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Reproductive biology of three caridean shrimp, *Rimicaris exoculata*, *Chorocaris chacei* and *Mirocaris fortunata* (Caridea: Decapoda), from hydrothermal vents

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The caridean shrimp *Rimicaris exoculata, Chorocaris chacei* and *Mirocaris fortunata*, together with bathymodiolid mussels, dominate the vent fauna along the Mid-Atlantic Ridge. Vent shrimp show the characteristic reproductive patterns of caridean decapods. The gonads are paired organs overlying the digestive gland under the carapace. In the ovaries, the oogonia (~20–30 μm diameter) proliferate in the germinal epithelium at the periphery of the gonad, developing into previtellogenic oocytes. The previtellogenic oocytes grow to 70–100 μm before undergoing vitellogenesis. The maximum size for mature oocytes ranged between 200 and 500 μm depending on the species and the sample. The oocyte size–frequency data show no evidence of synchrony in oogenesis at population level for any of the species studied. *Mirocaris fortunata* is the only species where gravid females are commonly collected. The brood is carried on the pleopods, and the number of eggs per female ranges from 25 to 503, with a mean egg length of 0.79 ±0.14 mm. There is a positive correlation between fecundity and body size, characteristic of crustaceans. One ovigerous *C. chacei* and two *R.exoculata* have been studied. The former was carrying 2510 eggs and the later 988 small eggs in an early stage of development. The fecundity of *M. fortunata*, *C. chacei* and *R. exoculata* is significantly higher than that of species from the *Acanthephyra* group collected in the north-east Atlantic.

INTRODUCTION

Almost ten years were to pass after the discovery of hydrothermal vents along the Galápagos Rift in 1977 before the existence of a hydrothermal vent fauna was demonstrated in the Atlantic. Rona et al. (1986) discovered black smokers, massive sulphide mounds and a vent biota in the rift valley of the Mid-Atlantic Ridge (MAR) at what is now called the TAG (Trans-Atlantic Geotraverse) vent field. Since then, seven hydrothermal vent fields have been sampled for fauna along the MAR south of the Azores triple junction: Menez Gwen (850 m depth), Lucky Strike (1690 m), Rainbow (2250 m), Broken Spur (2900 m), TAG (3650 m), Snake Pit (3480 m) and Logatchev (3000 m) (Figure 1).

In contrast to the fauna of the Pacific, mainly composed of the tube worm *Riftia pachyptila*, mussels, clams and other sessile invertebrates, the Atlantic vents are dominated by ubiquitous motile caridean shrimp and bathymodiolid mussels (Rona et al., 1986; Van Dover et al., 1996, 1988; Segonzac et al., 1993; Van Dover, 1995). The taxonomy of the caridean shrimp at the Atlantic vents is under constant review (Christofferson, 1989; Segonzac et al., 1993; Vereshchaka, 1996, 1997; Shank et al., 1998). This paper is concerned with the reproductive biology of *Rimicaris exoculata* Williams & Rona, 1986 and *Chorocaris chacei* (Williams & Rona 1986) (Family Alvinocarididae, Christofferson 1989), and *Mirocaris fortunata* (Martin & Christiansen, 1995) (Family Mirocarididae, Vereshchaka 1997).

Rimicaris exoculata is found at all Atlantic vent fields except Menez Gwen, being particularly abundant at TAG. This species requires both substratum and a source of hydrogen sulphide to survive (Copley et al., 1997). *Rimicaris exoculata* gains its energy by harvesting ectosymbiotic bacteria that live on modified structures, the scaphagnothites, within the carapace (Van Dover et al., 1988; Gebruk et al., 1993; Segonzac et al., 1993; Rieley et al., 1999), and recent studies have also shown the presence of endosymbiotic gut bacteria that may oxidize polymetal sulphides ingested by the shrimp (Polz et al., 1998). *Rimicaris exoculata* has no eyes, but has a dorsal organ believed to be maximally sensitive to low level illumination such as black-body radiation of 350°C vents (Pelli & Chamberlain, 1989; Van Dover et al., 1989; Kuenzler et al., 1997). In addition, there are sensillae on the antennae II capable of eliciting a behavioural response at picomolar levels of hydrogen sulphide (Renninger et al., 1995), which, together with the dorsal organ, allow the shrimp to keep their position swimming towards the emanating hydrothermal fluid. *Chorocaris chacei* is found at all Atlantic vents. This species has eyes and a small dorsal organ. They are scavengers and have been reported to be attracted to baited traps. However, *C. chacei* also has episymbiotic microorganisms along the respiratory current pathways (Segonzac et al., 1993). *Mirocaris fortunata* is found at all vents from Menez Gwen to Broken Spur. At vents deeper than Broken Spur it is replaced by *Mirocaris keldyshi* Vereschaka 1997. The validity of *M. keldyshi* as a separate species is currently under question and, as a

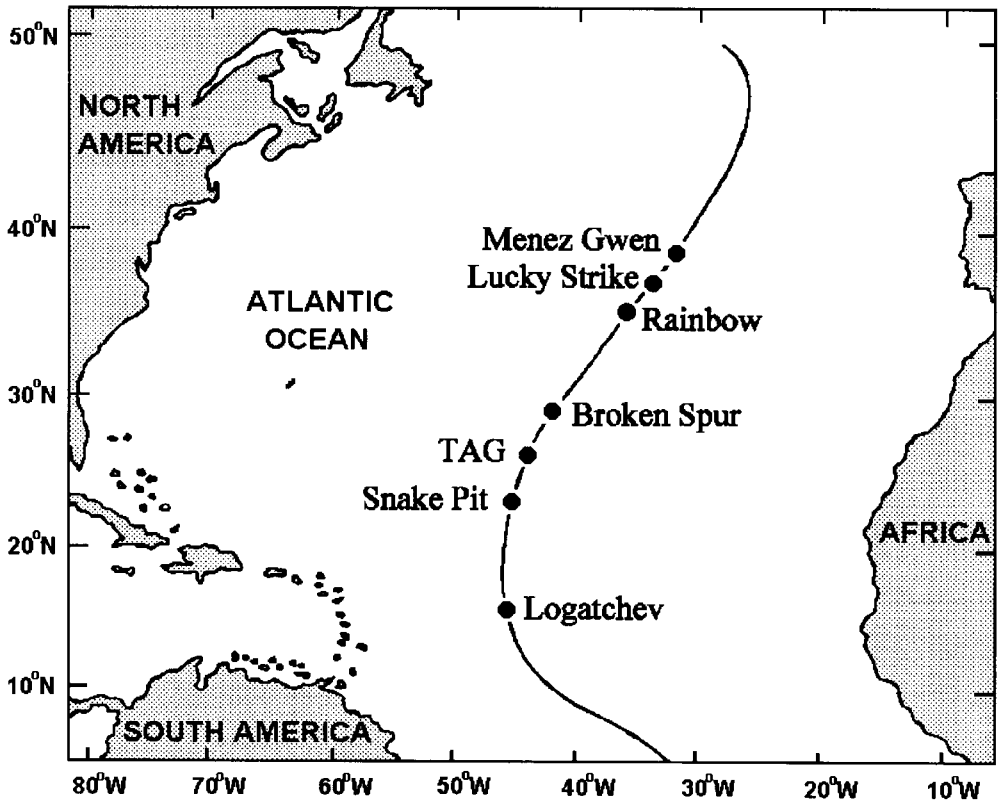

Figure 1. Location of hydrothermal vents on the Mid-Atlantic Ridge south of the Azores. Modified from Allen (1998).

