morphological abnormalities and were unable to suspend themselves in the water column. These non-viable zoeae were not enumerated.

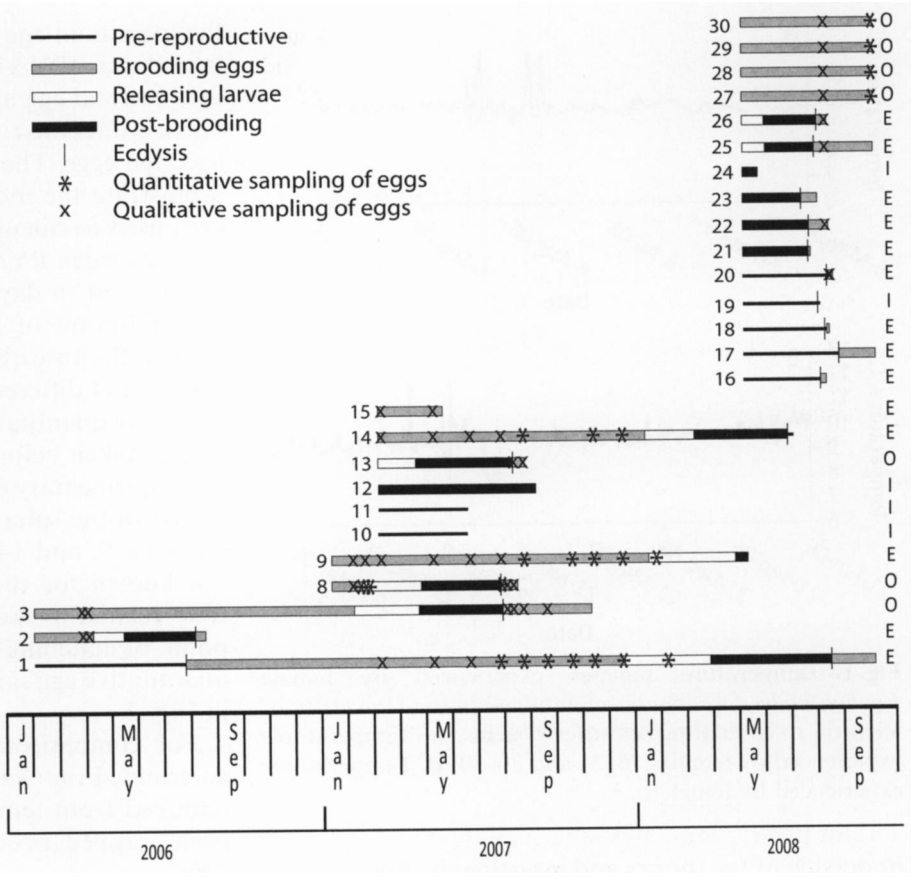


Fig. 2. Reproductive state of females of *Lopholithodes foraminatus* maintained in group tanks in the laboratory in the presence of at least one male. Each numbered horizontal line represents a single crab, beginning with capture, and terminating with death. Females 16–30 were captured north of Double Island at the entrance to Toba Inlet; all others were captured west of Twin Islands in the Northern Strait of Georgia (see "Methods"). Females were apparently releasing zoeae, molting, and mating either in even years (E), or in odd years (O). The reproductive timing of pre-reproductive and post-brooding females that did not extrude eggs in the lab was indeterminate (I). Samples of eggs were removed from females to calculate decrease in mean percentage yolk area in lateral view; the timing of this sampling is indicated by asterisks (*). The timing of egg sampling for qualitative observation is indicated by (x).

The mid-point of hatching for each female was calculated as

$$(\text{day of the year}) \times (\#\text{ of zoeae collected}) / (\text{total }\#\text{ of zoeae collected for that female})$$

In the one case where hatching began before January 1 (female 1), days in December were numbered in descending order beginning with day −1 (December 31). On the few occasions where zoeae were not collected on a daily basis the number of zoeae hatched on each day was calculated as

$$(\text{total}\#\text{ of zoeae collected}) / (\#\text{ of days since last collection})$$

The zoeae released by females 25 and 26 in 2008 were not enumerated, but the duration of hatching was recorded.

Results

Female reproductive status in the field

Reproductive status was determined for a total of 30 living females of *Lopholithodes foraminatus* collected in the field, and 16 preserved females from the Royal BC Museum collection. Twelve of the living females were pre-reproductive, five were post-brooding, and 13 were brooding eggs and/or releasing zoeae. Two of the preserved females were pre-reproductive, one was post-brooding, and 13 were brooding eggs. The mean (±SD), maximum, and minimum measured CW and calculated CL of pre-reproductive and brooding or post-brooding females are presented in Table 1. The largest pre-reproductive female had a CW of 11.1 cm (CL = 9.2 cm) while the smallest reproductive female had a CW of 8.8 cm (CL = 7.5 cm).

The 13 living brooding females fell into two distinct categories based on developmental stage of the embryos and condition of the exoskeleton. Eight were brooding embryos consisting of a bright orange ball of yolky cells lacking any differentiating larval tissues. These females had hard exoskeletons with slight epizootic growth and little staining. The other six females were brooding orange/brown eggs at an advanced stage of development. These eggs exhibited black-pigmented eyespots, red/orange chromatosomes, greatly reduced yolk volume, and transparent larval tissues undergoing differentiation. The exoskeletons of females in this second category had extensive epizootic growth, including tube building

Table 1. The mean (±standard deviation, SD), maximum, and minimum measured carapace width (CW) and calculated carapace length (CL) of pre-reproductive, brooding, and post-brooding female *Lopholithodes foraminatus*. Units are centimeters, and CL = (CW × 0.703)+1.3219. NA, not applicable.

