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Reproductive aspects of two bythograeid crab species from hydrothermal vents in the Pacific-Antarctic Ridge

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ABSTRACT: *Bythograea laubieri*, *B. vrijenhoeki* and alvinellid polychaetes dominate the vent fauna of the Pacific-Antarctic Ridge. We studied gonadal development in females of both crabs. They have ovary microstructures characteristic of brachyuran decapods. The ovaries are paired organs overlying the hepatopancreas beneath the carapace. Oogonia proliferate from the germinal epithelium and develop into previtellogenic oocytes that grow to 60 µm before undergoing vitellogenesis. The observed maximum sizes of mature oocytes were 209 µm in *B. laubieri* and 138 µm in *B. vrijenhoeki*. No ovigerous females were found in the samples, which agrees with the segregation behaviour of ovigerous females away from the direct influence of the active chimney in some related species. In contrast to other species of bythograeid crabs, the oocyte size-frequency data suggest that *B. laubieri* and *B. vrijenhoeki* lack synchrony in reproduction of the population as a whole. Synchrony and seasonality in reproduction of *B. thermydron* have been linked to the formation of phytoplankton blooms in surface waters. We suggest that the biogeography of bythograeid crabs is determined by contrasting oceanographic regimes that influence the reproductive patterns observed in different species.

KEY WORDS: Bythograeid crab · Gonad development · Hydrothermal vent · Pacific-Antarctic Ridge

INTRODUCTION

Since the discovery of hydrothermal vents along the Galapagos Rift in 1977, an increasing number of vent sites and their communities have been described (Tunnicliffe et al. 1998, 2003). More than 500 new species of mega- and macrofauna have been identified (Desbruyères et al. 2006) and a wealth of literature on the physiology, ecology, evolution and biogeography of vent organisms has been published (e.g. Childress & Fisher 1992, Van Dover 2000, Van Dover et al. 2002, Little & Vrijenhoek 2003). Although the study of life histories is widely recognized as essential to understanding the ecology, population dynamics, gene flow and resulting biogeography of vent organisms, research to date has been patchy, and only a small number of species have been the subject of primarily reproductive investigations (Tyler & Young 1999).

The family Bythograeidae, first described by Williams (1980) to accommodate *Bythograea thermydron* from vents in the eastern Pacific, is the only family of crabs truly endemic to deep-sea hydrothermal vents (reviewed by Martin & Haney 2005). Recent discoveries along the southern East Pacific Rise (EPR) and Pacific-Antarctic Ridge (PAR) have revealed a greater diversity of the genus *Bythograea* than previously realised, and 2 new species have been described: *B. laubieri* Guinot & Segonzac, 1997 found on vent sites between 17° S and 38° S, and *B. vrijenhoeki* Guinot & Hurtado, 2003 found on the PAR from 31° to 38° S. Because *B. thermydron* is the dominant crab species on most EPR vent sites between 21° N and 18° S and on the Galapagos Rift, it has been the subject of a number of ecological and physiological studies (e.g. Mickel & Childress 1982, Bennett & Turekian 1984, Sanders & Childress 1985, 1992, Vetter et al. 1987, Van Dover et

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al. 1987). Several aspects of its reproductive biology, including fecundity (Van Dover et al. 1985), gametogenesis (Perovich et al. 2003) and larval development (Van Dover et al. 1984, Epifanio et al. 1999, Martin & Dittel 2007) have also been described.

From the data available, it is apparent that the reproductive patterns of vent-associated decapods are primarily determined by phylogenetic constraints (Van Dover et al. 1985). Thus, it is expected that other species of bythograeid crabs have reproductive patterns generally similar to those of *Bythograea thermydron*. In this paper, we describe results from a study of the reproductive biology of *B. laubieri* and *B. vrijenhoeki* from the southernmost vent area known on the complex East Pacific Rise/Pacific-Antarctic Ridge. We investigated the gonadal development in female crabs of both species with the hypothesis that gametogenesis is phylogenetically constrained, and therefore characteristic of bythograeid crab species. The implications of different reproductive patterns in species dispersal and biogeography are discussed.