result, *M. fortunata* may extend to the deepest vents. *Mirocaris fortunata* is believed to feed on the faecal deposits of *Bathymodiolus* sp. (D. Dixon, personal communication) and has been observed feeding on mussels damaged by the arm of the submersible during collection (E. Ramirez Llodra, personal observation).

Although we have good information on the taxonomy, trophic ecology (Van Dover et al., 1988; Casanova et al., 1993; Gebruk et al., 1993; Segonzac et al., 1993; Pond et al., 1997b,c; Allen Copley et al., 1998) and sensory studies (Van Dover et al., 1989; Renninger et al., 1995; Charmantier-Daures & Segonzac, 1998) of the MAR vent shrimp, little is know about their reproductive biology. In order to understand the ecological processes driving a community, a thorough knowledge of the life history of its fauna is imperative. Reproductive patterns such as production and release of gametes, egg size, fecundity and larval development play a major role in the continuity of populations and their adaptation to the environment. Still, these processes do not respond to environmental factors in similar ways. One of the most important and lengthy processes during oogenesis is vitellogenesis, the synthesis and storage of energetic reserves in the egg. Three major vitellogenetic pathways are found amongst invertebrates: autosynthetic, heterosynthetic and mixed. In autosynthetic vitellogenesis there is an uptake of exogenous low molecular weight precursors by the cells, and a subsequent synthesis of vitellin by the oocyte proteosynthetic organelles. Conversely, heterosynthetic yolk production involves the transport of externally synthesized yolk proteins into the oocyte. Finally, the third mechanism is a combination of the two first (Eckelbarger, 1994). The vitellogenic pathways, which have major implications for the rate of egg production and larval development, are phylogenetically constrained, and therefore intrinsic to the species and non-affected by external factors (Eckelbarger, 1983, 1994, 1995). On the other hand, the reproductive output (number and quality of eggs) is affected by external factors such as food quantity and quality. Low food levels or poor quality can cause a decrease or even an interruption in yolk synthesis, slowing down the egg production rate and causing a reduction in fecundity (Qian & Chia, 1991; Levin et al., 1994; Eckelbarger & Walting, 1995). The characteristics of hydrothermal vents—with localized primary production, high levels of toxic compounds, high temperatures and high temporal and spatial variability (Tunnicliffe, 1991), together with a high energy availability—provide good experimental conditions to test the above postulates. Nevertheless, cost and technology limit sampling and experimental biology in the deep-sea, and little is known on the reproductive biology of many hydrothermal vent species.

In contrast, the reproductive patterns of non-vent caridean shrimp have been studied in detail. Oogenesis comprises a proliferative phase of oogonia production, followed by the differentiative phase where oogonia differentiate into previtellogenic oocytes, which then undergo vitellogenesis (Adiyodi & Subramonian, 1983). In decapods, mature oocytes are not stored in the ovaries, but transferred to the pleopods and fertilized (Krol et al., 1992). In males, the sperm is packed in spermatophores

in the vas deferens, and deposited with modified first pleopods on the ventral surface of the female (Baeur, 1986). Copulation takes place after ecdysis, and the ovigerous females incubate the batch of eggs on the pleopods, between lateral sclerites that usually enlarge at the pre-spawning moult forming a brood chamber (Adiyodi & Subramonian, 1983). In this paper, we describe the oogenesis and reproductive output of three species of hydrothermal vent shrimp under the hypothesis that gametogenesis is phylogenetically constrained and therefore will be characteristic of a caridean shrimp, while the reproductive output would be enhanced by an environment where there is a continuous and high energy availability. The fecundity, egg size, and their implication in dispersal abilities during the larval phase are also discussed.

MATERIALS AND METHODS

Three species of caridean shrimp, *Rimicaris exoculata*, *Chorocaris chacei* and *Mirocaris fortunata* were collected during several cruises along the Mid-Atlantic Ridge hydrothermal vent fields (Figure 1, Table 1). Shrimps were sampled by net or by slurp gun attached to the arm of the submersibles 'Mir 1' and 'Nautile'. All material was identified on-board, and fixed in 5% formaldehyde (BRAVEX material) or 10% formaldehyde (DIVA2, Microsmoke, MARVEL and PICO material) for 5–7 d, before being transferred to 70% isopropanol for storage.

In the laboratory, the carapace length (CL) of 20–25 females was measured with callipers to the nearest 0.1 mm and the specimens processed for histology. Whole shrimps were processed for *M. fortunata*, but only the cephalothorax was processed for the larger *C. chacei* and *R. exoculata*. The tissues were decalcified in Bouin's solution for 5 d, dehydrated in graded alcohols, cleared in Histoclear and embedded in paraffin wax. Sections were cut at 7 μm and stained with haematoxylin and eosin. From all the specimens analysed, only a maximum of nine females per species and sample provided good histological sections and were used for image analysis of the ovaries. All the oocytes (N=30–160) that had been sectioned through the nucleus were measured (feret diameter) with an image analysis programme (Matrox-Rainbow Runner/ Jandel Scientific SigmaScan Pro 4). The measurements were grouped into 25-μm classes in order to determine the oocyte size–frequency distribution for each individual. The pooled data for the nine females in each sample were also plotted, except for *C. chacei* collected during the MARVEL 97 cruise, where only three females were available. Differences on the mean size of vitellogenic oocytes between samples for each species were tested with the non-parametric Mann–Whitney test.

The carapace length and wet weight of ovigerous females were measured. The eggs carried on the pleopods were gently removed with a spatula and the egg mass weighed wet. The eggs were staged (early or late eggs depending on the morphological features of the eggs) and measured (egg length (EL) and egg width (EW)) using the Matrox-Rainbow Runner and SigmaScan Pro 4 software. The eggs were oval in shape, which is a common feature in caridean shrimp, and therefore egg volume (EV) was estimated as: $EV=EL\times\pi\times(EW/2)$ (Corey & Reid, 1991). Fecundity, estimated as number of eggs carried per female, was regressed against carapace length and the correlation analysed with the Pearson product moment correlation.