	Measured				Calculated			
	Mean CW	±SD	Min CW	Max CW	Mean CL	±SD	Min CL	Max CL
Pre-reproductive females ($n = 11$)	NA	NA	NA	11.1	NA	NA	NA	9.2
Brooding and post-brooding females ($n = 29$)	10.7	1.4	8.8	14.4	8.9	1.0	7.5	11.4

polychaetes, hydrozoan polyps, and minute bivalves. The distal segments of the legs, undersides of the chelae, and portions of the ventral surface were also stained black and the denticulations of the chelae were eroded. A similar shell condition was observed in post-brooding females, but never in males or pre-reproductive females. Females in both categories were caught together on three occasions at Twin Islands, and were also together in the group of crabs captured near Toba Inlet.

Female reproductive status in the laboratory

Eight pre-reproductive females, five post-brooding females, eight females with uneyed eggs, and five females with eyed or hatching eggs were maintained in the laboratory to determine the timing of reproductive events. Sixteen of these females molted in the laboratory, and almost all died shortly after molting. Only female 1 molted twice, completing an entire reproductive cycle in captivity (Fig. 2). This cycle consisted of molting, mating, and extrusion of eggs in late July of 2006; brooding for just >17 months; releasing larvae for 3 months in the late winter of 2008; and finally, 5 months of post-brooding status before molting, mating, and extruding eggs for a second time in August 2008.

Females 14 and 19 were the only individuals that did not extrude eggs immediately after molting. Female 14 was the only female that molted in a tank that did not contain a male and no male was introduced to the tank until 6 d post-molt. Female 14 died 7 d after molting, and mature eggs were found in her oviducts.

Mate guarding by males was observed for ≤7 d before and 1 d after female ecdysis. In all instances of pre-copulatory mate guarding, the male held the female by the merus of her major (right) cheliped with his minor (left) cheliped. In some cases, this position was observed in post-copulatory mate guarding, while in others the male positioned himself with both chelae spread over the dorsal surface of the female. Egg extrusion and fertilization apparently occurred within 48 h of ecdysis, and in some cases within 24 h. The actual sequence of spermatophore transfer by the male and egg extrusion by the female was never observed.

All 17 instances of female ecdysis occurred between June 28 and August 28. The mean molting date for all females (±SD) was August 2 ±13 d.

Analysis of development

The color of newly extruded eggs ranged from bright yellow to bright orange. On the day of extrusion and fertilization, the yolky eggs showed no sign of cleavage. Polar bodies were visible for some eggs by the second day post-extrusion. By the 3rd or 4th day after extrusion, some embryos had begun cleavage (Fig. 3A). Approximately 10 d post-extrusion, individual cells appeared polygonal, and were generally bordered in two dimensions by five to seven other cells (Fig. 3B). Nuclei were clearly apparent as irregularities within the homogenous yolky cytoplasm. By 2–3 weeks post-extrusion, embryonic cells appeared small, irregular, and yolky; nuclei were no longer apparent (Fig. 3C).

Very few qualitative changes to embryos were observed over the subsequent 11–12 months of embryogenesis (Fig. 3D). Development of the differentiating larva became apparent in some eggs ~12–13 months after fertilization, as a small transparent indentation into the yolk mass (Fig. 3E). By 14 months post-fertilization, some differentiating larvae had clearly developed optic lobes and appendages. At this stage, transparent larval tissues occupied as much as 20% of the egg area when viewed laterally; the balance consisted of opaque yolk (Fig. 3F). Black eye pigmentation and red chromatosomes became evident in some eggs by 15 months post-fertilization; and as eye and chromatosome pigmentation increased the color of the remaining yolk became lighter (Fig. 3G–I). By 16 months post-fertilization, all embryos had at least some eye pigment (Fig. 3J). At this stage, the most