MATERIALS AND METHODS

Individuals of *Bythograea laubieri* and *B. vrijenhoeki* were collected on the Sebastian's Steamer vent site (37° 47.48' S, 110° 54.85' W; 2204 m depth) on the Pacific-Antarctic Ridge between 21 March and 5 April 2005 during the PAR5 expedition aboard the RV 'Atlantis' (Fig. 1). This vent site is composed of 3 small mounds, up to 4 m high and 2 m wide that host several candlestick-shaped sulphide chimneys. The substratum consisted of glassy basalt with no sediment cover, suggesting that the lava emissions are very young. Using the deep-sea submersible 'Alvin', a baited trap was moored at the foot of an active sulphide edifice and retrieved after 30 h.

Shortly after capture, all specimens were identified to species level and sexed. A total of 238 specimens were collected: 110 specimens of *Bythograea laubieri* and 128 of *B. vrijenhoeki*. For both species, sex ratio was estimated and differences from 1:1 ratio were analysed with a χ^2 test.

Specimens were fixed in 4% formaldehyde for 96 h, with changes of fixative every 24 h, and then transferred to 70% ethanol. The carapace widths and lengths were measured to the nearest 0.05 mm with vernier calipers. The abdominal pleopods of each individual were examined, and all embryos found were counted and measured directly under a binocular dissecting microscope.

For the present study, 20 randomly chosen female specimens of each species were used. The entire gonad was dissected and processed for histology.

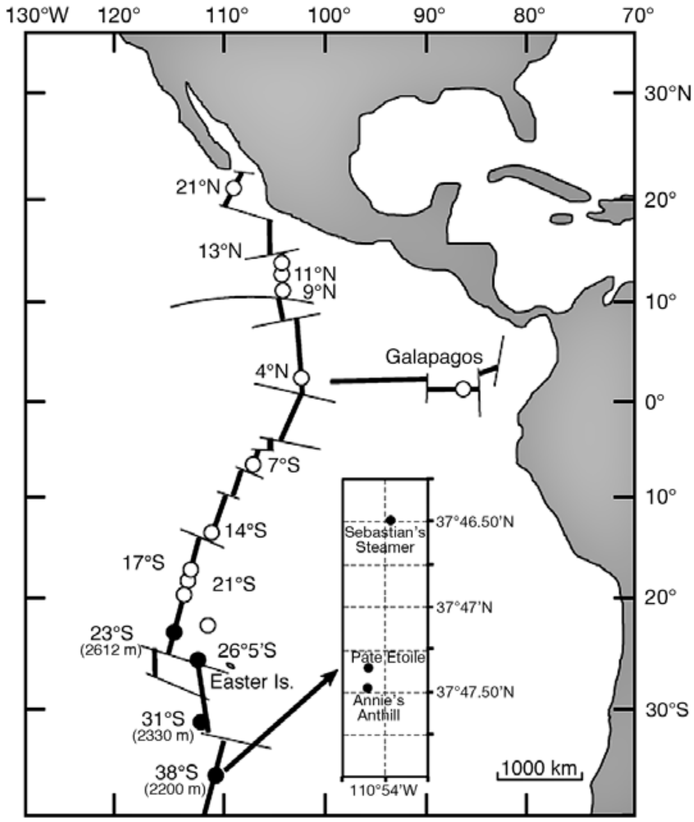

Fig. 1. East Pacific Rise and Pacific-Antarctic Ridge showing the hydrothermal vent sites, the vent sites visited during the PAR5 cruise (black dots) and the location of the sampling site (detail in rectangle) after Macpherson et al. 2005)

Sections of 5 µm were stained with Mayer's haematoxylin and eosin. All sections were examined on an Olympus BX40 compound microscope, and for each individual, the Feret diameters (diameters of hypothetical circles of area equal to the objects measured) of at least 100 oocytes that had been sectioned through the nuclei were measured using the SigmaScan Pro 4 image analysis system. Feret diameter was used to standardise variations in oocyte shape. Images of oocytes were calibrated from measurements of a stage micrometer at identical magnification. Oocyte sizes were grouped in 10 µm size classes and oocyte size-frequency diagrams were constructed for each individual.