RESULTS

General patterns of ovary morphology and oogenesis

The ovaries in the three species are similar, situated dorsally under the carapace, overlying the digestive gland. Each ovary consists of several layers of growing oocytes enveloped by a thin gonadal wall. The oogonia proliferate in the germinal epithelium at the periphery of

Table 1. *Location of sampling sites of three species of caridean shrimp along the Mid-Atlantic Ridge, showing cruises, date of collection and number of females examined.*

Species	Location	Latitude/Depth	Cruise	Date	Number of females examined
Rimicaris exoculata	TAG	26°N 3650 m	BRAVEX	September 1994	25
	Rainbow	36°N 2250 m	PICO	June–July 1998	25
	Snake Pit	23°N 3480 m	Microsmoke	November 1995	1
Chorocaris chacei	Lucky Strike	37°N 1690 m	DIVA2	June 1994	1
	Lucky Strike	37°N 1690 m	MARVEL	August–September 1997	20
	Lucky Strike	37°8 N 1690 m	PICO	June–July 1998	25
Mirocaris fortunata	Lucky Strike	37°N 1690 m	DIVA2	June 1994	19
	Lucky Strike	37°N 1690 m	MARVEL	August–September 1997	25
	Lucky Strike	37°N 1690 m	PICO	June–July 1998	37

Table 2. *Mean size and standard deviation of the three stages of oocyte development in* Rimicaris exoculata, Chorocaris chacei *and* Mirocaris fortunata *from different samples*.

Species	Oogonia	Previtellogenic oocytes	Vitellogenic oocytes
Rimicaris exoculata TAG, September 1994	21.9 ±3.4 μm	51.1 ±16.2 μm	166.9 ±48.7 μm
Rimicaris exoculata Rainbow, June 1998	25.2 ±3.8 μm	61.2 ±17.1 μm	122.5 ±37.2 μm
Chorocaris chacei Lucky Strike, September 1994	26.4 ±5.8 μm	62.5 ±18.9 μm	158.2 ±50.3 μm
Chorocaris chacei Lucky Strike, July 1998	31.9 ±5.8 μm	66.8 ±17.6 μm	122.0 ±26.0 μm
Mirocaris fortunata Lucky Strike, September 1994	24.1 ±4.3 μm	51.2 ±17.3 μm	149.7 ±56.3 μm
Mirocaris fortunata Lucky Strike, July 1998	27.8 ±4.8 μm	58.4 ±17.7 μm	249.9 ±89.5 μm

the gonad, developing into previtellogenic oocytes (Figure 2D). The previtellogenic oocytes migrate to the growth zone between large vitellogenic oocytes and undergo vitellogenesis (Figure 2A, C & D). Yolk production is identified by the presence of yolk granules spreading from the periphery of the oocyte towards the nucleus (Figure 2B). The yolk granules occupy most of the ooplasm in mature oocytes. A layer of flattened accessory cells involved in the vitellogenetic processes surrounds the vitellogenic oocytes (Figure 2B). The gameto-genetic patterns are similar in the three species, although there is some variability in the mean size of the oocyte stages (Table 2).

Oogenesis and oocyte size–frequency distribution of Rimicaris exoculata

Nine females of *Rimicaris exoculata* from TAG (September 1994) and nine from Rainbow (June 1998) where analysed. The oogonia are small cells of around

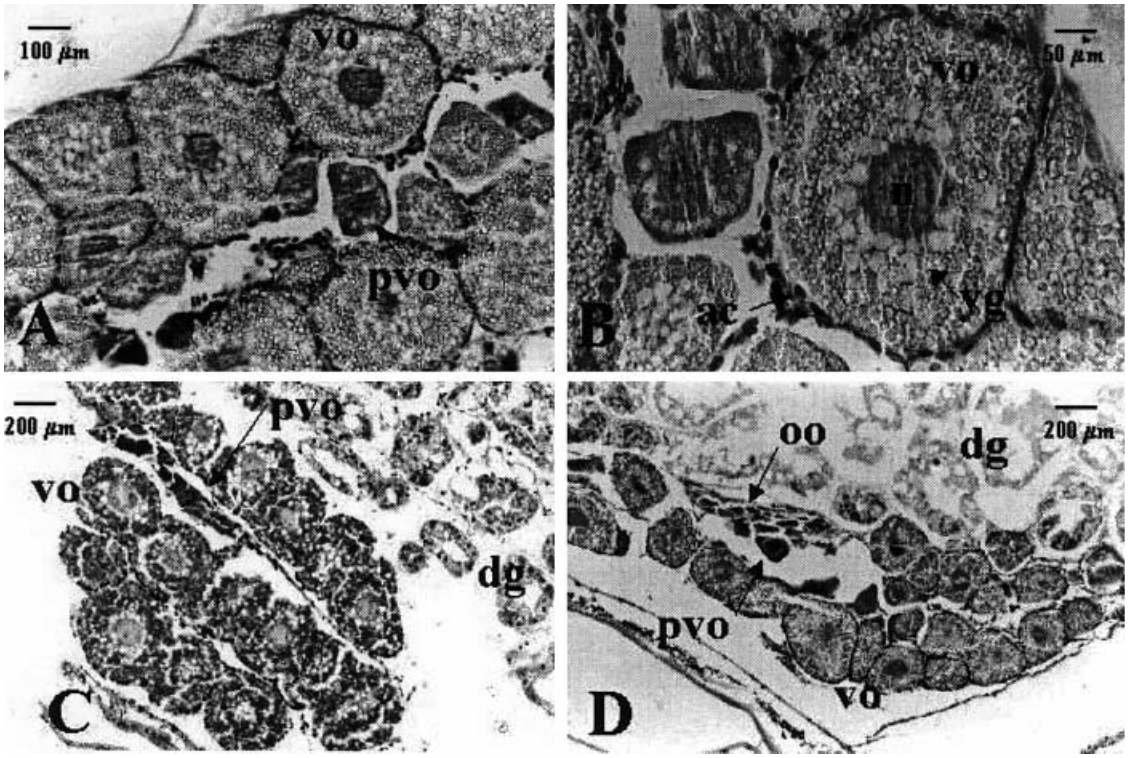

Figure 2. Microphotography of ovary sections (haematoxylin and eosin). (A) *Chorocaris chacei*: ovary showing vitellogenic oocytes (vo) and previtellogenic oocytes (pvo). (B) Detail of the ovary of *C. chacei* showing a large vitellogenic oocyte (vo) surrounded by accessory cells (ac) and with yolk granules (yg) spreading in the cytoplasm. (C) *Rimicaris exoculata*: ovary showing previtellogenic (pvo) oocytes developing between vitellogenic oocytes (vo). (D) *Mirocaris fortunata*: section of ovary showing oogonia (oo) and previtellogenic oocytes (pvo) surrounded by large vitellogenic oocytes (vo); dg, digestive gland; n, nucleus.