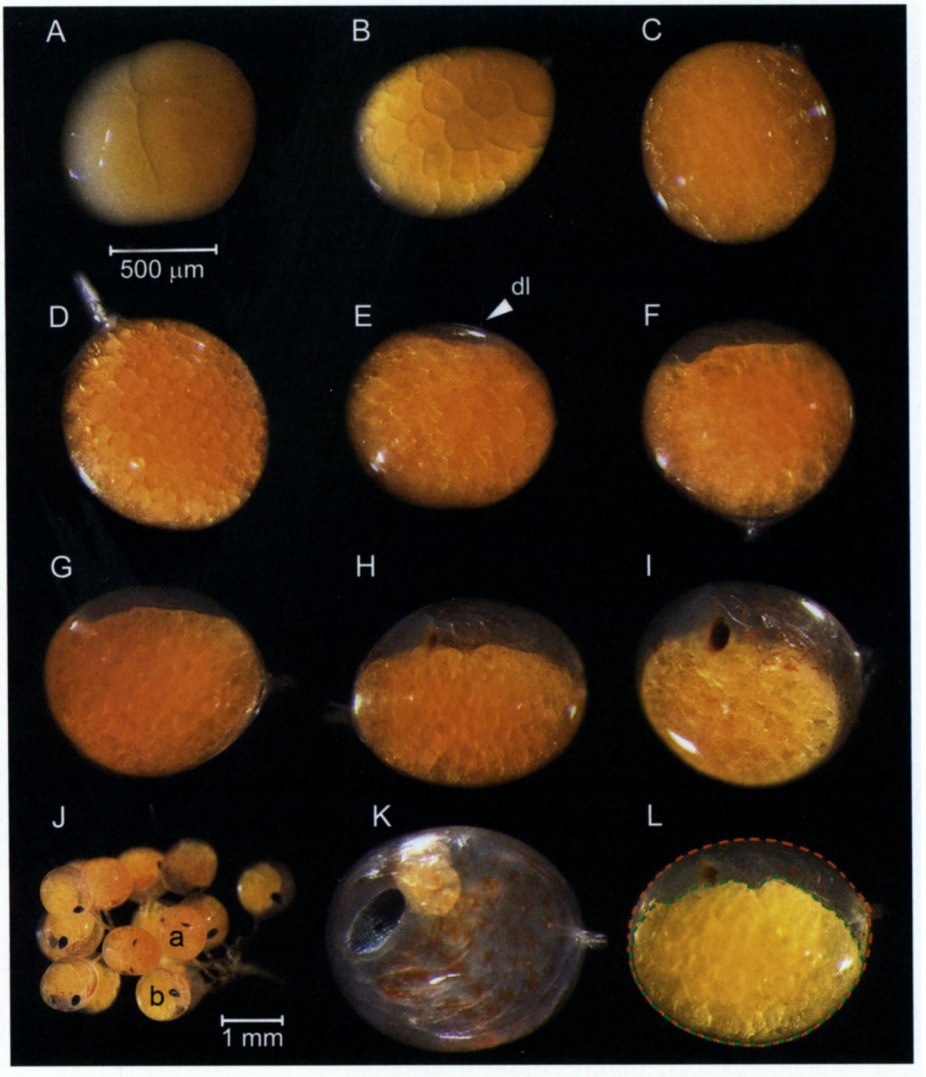


Fig. 3. Embryos removed from the broods of females of *Lopholithodes foraminatus* throughout embryogenesis. **A.** Female 20, 4 d post-extrusion (PE). **B.** Female 3, embryo removed 4 d PE, photographed 11 d PE. **C.** Female 25, 13 d PE. **D.** Female 1, ~11 months PE. **E.** Female 1, ~13 months PE. **F.** Female 1, ~14 months PE. **G–I.** Female 1, three eggs from the same sample, ~15 months PE. **J.** Female 1, clump of embryos containing (a) less developed and (b) more developed eggs ~16 months PE. **K.** Female 1, ~18 months PE, 1 d after the mid-point of hatching. **L.** Female 27, October 9, 2008. The red line indicates the "egg area" of this embryo, and the green line indicates "yolk area." These measurements were used to calculate percentage yolk area in lateral view (see "Methods"). The scale for A applies to all images except for J. dl, differentiating larva.

advanced differentiating larvae occupied almost half of the egg area in lateral view. Over the subsequent 2 months, the size of the pigmented portion of the eye and degree of chromatosome pigmentation continued to increase while yolk volume decreased; by the mid-point of hatching most eggs had little yolk remaining (Fig. 3K).

Eggs in close proximity to each other within the egg mass were observed to be at different developmental stages during the entire period of rapid development from 13–18 months post-fertilization. This heterogeneity in developmental stage is illustrated in Fig. 3G–I by the difference between three eggs removed from female 1 in October of 2007, 15 months post-fertilization. At this time, some differentiating larvae were completely transparent with small optic lobes (Fig. 3G), while others had pigmented eyes, red chromatosomes, and well-developed appendages (Fig. 3I). In clumps of eggs at 16 months post-extrusion, embryos with barely evident eye pigmentation (Fig. 3J, a) were directly adjacent to embryos at a much more advanced stage of development (Fig. 3J, b).

Percentage lateral yolk area remained between 95% and 100% until ~13 months post-fertilization (5 months before the mid-point of hatching). Yolk area was not 100% during this period due to a small separation between the embryo and egg membrane. The size of this separation varied among eggs and among females. A rapid decrease in mean PYA began ~5 months before the mid-point of hatching (Fig. 4). Mean PYA decreased steadily to ~50% by 50 d before the mid-point of hatching, and to just >25% at the mid-point of hatching.

On October 9, 2008, some of the eggs removed from females 28–30 were beginning to show develop-