Mean frequencies of each oocyte size class were plotted to visualize oocyte size-frequency distribution for the population of each species. Mean values for each oocyte size class were compared between 2 species using a non-parametric Mann-Whitney test with a significance level of $\alpha = 0.05$. Non-parametric analysis was used because initial inspection of the data indicated that the variables were not normally distributed (Kolmogorov-Smirnov test of normality).

RESULTS

Sex ratio

The sex ratio of *Bythograea laubieri* was significantly biased towards females, with 85 females and 25 males ($\chi^2 = 32.723$, 1 df, $p < 0.001$). In contrast, the sex ratio of *B. vrijenhoeki* did not differ significantly from unity, with 63 females and 65 males ($\chi^2 = 0.031$, 1 df, $p > 0.05$).

Ovarian structure

Histological analysis indicated that, as in *Bythograea thermydron* from the East Pacific Rise (Perovich et al. 2003), the ovarian microstructures in *B. laubieri* and *B. vrijenhoeki* were similar to that of shallow water brachyuran crabs (Johnson 1980). The ovaries consist of several layers of developing oocytes enveloped by a thin gonad wall. Longitudinal strands of oogonia proliferate from the germinal epithelium and develop into previtellogenic oocytes. Previtellogenic oocytes contained little basophilic cytoplasm. Nuclei were large in relation to cell volume, and >1 nucleolus (usually 2 to 3) were frequently observed (Fig. 2). In both species, vitellogenesis began when the oocytes measured approximately 60 µm in diameter. Vitellogenesis was identified by the presence of yolk granules appearing in the cytoplasm. Early vitellogenic oocytes (60 to 100 µm diameter) had a basophilic granular cytoplasm. Vitellogenic (mature) oocytes (>100 µm diameter) had an acidophilic cytoplasm and were completely granular in appearance. The observed maximum oocyte size was 209 µm in *B. laubieri* and 138 µm in *B. vrijenhoeki*.

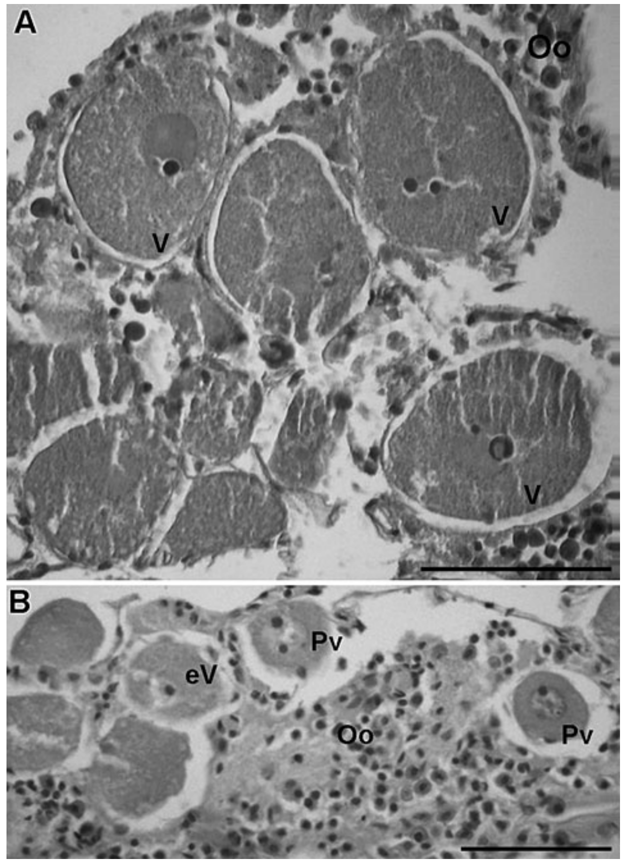

Fig. 2. *Bythograea laubieri* and *B. vrijenhoeki*. Light micrographs of histological sections through the ovary of (A) *B. laubieri* and (B) *B. vrijenhoeki*. eV: early vitellogenic; Oo: oogonia; Pv: previtellogenic; V: vitellogenic. Scale bar = 100 µm