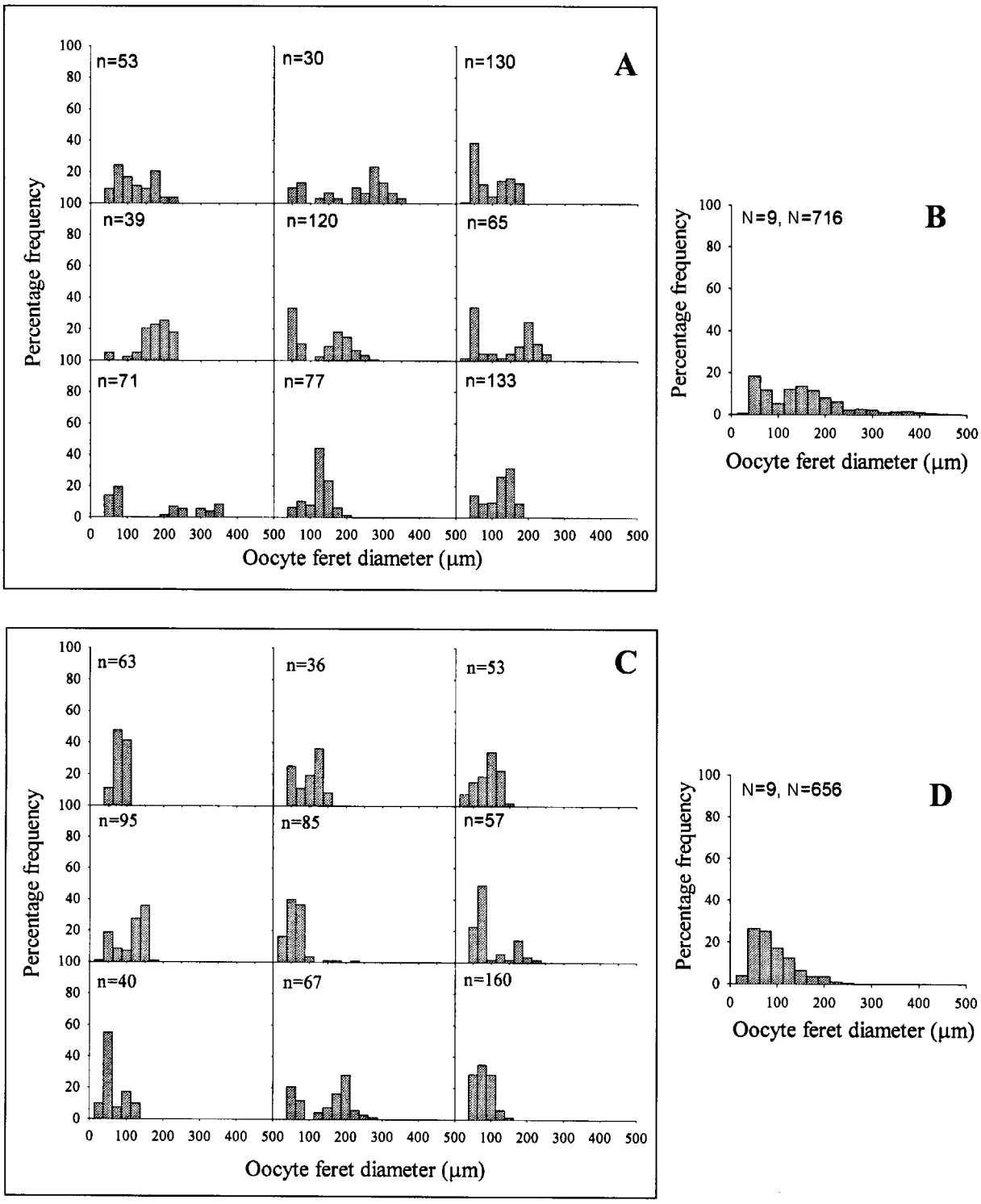

Figure 3. Oocyte size–frequency distribution of *Rimicaris exoculata*. (A) Oocyte size–frequency of individuals from September 1994. (B) Summated oocyte size–frequency distribution for nine individuals of *R. exoculata* from September 1994. (C) Oocyte size–frequency of individuals from July 1998. (D) Summated oocyte size–frequency distribution for nine individuals of *R. exoculata* from July 1998. N, number of individuals analysed; n, number of oocytes measured.

20 μm with a dark stained nucleus occupying the entire cell. These cells grow to 25–35 μm and then develop into previtellogenic oocytes. Previtellogenic oocytes are identified by their large nucleus/cytoplasm ratio and basophilic cytoplasm. Vitellogenesis begins at 85–100 μm, indicated by yolk vesicles appearing at the periphery of the oocytes, and a change to acidophilia in the cytoplasm. As vitellogenesis progresses, the yolk granules spread towards the nucleus, occupying most of the cytoplasm in mature oocytes. The maximum oocyte size observed was 455.1 μm in the females from TAG, and 206.2 μm in the specimens from Rainbow. In the samples analysed, most of the gonad volume was occupied by vitellogenic oocytes surrounding patches of developing previtellogenic oocytes.