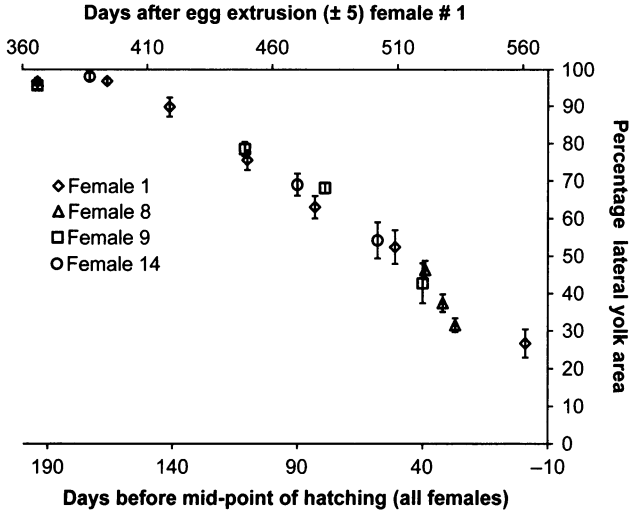


Fig. 4. Decrease in mean percentage yolk area in lateral view (PYA) of subsamples of at least ten eggs (maximum 58, mean 20) removed from the pleopods of females of *Lopholithodes foraminatus* during the final 200 d of embryogenesis. The dates of egg extrusion and the mid-point of hatching are known for female 1, therefore data for this female are plotted against both the top and bottom *x*-axes. As the dates of egg extrusion are not known for females 8, 9, and 14, these data are plotted against the bottom *x*-axis only (days before the mid-point of hatching). Error bars indicate ±95% confidence intervals. The time of year of sampling is indicated in Fig. 2.

ment of differentiating larval structures, and in a few cases optic lobes were evident. The eggs removed from female 27 were at a more advanced stage of development; most exhibited eye and chromatosome pigmentation (Fig. 3L). They were at a similar stage to those removed from female 1 on October 19, 2007 (Fig. 3G–I). The mean PYA (±95% confidence intervals) of the samples of eggs removed from females 27 to 30 were 74±3%, 94±2%, 94±2%, and 91±2%, respectively. Based on the PYA observed at the same time of year for females 1, 9, and 13, it is likely that females 27–30 would have released larvae in the late winter or early spring of 2009.

Egg size stayed relatively constant for the majority of embryogenesis before increasing during the last 3 months before hatching. Two days post-fertilization, the area (±SD) and maximum diameter (±SD) of the eggs of female 8 were 0.75 (±0.02) mm^2 and 1.07 (±0.03) mm, respectively. At 477 d post-extrusion, the eggs of female 1 had an area of 0.81 (±0.03) mm^2 and maximum diameter of 1.06 (±0.03) mm; by the mid-point of hatching this had increased to an area of 0.97 (±0.05) mm^2 and maximum diameter of 1.17 (±0.04) mm.

Timing and magnitude of larval release

Daily release of zoeae by five females is shown in Fig. 5. In all cases, larval hatching was very protracted, with a relatively small number of larvae released each day. Duration of hatching for these females ranged from 38–106 d with a mean of 69±25 d. Females 25 and 26 were releasing zoeae when they were obtained from the Pacific Biological Station on May 7, 2008. They continued to release a few zoeae daily until approximately June 2.