Synchronicity of ovarian development

Of the 20 females of each species used for histological analyses, 10 of *Bythograea laubieri* and 12 of *B. vrijenhoeki* showed evidence of recent release of their broods, including unhatched embryos, empty egg capsules and attachment stalks still present on the abdominal pleopods. None of the unhatched eggs showed signs of cleavage and could therefore have been unfertilized eggs or zygotes that did not develop. In either case, their size would have been similar to embryos in an early developmental stage. Unhatched eggs were approximately spherical in shape; the greatest and smallest mean diameters (±SD) were, respectively, 0.50 ± 0.03 mm and 0.46 ± 0.04 in *B. laubieri*, and 0.52 ± 0.04 mm and 0.05 ± 0.04 mm in *B. vrijenhoeki*. No ovigerous females were found among the 148 females (85 of *B. laubieri* and 63 of *B. vrijenhoeki*) analysed.

Of the 40 females used for histological studies, we obtained good sections of the ovaries for 19 *Bythograea laubieri* and 16 *Bythograea vrijenhoeki* individuals. The oocyte size-frequency distributions of both species fit 3 patterns. The first pattern (previtellogenic) was characterized by a unimodal distribution of oogonia and previtellogenic oocytes (<60 µm) (Fig. 3A–C and Fig. 4A,B) ; the second pattern (vitellogenic) was characterized by a unimodal distribution of previtellogenic oocytes and young vitellogenic oocytes (<100 µm) (Fig. 3D–M and Fig. 4C–N); the third pattern was characterized by a bimodal distribution with a large cohort of mature oocytes (>100 µm) and a smaller cohort of previtellogenic oocytes (Fig. 3N–S and Fig. 4O–P). Table 1 shows the numbers of females of both species in each of the 3 patterns. The presence of previtellogenic, vitellogenic and mature females at a single time suggests asynchronous oogenesis.

Inter-specific variability

Bythograea laubieri has a greater mean oocyte diameter than *B. vrijenhoeki* (Fig. 5). This was supported by a Mann-Whitney test that indicated a significant difference in the mean oocyte size of the 2 species (U = 2 875 242, $p < 0.001$). A chi-square test showed that the proportions of the 3 oocyte size-frequency distribution patterns (previtellogenic, vitellogenic and mature) were not significantly different between *B. laubieri* and *B. vrijenhoeki* ($\chi^2 = 0.343$, 2df, $p > 0.05$), suggesting that differences found in mean oocyte size were not due to a more advanced stage of gonad development in the entire population of *B. laubieri*.

DISCUSSION

The populations of *Bythograea laubieri* and *B. vrijenhoeki* collected at the Sebastian's Steamer vent site showed a sex ratio biased towards females and a 1:1 sex ratio, respectively. Perovich et al. (2003) observed a