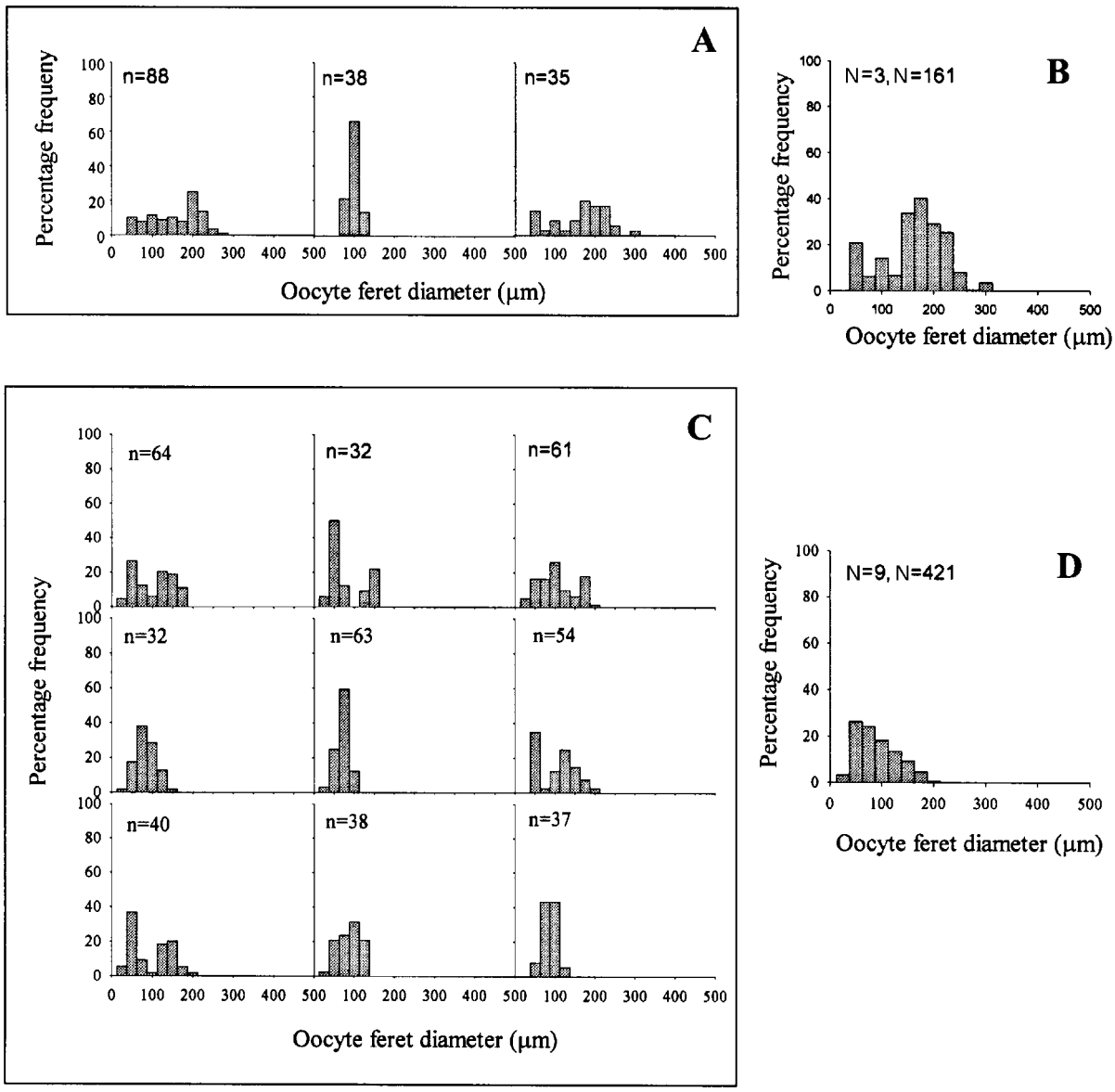

Figure 4. Oocyte size–frequency distribution of *Chorocaris chacei*. (A) Oocyte size–frequency of individuals from September 1997. (B) Summated oocyte size–frequency distribution for nine individuals of *C. chacei* from September 1997. (C) Oocyte size–frequency of individuals from July 1998. (D) Summated oocyte size–frequency distribution for nine individuals of *C. chacei* from July 1998. N, number of individuals analysed; n, number of oocytes measured.

The oocyte size–frequency distributions show no evidence of synchronous oogenesis. Although there is variability between individuals, there is a common pattern in oocyte size distribution, with a first peak of oogonia and previtellogenic oocytes ($<100\,\mu$m), and most specimens showing a second peak of vitellogenic oocytes ($>100\,\mu$m) (Figure 3A & C). The females from TAG in September 1994 (Figure 3B) have gonads with significantly larger vitellogenic oocytes (Mann–Whitney U-test, U=853.0, $P<0.0001$) than the gonads from individuals collected at Rainbow in June 1998 (Figure 3D), suggesting that the former were in a more advanced stage of development.

Oogenesis and oocyte size–frequency distribution of Chorocaris chacei

Only three females of *Chorocaris chacei* collected from Lucky Strike in September 1997 provided good histological sections, while nine females from July 1998 were analysed. The oogonia grow to 30–40 μm and then develop into previtellogenic oocytes. These oocytes migrate to the growth zone between the larger vitellogenic oocytes, and grow to a size of 70–100 μm before undergoing vitellogenesis. The vitellogenetic processes are again characterised by the presence of yolk granules spreading from the periphery of the oocyte towards the nucleus. The maximum size observed for a vitellogenic oocyte was 282.7 μm in September 1997 and 184.3 μm in July 1998.

In the sample from September 1997, the oocyte size–frequency diagrams show a large spread of oocyte sizes in two individuals, but a dominance of young vitellogenic oocytes in the other individual (Figure 4A). Because of the low number of specimens available, these results should be interpreted cautiously. In the females collected from Lucky Strike in July 1998, most of the ovary volume was occupied by previtellogenic and young vitellogenic