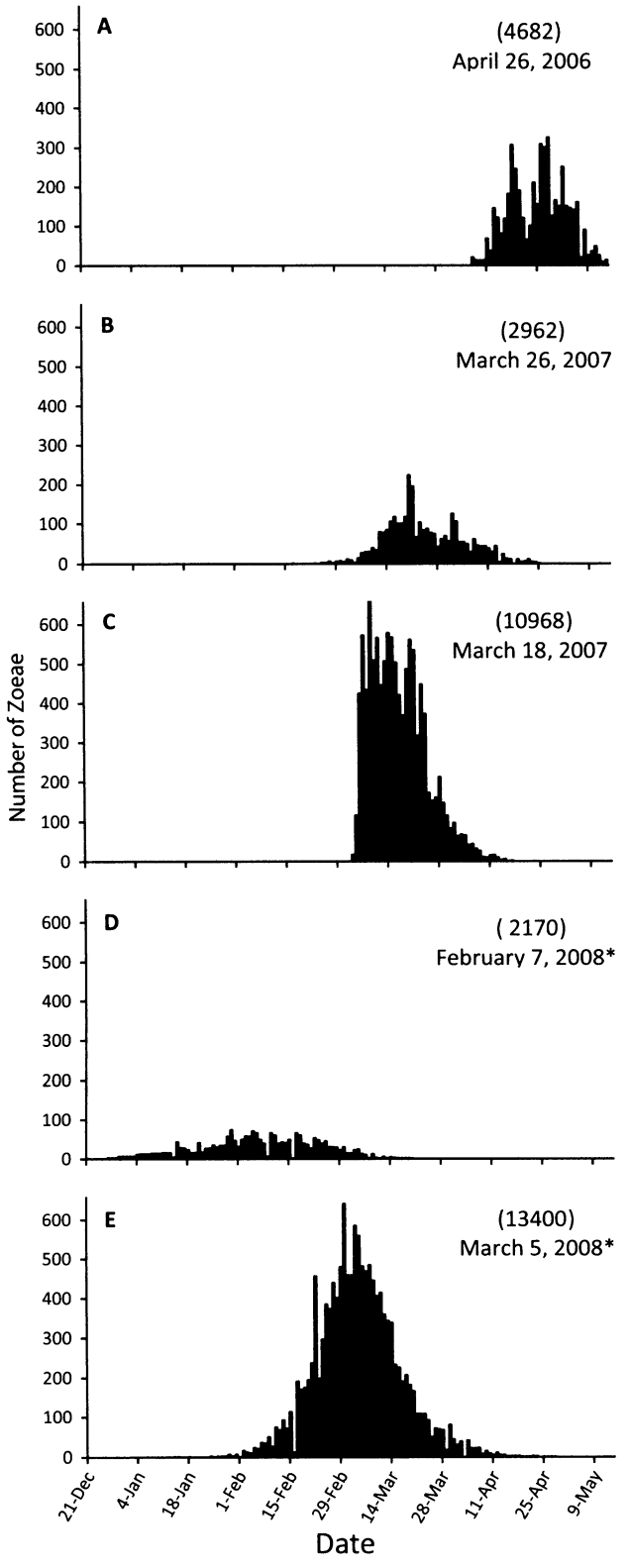
Discussion

Biennial reproductive cycles

The field and laboratory observations reported here suggest that brown box crabs in British Columbia waters have a biennial reproductive cycle. Females molt, extrude eggs, and mate in mid- to late-summer, brood eggs for ~18 months, and release larvae in the late winter or spring of the second year after mating. During any one summer, some mature females will mate, whereas the remainder will still be brooding immature eggs resulting from mating during the previous summer. This interpretation is consistent with the observation that box crabs collected on four separate occasions during the spring included brooding females with eggs in either an early or late stage of development. Although this observation could be evidence for asynchronous mating, the almost complete lack of post-brooding females outside of the late spring to mid-summer period makes this unlikely. The single exception, female 39, which was post-brooding when collected in the fall (specimen 985-28-5 from the Royal B.C. Museum), could have been due to premature brood loss, as observed in the present study for females 3 and 14.

The strongest support for summer mating and a biennial reproductive cycle was provided by the timing of reproductive events for females of *Lopholithodes foraminatus* maintained in the laboratory. While only female 1 underwent a complete reproductive cycle, the status of all other females maintained in captivity corresponded with expectations based on a biennial pattern. All 17 female molting events occurred during a 2-month window in mid-summer (Fig. 2). This was the case regardless of whether females had been caught the same year (females 1, 2, 8, 13, 16–23, and 25–26) or in a previous year (females 1, 3, and 14). All individuals, with the exception of females 14 and 19, extruded eggs after molting. Female 19 was only 7.4 cm in CL after molting and was probably not functionally mature. Female 14 had

mature oocytes in her oviducts and presumably would have extruded eggs if a male had been present in her tank at the time of molting.



The three females caught in the winter and early spring with uneyed eggs and held in the lab until hatching (females 3, 9, and 14) did not release larvae until the following late winter or early spring. Similarly, eggs of females 27–30, which were in the uneyed stage when the females were caught in March of 2008, commenced rapid embryonic development in the fall of 2008. These females would almost certainly have released larvae in the late winter and spring of 2009. Given the timing of female ecdysis in the laboratory it seems very likely that all females captured with uneyed eggs had molted, extruded eggs, and mated the previous summer.

Interpretations of life-history parameters from captive animals may be subject to error due to unnatural conditions experienced in the laboratory (Reid et al. 2007). The temperature experienced by brooded embryos in this study was generally between 9.5°C–10°C, while the mean temperature in the Northern Strait of Georgia at ~120 m depth ranges from 8.5°C–9.5°C over the course of the year (Fisheries & Oceans Canada 2008). Elevated temperature during embryogenesis has been shown to lead to earlier hatching in *Paralithodes camtschaticus* (Shirley et al. 1990), *Paralithodes platypus* (Stevens et al. 2008), and the brachyuran *Chionoecetes opilio* (Fabricius 1788) (Webb et al. 2007). The mid-points of hatching for females that brooded in the laboratory for > 10 months (females 1 [February 7], 3 [March 7], 9 [March 5], and 14 [February 13]) were all earlier than those for females that released larvae within 2 months of capture (females 2 [April 26], 8 [March 26], and 13 [March 18]). It is possible that elevated incubation temperatures in the lab may have accelerated embryogenesis. However, Stevens et al. (2008) found that a difference of 3.8°C in mean temperature during brooding by females of *P. platypus* resulted in only a 23 d increase in the time required for embryogenesis (410–433 d). Also, while low temperatures early in embryogenesis may induce a diapause mediated switch from a 1- to 2-year period of incubation

Fig. 5. Number of swimming zoeae released daily by females of *Lopholithodes foraminatus*. **A.** Female 2, which released larvae in the spring of 2006. **B.** Female 8, spring of 2007. **C.** Female 13, spring of 2007. **D.** Female 1, spring of 2008. **E.** Female 9, spring of 2008. The total number of larvae released by each female is indicated in parentheses; dates indicate the mid-point of hatching. The asterisks (*) indicate that dates on the *x*-axis do not account for 2008 being a leap year; therefore, daily larval release numbers for females 1 and 9 after February 28 are reported 1 d later than they occurred (e.g., data for February 29, 2008, are reported as occurring on March 1, 2008).

in *C. opilio* (Moriyasu & Lanteigne 1998), after 2–3 months post-extrusion, changes in temperature can no longer induce this switch (Webb et al. 2007). Given that similar timing of reproductive events was observed for females of *L. foraminatus* held in the lab for both long and short periods, it seems unlikely that the slightly elevated temperatures experienced during brooding were sufficient to lead to an incorrect interpretation of the reproductive cycle.