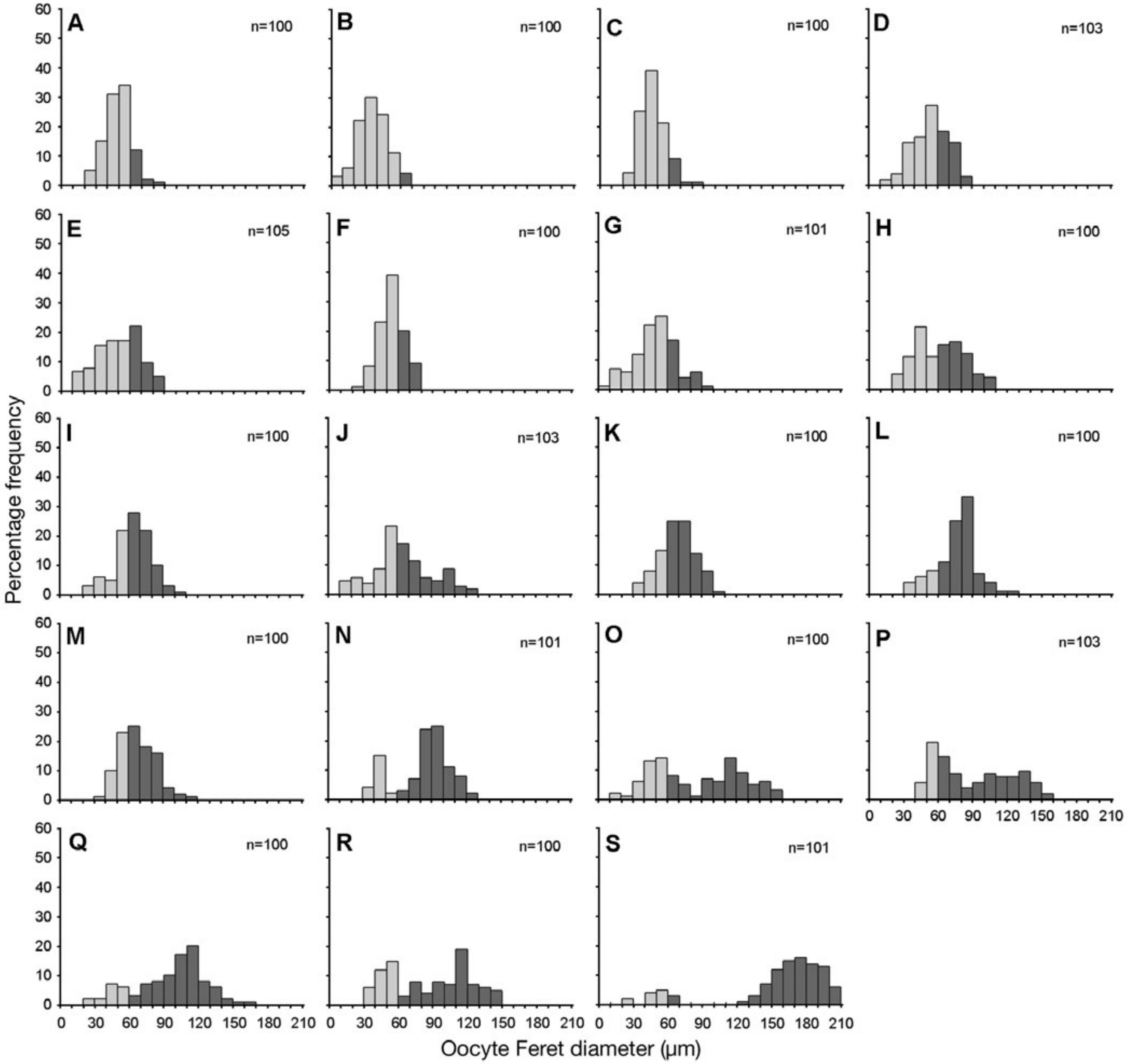

Fig. 3. *Bythograea laubieri.* Oocyte size-frequency distribution for each female. ☐: oogonia and pre-vitellogenic oocytes; ■: vitellogenic oocytes