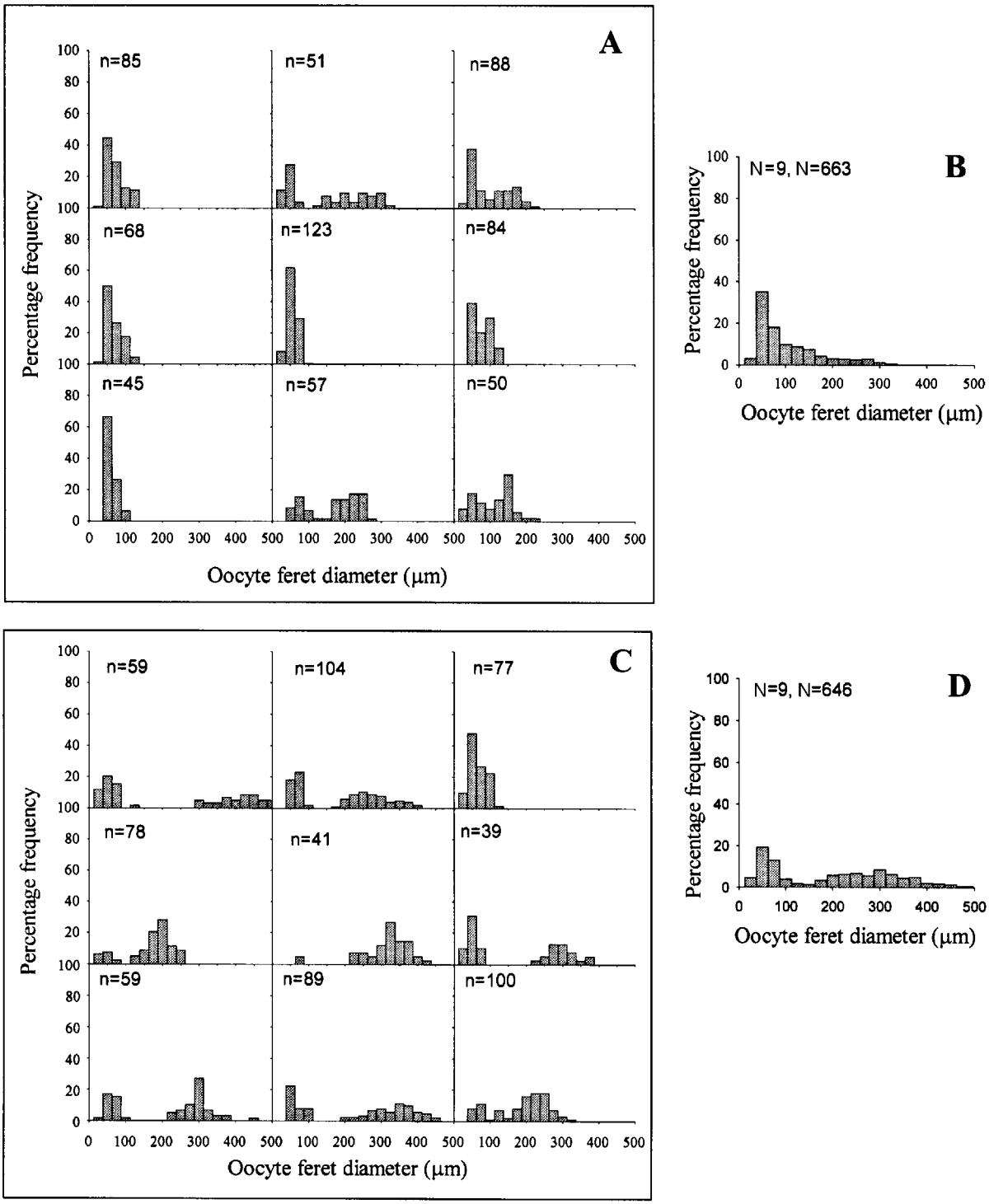

Figure 5. Oocyte size–frequency distribution of *Mirocaris fortunata*. (A) Oocyte size–frequency of individuals from September 1997. (B) Summated oocyte size–frequency distribution for nine individuals of *M. fortunata* from September 1997. (C) Oocyte size–frequency of individuals from July 1998. (D) Summated oocyte size–frequency distribution for nine individuals of *M. fortunata* from July 1998. N, number of individuals analysed; n, number of oocytes measured.

oocytes. In five individuals, a bimodal oocyte size distribution can be distinguished, the first peak corresponding to previtellogenic oocytes ($<100\,\mu$m) and the second one to vitellogenic oocytes ($>100\,\mu$m) (Figure 4C). The vitellogenic oocytes from the samples collected during July 1998 (Figure 4D) are significantly smaller than the vitellogenic oocytes in the ovaries of females collected in September 1997 (Figure 4B) (Mann–Whitney *U*-test, $U=4095.0$, $P<0.0001$).

Oogenesis and oocyte size–frequency distribution of

Mirocaris fortunata

Nine females of *Mirocaris fortunata* collected at Lucky Strike in September 1997 and nine collected from the same location in July 1998 were examined. The oogonia develop into previtellogenic oocytes at a size of 25–30 μm. The previtellogenic oocytes grow to 85–95 μm and then undergo vitellogenesis, with yolk granules spreading from

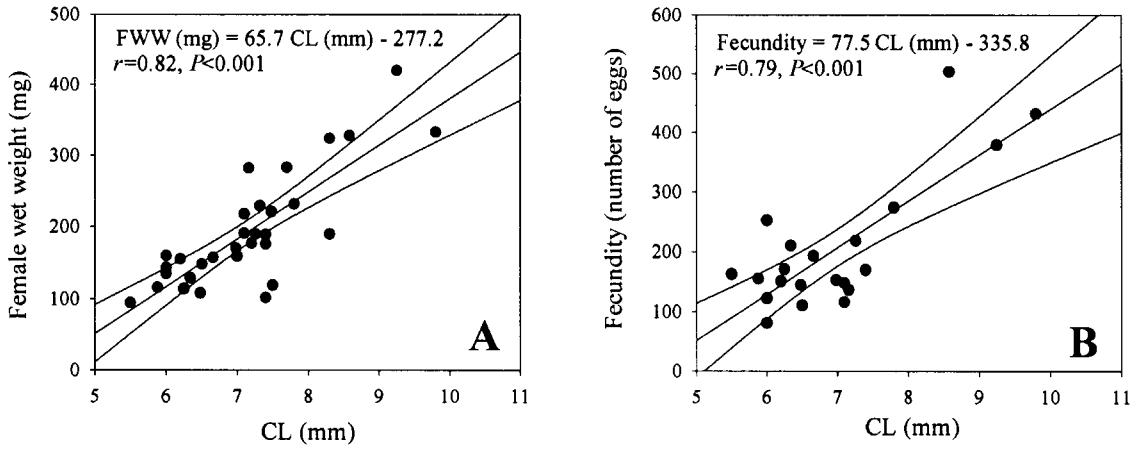

Figure 6. Fecundity of *Mirocaris fortunata*. (A) Simple regression of female wet weight (FWW) in mg against carapace length (CL) in mm, showing 95% confidence interval, linear regression equation and Pearson's coefficient of correlation. (B) Simple regression of fecundity (number of eggs per female) against carapace length (CL) in mm, showing 95% confidence interval, linear regression equation and Pearson's coefficient of correlation.

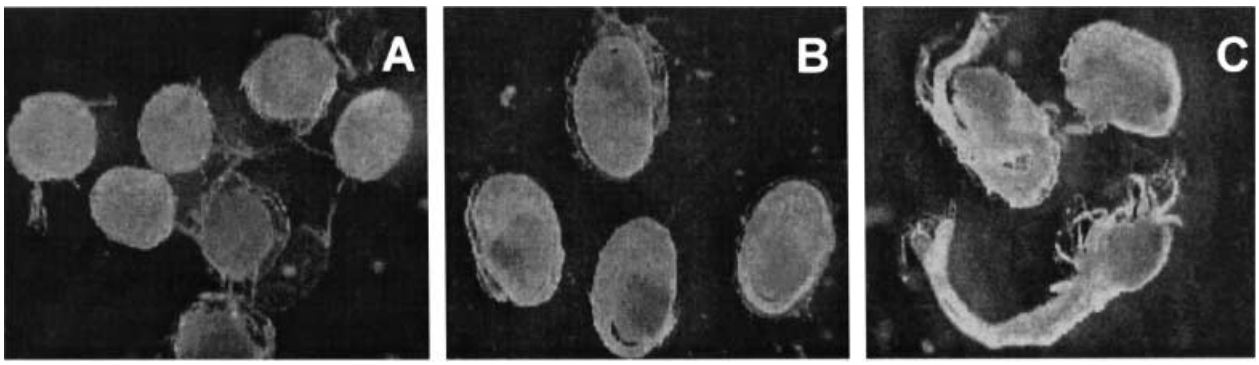

Figure 7. Egg stages in the broods of *Mirocaris fortunata*. (A) Early embryos; (B) late embryos; (C) late eggs with larvae ready to hatch.

the periphery of the oocytes towards the nucleus. The maximum size observed for vitellogenic oocytes was 319.5 μm in September 1997 and 498.9 μm in July 1998.