In the 2001 British Columbia test fishery, both new shell and old shell females of *L. foraminatus* were encountered bearing apparently new (yellowish) broods, which poses a problem for the biennial reproduction hypothesis. This observation led to the interpretation that mating might be possible for both hard- and soft-shelled females (Zhang 2001), which would make it unique among lithodid crabs. We suggest that this anomalous observation derives from two factors: (1) the fact that Zhang (2001) was unaware of the prolonged diapause that occurs during embryogenesis of *L. foraminatus,* and (2) Zhang (2001) grouped together "old shell" and "real old shell [sic]" crabs into a single "old shell" category. It is therefore probable that some of the females placed in the "old shell category" had been brooding for a sufficiently long period to acquire some encrusting organisms on the exoskeleton, but their diapause-arrested embryos still had plentiful, yellow-colored yolk.

Based on the smallest reproductive and largest pre-reproductive females observed in the present study (Table 1), mating likely occurs for the first time at between 7.5–9.2 cm CL. This is similar to previous estimates of size at functional maturity for females of *L. foraminatus* of ~8 cm CL (Zhang et al. 1999; Zhang 2001).

Embryonic development

The timing of early egg cleavages observed in this study was similar to that observed for embryos of *P. platypus* (Stevens 2006a) and *P. camtschaticus* (Nakanishi 1987). By 3 weeks post-fertilization, embryos of *L. foraminatus* had reached a stage characterized by small irregular-shaped yolky cells. This stage was similar to Stage 2 (blastula–gastrula) of *P. platypus* (Stevens 2006b), Embryonic Stage II of *Paralomis granulosa* (although without a whitish mass of cells on the yolk surface; Lovrich & Vinuesa 1993), and Stages 3/4 (cleavage and blastula/gastrula) of the brachyuran *C. opilio* (Moriyasu & Lanteigne 1998).

Embryos did not begin to show yolk reduction and development of transparent, differentiating larval structures until ~12–13 months post-fertilization (female 1) or 5–6 months before the mid-point of hatching (Fig. 2). The stage at which an indentation in the yolk first became apparent was similar to Stage 4 (pre-nauplius) of embryos of *P. platypus* (Stevens 2006b) and Stage 6 (pre-nauplius) of embryos of *C. opilio* (Moriyasu & Lanteigne 1998). When diapause early in embryogenesis has been described for other decapod species, it occurs during the gastrula stage (Wear 1974; Lovrich & Vinuesa 1993; Petersen & Anger 1997; Moriyasu & Lanteigne 1998; Swiney 2008). Similarly, our observations suggest that embryos of *L. foraminatus* experience a diapause at the gastrula stage, which lasts ~12 months. According to this interpretation, females 3, 9, 14, 15, and 27–30 were obtained from the field while their broods were in this period of diapause.

Explaining reproductive timing

It is difficult to understand what adaptive significance biennial reproduction and extended diapause could have in the life history of *L. foraminatus*. The lithodid *P. camtschaticus,* which also produces planktotrophic zoeae, has an annual reproductive cycle and completes embryogenesis within a single year at 7.2°C (Stevens & Swiney 2007). Even some lithodid species with large eggs and lecithotrophic larvae complete embryogenesis within a year, e.g., *Lithodes santolla* (Lovrich & Vinuesa 1999) and *Lithodes aequispinus* (Paul & Paul 2001). Females of *P. platypus* have a biennial reproductive cycle (Sasakawa 1975; Somerton & MacIntosh 1985; Jensen & Armstrong 1989) but still complete embryogenesis in less time than *L. foraminatus,* despite brooding at a lower temperature (395 d at 5.2°C, Stevens 2006b; 410 d at 6.1°C, Stevens et al. 2008). These results suggest that there is no unusual biochemical or physiological constraint on the rate of embryonic development in lithodid crabs. Comparison between *L. foraminatus* and other lithodids regarding reproductive cycles and natural history characteristics suggests several possibilities, as discussed below.

Synchronized annual larval release can be explained for relatively shallow water species with either planktotrophic or lecithotrophic larvae as it facilitates larval access to phytoplankton (Shirley & Shirley 1989; Shirley et al. 1990; Stevens & Swiney 2007) and juvenile access to seasonal benthic production (Reid et al. 2007), respectively. By contrast, relatively deep water representatives of the genera *Lithodes* and *Paralomis* release larvae throughout the year, presumably because seasonal phytoplankton is not necessary for the non-feeding larvae or the juveniles of these species (Somerton 1981; Sloan 1985; Paul & Paul 2001; Reid et al. 2007).

Explaining synchronous mating and biennial reproduction of *P. platypus* has been more problematic, given that a sympatric congener (*P. camtschaticus*) exhibits annual reproduction. Somerton & MacIntosh (1985) suggested that biennial reproduction in *P. platypus,* a species in which adults are large in body size, represents a "low-frequency reproduction (LFR)" strategy as described by Bull & Shine (1979). Greater energy investment per brood, larger larvae, and a longer reproductive life associated with less frequent molting compensates for reduced frequency of reproduction. Jensen & Armstrong (1989) disagreed with the hypothesis of an adaptive LFR strategy and proposed that biennial reproduction in *P. platypus* results from the inability of large females to acquire adequate energy to produce a brood within a single year. They suggested that females of *P. platypus* may occupy poorer quality habitat or colder water than females of *P. camtschaticus* within the same range. They identified inaccuracies in the brood investment calculations of Somerton & MacIntosh (1985), and they pointed out that small females of *P. platypus* can reproduce annually.

The biennial reproductive cycle of *P. granulosa* (Lovrich & Vinuesa 1993) has also proved difficult to interpret. Females of a sympatric species (*L. santolla*) not only have annual molting and reproduction, but also higher fecundity. Lovrich & Vinuesa (1999) suggested that biennial reproduction in *P. granulosa* could be due to occupation of relatively poor-quality habitat.