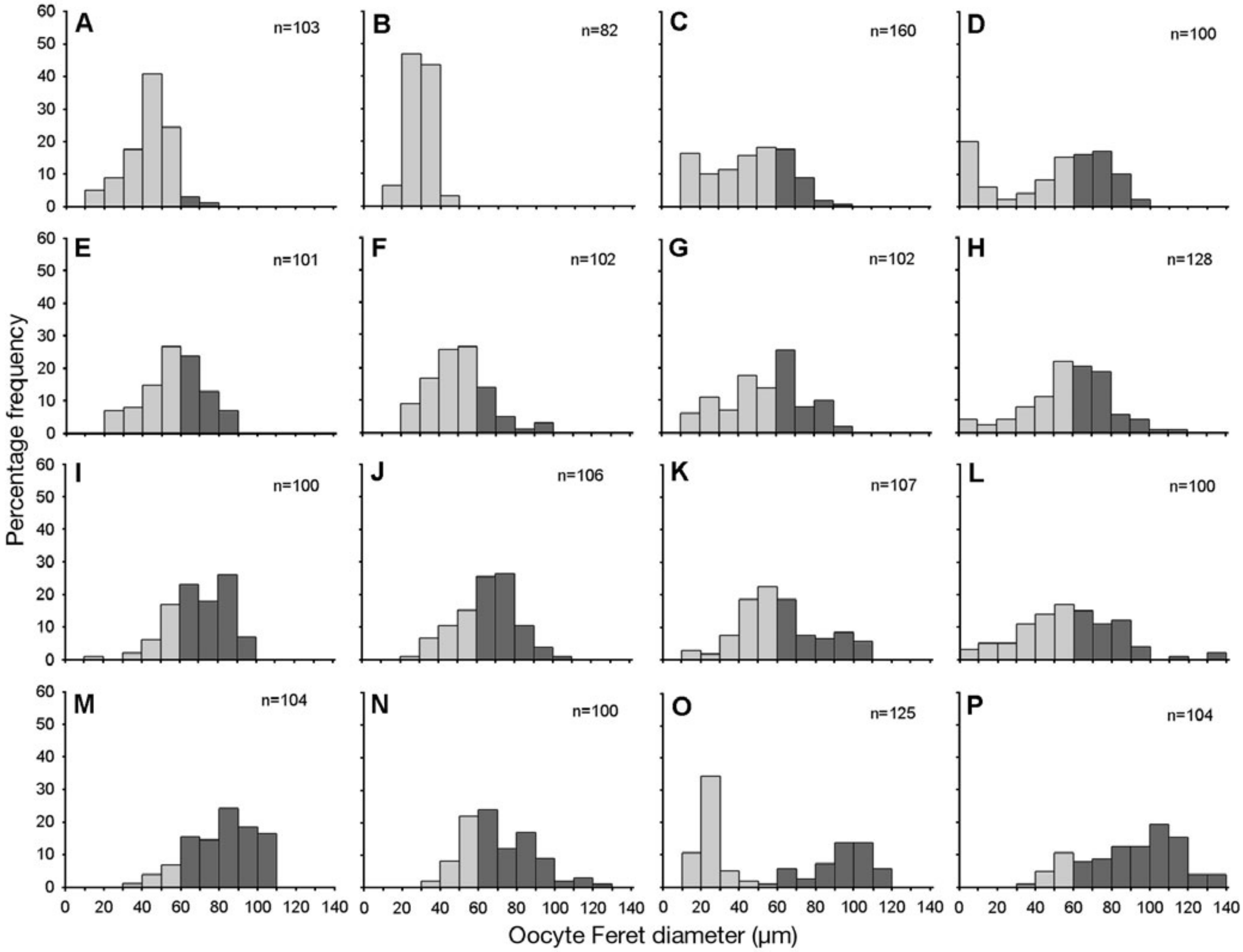

Fig. 4. *Bythograea vrijenhoeki.* Oocyte size-frequency distribution for each female. ☐: oogonia and pre-vitellogenic oocytes; ■: vitellogenic oocytes

bias towards females in populations of *B. thermydron* collected from the periphery of vent sites, and suggested that females move to the periphery during the brooding period to avoid the hydrothermal fluids rich in sulphide and heavy metals that may be toxic to the embryos and larvae. Such behaviour has also been suggested for the caridean shrimp *Rimicaris exoculata* at vents on the Mid-Atlantic Ridge (Ramirez-Llodra et al. 2000). Although this behaviour may explain the absence of ovigerous females in the samples collected for the present study, it does not explain the bias towards females found in the population of *Bythograea laubieri* since the sample was collected in an active area of the vent field. Further studies are necessary to determine the processes causing sex ratio bias in *B. laubieri*, although this may be purely stochastic.

Table 1. *Bythograea laubieri* and *B. vrijenhoeki*. Numbers of females in 3 categories of oocyte size-frequency distribution

	Previtellogenic	Vitellogenic	Mature
B. laubieri (n = 19)	3	10	6
B. vrijenhoeki (n = 16)	2	12	2

The reproductive traits of *Bythograea laubieri* and *B. vrijenhoeki* were expected to be similar to those of other members of the genus, as many reproductive and life history traits of decapod crustaceans from hydrothermal vents are thought to have strong phylogenetic constraints (Van Dover et al. 1985, Tyler & Young 1999, Perovich et al. 2003).