The oocyte size–frequency diagrams from both samples (Figure 5A & C) show the presence of a pool of previtellogenic and early vitellogenic oocytes in most individuals. Nevertheless, most females had well-developed gonads with a bimodal oocyte size distribution, the first mode corresponding to previtellogenic oocytes ($<100\,\mu$m) and the second to vitellogenic oocytes ($>100\,\mu$m). *Mirocaris fortunata* is the only species examined that presented significantly larger vitellogenic oocytes in July 1998 (Figure 5D) than in the September samples (Figure 5B) (Mann–Whitney *U*-test, $U=18580$, $P<0.0001$).

Fecundity and egg sizes of M. fortunata, C. chacei *and* R. exoculata

The mean carapace length of 31 ovigerous *M. fortunata* analysed was 7.16 ±0.18 mm. The mean female wet weight (not including egg mass) was 0.19 ±0.08 g. There is a significant positive correlation (Pearson correlation, $r=0.82$, $P<0.001$) between female wet weight and carapace length, indicating that the carapace length is a good measure for body size (Figure 6A). From the 31 females available, four showed signs of body damage and were not included in the following analysis. Three stages of egg development were present in the different broods: early embryos with no eye spots (Figure 7A) and two stages of late development. The first corresponds to embryos with a clear formation of the abdomen (Figure 7B), and the second to broods with embryos ready to hatch, showing eyespots, clear larval features and the egg membrane breaking down (Figure 7C). Within a brood, the embryos develop synchronously and all the eggs in one batch are at the same stage. In the sample, twenty specimens had broods with early eggs, seven carried late eggs with late embryos and four females were carrying larvae ready to hatch. The mean egg mass wet weight was 0.023 ±0.02 g. The number of eggs carried per female ranged from 25 eggs in females with late broods to 503 in females carrying early embryos. The four females carrying embryos ready to hatch showed evidences of damaged broods, and were therefore not included in the analysis. Mean fecundity (quantified as number of eggs per female in non-damaged broods) was 174.7 ±22.8 eggs per female. There is a significant positive correlation (Pearson correlation, $r=0.79$, $P<0.001$) between fecundity and carapace

length (Fecundity=77.5 CL (mm) − 335.8) (Figure 6B). The eggs of *M. fortunata* are small, with a mean egg volume of 0.21 ±0.08 mm^3 (mean egg length=0.79 ±0.14 mm and a mean egg width=0.57 ±0.07 mm).

Very few ovigerous *C. chacei* have been collected to date, and only one specimen collected at Lucky Strike in June 1994 and provided by IFREMER (Brest, France) was available for analysis. This female has a carapace length of 16.8 mm, a body weight of 2.26 g and an egg mass wet weight of 0.231 g. The brood consisted of 2510 eggs carried on the pleopods in an advanced stage of development, where the abdomen and appendages can be distinguished. The mean egg volume is 0.13 ±0.03 mm^3 (mean egg length=0.70 ±0.1 mm and mean egg width=0.49 ±0.04 mm).

One of the few ovigerous *R. exoculata* that have been collected to date was analysed during a visit to IFREMER (Brest, France). This specimen has a carapace length of 16.4 mm, and carries 988 eggs. The female wet weight is 1.64 g and the egg mass wet weight is 0.107 g. The eggs are small (around 0.6 mm in length) and in an early stage of development, as no eye spots or other structural features are present in the embryos. These data are consistent with the observations on two ovigerous females collected from TAG, one during the NOAA VENTS cruise (August 1985) and one during the BRAVEX cruise (September 1994). The former had a carapace length of 17.3 mm and the eggs measured 0.62×0.72 mm (N=10) (Williams & Rona, 1986). During BRAVEX 94, two ovigerous *R. exoculata* were found in a sample of over 500 specimens, and one was analysed by Copley (1998). This female had a carapace length of 17.7 mm, and was carrying 836 eggs in an early blastula stage of development.

DISCUSSION

The ovaries of *Rimicaris exoculata*, *Chorocaris chacei* and *Mirocaris fortunata* are located under the carapace, as in non-vent caridean shrimps, and can be seen through the exoskeleton in fresh specimens. The examination of gonad sections show a very similar gametogenic pattern for the three species, with oogonia (~20–30 μm) proliferating in the germinal epithelium at the periphery of the ovary, developing into previtellogenic oocytes, which then migrate to the growth zone between the large vitellogenic oocytes. These previtellogenic oocytes grow to around 70–100 μm and then undergo vitellogenesis. The yolk granules spread from the periphery of the cell towards the nucleus, occupying most of the ooplasm in mature oocytes. Vitellogenic oocytes are covered by a layer of flattened follicle cells involved in the vitellogenic processes. The maximum size for mature oocytes ranged between 300 and 500 μm.

The oocyte size–frequency diagrams show no evidence of gametogenic synchrony in oogenesis for any of the species studied. All stages of developing oocytes, from oogonia to large vitellogenic oocytes were present in the gonads at a single time. However, different individuals show different patterns of oocyte sizes. Most females of *M. fortunata* show a bimodal distribution corresponding to two different cohorts of developing oocytes, and this, together with the observation that all the embryos within a brood are at the same developmental stage, suggest a periodic production of eggs. Most specimens of *R. exoculata* and *C. chacei* present a more or less accentuated bimodal oocyte size distribution, but did not have oocytes in the largest classes. Nevertheless, the ovaries contained all stages of oocyte development, with a cohort of young cells (oogonia and previtellogenic oocytes) followed by a cohort of vitellogenic oocytes. The bimodal distribution of oocyte sizes, as well as the presence of two cohorts of developing oocytes in all specimens, suggest iteroparity and a lack of synchrony in reproduction for the population as a whole. An environment such as hydrothermal vents, where there is a continuous energy supply introduced in the food web by the chemoautotrophic bacteria, can support the asynchronous or quasi-continuous production of eggs. Nevertheless, Copley (1998) found a polymodal population structure for *R. exoculata*, indicating a discrete pattern of recruitment, contrasting with the continuous reproductive output that would be expected from a population with an asynchronous reproductive strategy. The ecology of the larval phase may explain this contradiction. Postlarvae identified as belonging to *R. exoculata*, *C. chacei* and *Alvinocaris markensis* by ribosomal DNA markers (Dixon & Dixon, 1996; Herring, 1996) have been collected from the water column above Broken Spur. These postlarvae possess a substantial wax-ester reserve, compound eyes and their lipid composition is derived from a diet of photosynthetic material, contrasting with the small or non-existent eyes and bacterial-derived lipids of the adults (Pond et al., 1997a,b,c; Allen, 1998; Allen Copley et al., 1998). These observations suggest a long planktotrophic phase with large migratory abilities towards the surface. The hypothesis of a high dispersal potential during the larval stage is also supported by genetic studies on vent shrimp populations from Broken Spur and TAG, where a high gene flow between the two vent fields with a N_m (number of migrants per generation) of 250 was calculated (Creasey et al., 1996; Shank et al., 1998). Although the production of larvae might be quasi-continuous at population scale, the recruitment could be affected by environmental factors found by the larvae during their extended planktotrophic stage in the water column. Factors such as favourable hydrodynamic conditions or variability in the phytodetritus concentration could be used as settlement cues, causing the discrete recruitment found by Copley (1998).