It is not possible to attribute biennial reproduction of females of *L. foraminatus* in Southern British Columbia to a harsh environment characterized by extremely low temperatures and a short growing season, as suggested for *P. platypus* by Jensen & Armstrong (1989). However, it is possible that the relatively deep water, soft substrate habitat occupied by *L. foraminatus* (Jensen 1995; Zhang 2001) has limited food resources relative to shallower, hard substrate habitats. The Pacific Northwest has a high diversity of large predatory crabs such as *Cancer magister, Cancer productus* Randall 1840 and *Cancer antennarius* Stimpson 1856. It has been suggested that these cancrids exclude introduced green crabs (*Carcinus maenas* (Linnaeus 1758)) from habitat they might otherwise occupy (Jensen et al. 2007). Similarly, these predatory cancrids presumably influence the niche space occupied by native decapods. It is possible that members of *L. foraminatus* occupy an ecological niche of lower productivity, lower competition, and reduced predation risk at the expense of high reproductive output.

Puget Sound king crabs (*Lopholithodes mandtii* (Brandt 1849)) are found on hard substrates in generally shallower and higher current areas than members of *L. foraminatus,* and also grow considerably larger ($\leq$30 cm CW). The complete reproductive cycle of *L. mandtii* is not known, but adults of this species have been observed to breed in shallow water in the late winter or early spring (Jensen 1995). This mating season is similar to that of members of *P. camtschaticus,* which exhibit annual reproduction (Stevens & Swiney 2007). If females of *L. mandtii* are found to have annual reproduction, it would be the third known instance where sympatric pairs of lithodid species with the same type of larval development exhibit divergent reproductive periodicity (and the second instance where both members of the pair are congeners). This illustrates how, as our knowledge of lithodid reproduction becomes broader, we will be better placed to address questions about the life-history adaptations of this group.

An outstanding question regarding the reproductive cycle of *L. foraminatus* is why embryos should undergo a 12-month diapause early in development. Embryonic diapause in decapods may serve to synchronize hatching with seasonal food availability (Wear 1974; Petersen & Anger 1997; Stevens et al. 2008; Swiney 2008). For example, Stevens et al. (2008) found that embryos of *P. platypus* experienced a period of diapause late in embryogenesis when brooded at 4°C and 6°C, but not at 2°C. The authors suggested that this diapause may allow *P. platypus* to compensate for elevated water temperature that could otherwise lead to inappropriate time of hatching. An opposite effect was observed in the development of the brachyuran *C. opilio* in the cold water of the Gulf of St. Laurence (Moriyasu & Lanteigne 1998). Two periods of diapause (during the gastrula stage and eye pigment formation stage) apparently prolonged embryogenesis by 9–10 months, leading to a biennial reproductive cycle. In warmer water, embryos of *C. opilio* hatch within 1 year and exhibit only brief periods of diapause late in development, which likely synchronize hatching with the spring phytoplankton bloom (Webb et al. 2007).

Diapause during embryogenesis of *L. foraminatus* presumably has a different purpose than in the above examples. As discussed earlier, it seems unlikely that embryogenesis cannot be completed within 1 year due to biochemical or physiological constraints. If the biennial reproductive cycle is caused by limiting energy resources, as Jensen & Armstrong (1989) proposed for *P. platypus,* then it is surprising that the life history of *L. foraminatus* does not follow the same pattern as that described for *P. platypus,* where mat-

ing, brooding, and larval release are completed within a single year, but occur only in alternate years (Jensen & Armstrong 1989; Stevens 2006a; Stevens et al. 2008), Brooding eggs has been shown to entail energetic expenses for female crabs (Baeza & Fernández 2002; Fernández & Brante 2003). In addition, embryos that are brooded for an extended period of time may use up more of their own metabolic reserves than those brooded for a shorter period (Petersen & Anger 1997). A long brooding period also increases the exposure time of embryos to pathogens and egg parasites.

A period of embryonic diapause similar to that observed in the present study occurs during biennial reproduction of females of *P. granulosa* off the southern tip of South America (Lovrich & Vinuesa 1993, 1999). We are not aware of any hypotheses that have been advanced to explain this phenomenon. Hopefully the acquisition of more life-history data will shed light on the adaptive significance of this enigmatic life-history character.

Extended hatching

Hatching occurs over a very extended period for all lithodid species investigated: 34 d (mean) for *L. aequispinus* (Paul & Paul 2001); 13–61 d for *P. granulosa* (Thatje et al. 2003); 35–41 d for *L. santolla* (Thatje et al. 2003); 29 d (mean) (Stevens 2006b) or 46.7 d (mean) (Stevens et al. 2008) for *P. platypus;* and 31.6 d (mean) for *P. camtschaticus* (Stevens & Swiney 2007). The hatching duration reported here for *L. foraminatus* (mean 69 d), is to our knowledge the longest reported for any decapod, although other authors indicate that they may have underestimated hatching duration (Thatje et al. 2003; Reid et al. 2007).