The general gametogenic process of the 2 species studied was similar to that reported for *Bythograea thermydron*, but vitellogenic oocyte size (>100 µm)

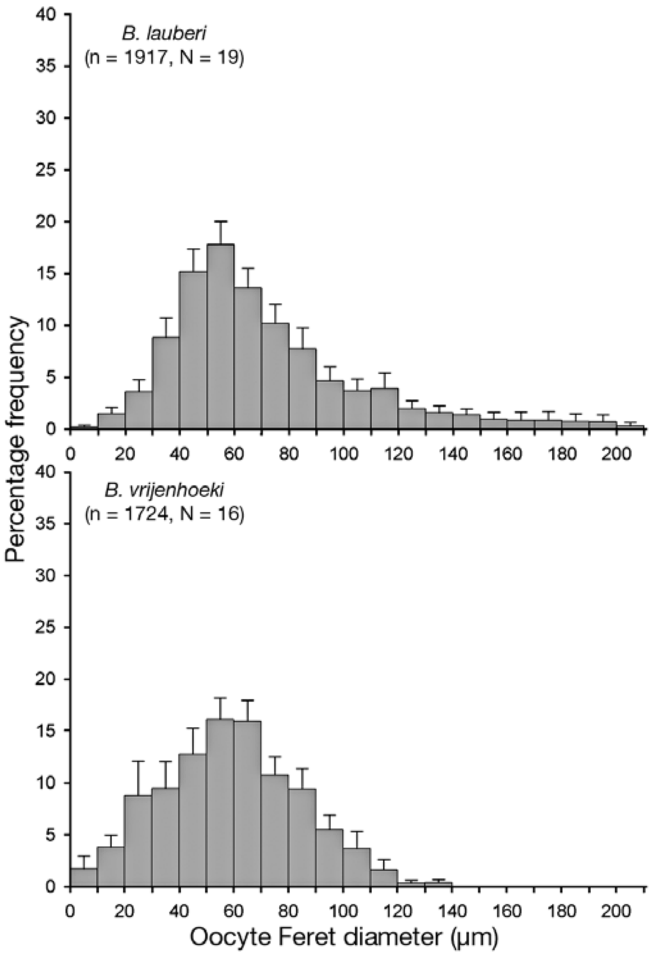

Fig. 5. *Bythograea laubieri* and *B. vrijenhoeki*. Mean size-frequencies of oocytes. Means + SE. n: number of oocytes measured; N: number of individuals examined

and oocyte size at onset of vitellogenesis (60 µm) were smaller than those reported by Perovich et al. (2003) (~500 and 150 µm, respectively). Because histological processing can cause tissue shrinkage of up to 20%, the differences in oocyte sizes could be a consequence of differing methodologies. However, even when accounting for these 20%, vitellogenic oocyte size and oocyte size at onset of vitellogenesis in *B. laubieri* and *B. vrijenhoeki* would still be significantly smaller than in *B. thermydron*. Because the 3 species have a very similar morphology and size (Desbruyères et al. 2006), morphology can also be ruled out as a contributor to interspecific differences in maximum oocyte size.

At the individual level, the duration of oogenesis depends on the mechanisms of yolk deposition and on the number of egg cohorts developing at any given time (reviewed by Eckelbarger 1994). The mechanism of vitellogenesis is conserved in some groups, but in others selection can modify the timing and speed of gametogenesis to produce life cycles that reflect conditions of the environment in which the animal lives. Orton (1920) predicted that the reproduction of deep-sea species would be continuous as a consequence of the constant temperature of their environment. Although the majority of non-vent deep-sea species have continuous asynchronous reproduction, there are examples of seasonal reproduction linked to variations in food supply at all latitudes and to depths reaching several thousand meters (reviewed by Young 2003). *In situ* primary production in chemosynthetic ecosystems in general, and in hydrothermal vents in particular, is not known to vary seasonally and is usually orders of magnitude greater than organic matter input from the photic zone. Seasonal variation in phytodetritus supply is therefore unlikely to influence the reproductive timing of species in these ecosystems directly through their energetics. However, species with planktotrophic larvae that disperse away from the chemosynthetic environment might still exhibit seasonal reproductive patterns. Seasonal reproduction at vents and seeps has been documented in bivalves (Le Pennec & Beninger 1997, Lisin et al. 1997, Dixon et al. 2006, Tyler et al. 2007) and decapods (Perovich et al. 2003, Copley & Young 2006). In the case of *Bythograea thermydron*, hatching of planktotrophic larvae coincides with the seasonal (spring and summer) phytoplankton blooms in surface waters (Perovich et al. 2003).