One of the most intriguing observations on the reproduction of the vent shrimps is the almost complete lack of ovigerous *C. chacei* and *R. exoculata* in the samples, while *M. fortunata* are known to provide gravid females regularly (Van Dover et al., 1996; P.A. Tyler, personal observation). We believe that *R. exoculata* occupies a different habitat while brooding, to protect the embryos from hydrothermal fluids and from the risk of mechanical damage caused in the highly active aggregations of shrimp around black smokers. Gravid females of *M. fortunata* have been sampled over mussel beds and close to the shimmering waters. They live, however, in less dense populations than *R. exoculata*, with fewer physical interactions between individuals and lower contact with the very hot and toxic hydrothermal fluid. If *Rimicaris exoculata* and *C. chacei* move to the periphery of the vents while

carrying eggs, samples from these external habitats should confirm their presence. An alternative hypothesis would be that we have been missing the ovigerous *R. exoculata* because of limitation of sampling to the summer and early autumn months. *R. exoculata* could brood their embryos in a different time of the year than *M. fortunata*, although the data on gametogenesis presented here does not support the idea of a seasonal reproduction for any of the species studied.

In crustaceans in general, and in caridean shrimp in particular, an important factor related to the number of eggs produced is adult body size. A positive correlation is found between carapace length and body size (Clarke 1979, 1993b; King & Bulter 1985; Bell & Fish 1996, Stella et al., 1996; Ohtomi, 1997; Thessalou-Legaki & Kiortsis, 1997). This correlation is a result of the physical space limitation between the pleopods for attachment of eggs (King & Butler. 1985; Corey, 1987; Corey & Reid, 1991; Clarke, 1993b). The ovigerous *M. fortunata* analysed follow this pattern, with a positive correlation between carapace length and fecundity. This correlation was stronger when the specimens with larvae ready to hatch were not included in the data. It is possible that egg loss occurs in late stages of development, naturally and during collection and storage. Broods from these females had very few eggs, ranging from 25 to 60 eggs, while females carrying early broods had a mean fecundity of 193.7 eggs per female.

The eggs are amongst the largest cells in the organism and show a wide variability between and within species. Because the energy required to produce eggs is limited, invertebrates produce either a small number of large, rich eggs or a high number of small eggs (Menge, 1975; Clarke, 1993a; Podolsky & Strathmann, 1996). This trade-off between egg size and fecundity is very clear in caridean shrimp (Herring, 1974a,b; Clarke, 1993b; Ohtomi, 1997). The effects and consequences that this range of sizes might have on energy content, parental investment, fertilization success and larval development is what has been interesting life history biologists and ecologists for decades. Vance (1973) proposed a theoretical model predicting an optimal egg size following a bimodal distribution corresponding to larval developmental type (i.e. planktotrophy for small eggs and lecithotrophy for large ones). Later studies suggest that the evolution of egg sizes is related to prezygotic factors, such as higher fertilization rates in large eggs offering larger targets for sperm (Levitan, 1996), and postzygotic factors, such as larval mortality and developmental time (Podolsky & Strahmann, 1996). In deep sea species with migrating larvae, the mortality risk while in the water column increases with depth. It has been proposed that these species reduce, in part, that risk by producing larger eggs, which will hatch into larger and more advanced larvae with higher survival probabilities during their migratory movements (Clarke, 1979; King & Butler, 1985; King, 1987; Clarke, 1993a). However, *M. fortunata* and the few *C. chacei* and *R. exoculata* examined have a high number (around 200 for *M. fortunata*, 2500 for *C. chacei* and 1000 for *R. exoculata*) of small eggs (around 0.5–0.8 mm in length). These eggs have similar sizes than the eggs brooded by the deep-water pelagic caridean shrimp *Acanthephyra* sp. (Herring, 1974b; E. Ramirez Llodra, personal observation). The small size of the eggs, together with the genetic and biochemical data (Creasey et al., 1996; Pond et al., 1997a,b,c; Allen, 1998; Allen Copley et al., 1998; Shank et al., 1998), suggest a short embryonic development with larvae hatching in an early stage and undergoing a relatively long planktotrophic stage. Moreover, fecundity is higher in the three vent shrimp than in the small-egged, non-vent species *Acanthephyra* sp. (E. Ramirez Llodra, personal observation). In order to compare broods between different species of caridean shrimp, fecundity needs to be expressed as number of eggs related to female body weight. When calculating fecundity as number of eggs per 1g of female body weight, *M. fortunata*, *C. chacei* and *R. exoculata* produce 2.5, 2 and 1.5 times more eggs respectively than the species of *Acanthephyra* from the north-east Atlantic (E. Ramirez Llodra, unpublished data). This high production of eggs can be supported by the rich hydrothermal vent environment, where the chemoautotrophic bacteria provide the trophic web with a high and continuous primary production. There is therefore a high number of feeding larvae hatching from these small eggs, which will be able to spend long periods in the water column, incrementing the dispersal and colonisation potential of the species.

We believe that the hydrothermal vent caridean shrimp *M. fortunata*, *C. chacei* and *R. exoculata* have phylogenetically constrained gametogenesis, but that their fecundity is enhanced as a consequence of living in a rich environment with a continuous energy supply. Furthermore, the small eggs developing into planktotrophic larvae capable of long residence times in the water column would allow for the colonization of new vent fields in an environment characterized by its patchiness and the instability caused by the extinction/reactivation of vent sites (Langumir et al., 1997).

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