Two hypotheses have been advanced to explain extended hatching in lithodid crabs. The first states that oxygen gradients within the egg mass might result in differential rates of embryonic development, resulting in extended hatching. This hypothesis was proposed for southern ocean lithodids with lecithotrophic development, for which larval release need not be synchronous with plankton availability (Thatje et al. 2003; Thatje 2004; Reid et al. 2007). Egg mass oxygen gradients have indeed been reported for other marine invertebrates, including gastropods (e.g., Cohen & Strathmann 1996) and brachyuran crabs (Naylor et al. 1999; Baeza & Fernández 2002). Fernández et al. (2003) found a correlation between low oxygen partial pressure in the center of egg masses from two brachyuran species and slowed development rate (indicated by percentage yolk volume). More recently, Romero et al. (2010) demonstrated a gradient in oxygen availability and hatch timing in the egg clutches of *P. platypus,* a northern hemisphere lithodid species with planktotrophic larvae. However, measured metabolic rates for embryos within different areas of the brooded egg mass showed no differences.

The oxygen gradient hypothesis of extended hatching was called into question by Stevens (2006b), who pointed out that extended hatching is not limited to lithodid crabs with lecithotrophic development, and that lithodids, like brachyurans, are capable of ventilating their egg mass through abdominal flapping. Stevens suggested the alternative hypothesis that extended hatching in lithodids could be a "diversified bet-hedging" strategy (Slatkin 1974) to ensure that at least some larvae encounter optimum conditions (Stevens & Swiney 2007; Stevens et al. 2008).

Our observations are inconsistent with an oxygen gradient being the sole explanation for extended hatching in broods of *L. foraminatus*. Females 3 and 14 experienced near total loss of their broods by 6 and 3 months before the mid-point of hatching, respectively. If extended hatching was a consequence of an oxygen gradient in the egg mass alone, then reduction of that gradient in these two females should have resulted in abbreviated duration of hatching. Although the period during which most of the brood was absent was relatively short, it is this latter part of the brooding period that is characterized by the highest embryonic oxygen consumption (Naylor et al. 1999; Baeza & Fernández 2002). In fact the durations of hatching for females 3 and 14 were 75 and 57 d, respectively, well within the range of durations for females with full broods. Within the broods of *L. foraminatus,* the occurrence in close proximity of embryos (eggs) at different stages of development (see Fig. 3J) is also inconsistent with the oxygen gradient hypothesis of extended hatching. If a gradient in oxygen availability results in differential development rates, embryos in close proximity would be expected to be at a similar developmental stage.

Romero et al. (2010) suggest that oxygen gradients in lithodid egg masses are responsible for extended hatching. However the results of the present study strongly suggest that in egg masses of *L. foraminatus,* intrinsic factors also play a part. If the variability in development rate of lithodid embryos within a brood is indeed partially independent of oxygen consumption, then the mechanism underlying this variability warrants further investigation.

Management implications

Biennial reproduction of adults of *L. foraminatus* off the coast of British Columbia has implications for

fisheries management. Recent work on skipped spawning cycles in iteroparous marine fish has highlighted the importance of reproductive periodicity to fisheries management models (e.g., Engelhard & Heino 2005). The presence of non-reproductive individuals in a population can lead to an overestimation of spawning stock biomass (Rideout et al. 2005; Jørgensen et al. 2006). If not recognized, biennial reproduction could have the same effect, as estimates of the potential rate of increase of the population based on annual reproduction would be double the actual values.

Marine species exhibiting late maturation, long life, and slow potential rate of increase are particularly vulnerable to overfishing (Adams 1980; Jennings et al. 1998, 1999). These life-history characters may be linked to occupation of low-productivity habitats, as is the case for deep sea fishes (Koslow et al. 2000). While the inshore waters of the Pacific Northwest are not a low-productivity system, it is possible that biennial reproduction of females of *L. foraminatus* is a response to occupation of a lower productivity niche within this system. Given the diversity of reproductive traits among lithodid crabs, and their history of fishing related stock collapse, caution is clearly warranted in the development of new lithodid fisheries.

While recreational harvest of *L. foraminatus* within current limits (one crab per person per day, Fisheries & Oceans Canada 2011) seems unlikely to threaten stocks, development of a commercial fishery in British Columbia would not be advisable. Other jurisdictions in the Pacific Northwest should also be wary of permitting commercial harvest. Despite the fact that most commercial crab fisheries are male-only, the reproductive potential of a stock can still be impacted due to inability of females to find mates, and inability of males to produce adequate sperm for multiple matings (Sato et al. 2007). This is particularly true for lithodid crabs, which have only a narrow window after female molting during which eggs can be fertilized (Powell et al. 1974; Sato et al. 2005). A more immediate threat to stocks of *L. foraminatus* may be by-catch mortality in groundfish and shrimp trawl fisheries. Such fisheries may affect both males and females. Direct by-catch mortality caused by trawl gear (e.g., Broadhurst et al. 2006) and ecosystem level effects of trawling on biodiversity (e.g., Thrush & Dayton 2002) are subjects of global concern. *Lopholithodes foraminatus* is just one of many species threatened by trawl fisheries in the Pacific Northwest.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Table S1. Origins, sizes, reproductive status upon collection, and types of data collected for living females of *Lopholithodes foraminatus* examined in this study.

Table S2. Origins, sizes, and reproductive status of females of *Lopholithodes foraminatus* in the Royal British Columbia Museum (RBCM) invertebrate collection. Data were not recorded for individuals smaller than 3.5 cm or for individuals in which reproductive status could not be determined (dry specimens).

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