In contrast to *Bythograea thermydron*, females of *B. laubieri* and *B. vrijenhoeki* collected simultaneously from the Pacific-Antarctic Ridge contained oocytes in all stages of development, suggesting a lack of synchrony in reproduction for the population as a whole. The vent fields in the southern East Pacific Rise (31° and 32° S) and in the Pacific-Antarctic Ridge (38° S) that have been explored so far are situated within the oligotrophic South Pacific Subtropical Gyre (SPSG). This gyre, located roughly between 20° and 40° S, is the most uniform and seasonally stable region of the open oceans; the nutrient-bearing waters are suppressed far below the euphotic zone, severely limiting phytoplankton production and yielding a very small flux of particulate organic carbon to the deep-sea floor (Tomczak & Godfrey 1994). These features may therefore preclude possible cues for reproductive seasonality.

Guinot & Hurtado (2003) showed a clear phylogenetic separation between 2 pairs of *Bythograea* species and placed *B. thermydron* and *B. galapagensis* in one group and *B. laubieri* and *B. vrijenhoeki* in another. The SPSG coincides with the distributional boundaries of these 2 groups. The *B. thermydron*/*B.galapagensis* clade is endemic to vents north of the gyre and the *B. laubieri*/*B. vrijenhoeki* clade is endemic to vents located within the gyre. Although the life history of *B. galapagensis* has not been investigated, the differences found between the *B. laubieri*/*B. vrijenhoeki* group and *B. thermydron* suggest that the SPSG can function as a dispersal barrier to bythograeid crabs. Attempts to understand the biogeography and gene flow between the insular hydrothermal vent ecosystems have tended to focus on the potential roles of topographical discontinuities (e.g. transform faults, microplates, bathymetric inflation, seamounts) and cross-axis currents as barriers to dispersal (Tyler et al. 2002, Van Dover et al. 2002). However, recent studies (Copley & Young 2006, Copley et al. 2007) have suggested that links between surface productivity and ecological patterns in deep-sea chemosynthetic ecosystems, and features like oligotrophic gyres, might also influence the dispersal, gene flow and biogeography of some species.

CONCLUSIONS

The study of *Bythograea laubieri* and *B. vrijenhoeki* collected from the Sebastian's Steamer vent field at 38° S in Pacific-Antarctic Ridge showed that these 2 species have reproductive features that are phylogenetically conserved, but also specific characteristics that reflect the environmental condition in which they live. The ovary microstructure and general pattern of vitellogenesis is characteristic of brachyuran decapods, and our results suggest that, like other bythograeid species, ovigerous females of *B. laubieri* and *B. vrijenhoeki* gather outside of the direct influence of the vent field. On the other hand, and in contrast to *B. thermydron*, these 2 sister species seem to lack synchrony in gonad development. These differences in the reproductive pattern of species belonging to the same genus suggest that the timing of gametogenesis in bythograeid crabs may not be phylogenetically constrained.

Although the nature of the cue synchronizing the gametogenic pattern of some vent species remains unknown, previous studies have linked the synchrony of reproduction in *Bythograea thermydron* with the seasonal formation of phytoplankton blooms in surface waters. The geographical distribution of *B. laubieri* and *B. vrijenhoeki* falls within the boundaries of the SPSG, where the absence of blooms and constant oligotrophy may preclude environmental cues for seasonal reproduction. This oceanographic feature may also function as a dispersal barrier determining the biogeographic patterns of *Bythograea* species.

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