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Review

Reproductive characteristics and strategies of reducing-system bivalves

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Abstract

The reproductive biology of Type 3 reducing-system bivalves (those whose pallial cavity is irrigated with water rich in reducing substances) is reviewed, with respect to size-at-maturity, sexuality, reproductive cycle, gamete size, symbiont transmission, and larval development/dispersal strategies. The pattern which emerges from the fragmentary data is that these organisms present reproductive particularities associated with their habitat, and with their degree of reliance on bacterial endosymbionts. A partial exception to this pattern is the genus *Bathymodiolus*, which also presents fewer trophic adaptations to the reducing environment, suggesting a bivalent adaptive strategy. A more complete understanding of the reproductive biology of Type 3 bivalves requires much more data, which may not be feasible for some aspects in the deep-sea species. © 2000 Elsevier Science Inc. All rights reserved.

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1. Introduction

Interest in the biology of marine reducing systems has surged since the discovery of deep-sea vents and associated fauna (Corliss et al., 1979). One of the most conspicuous taxa in these habitats is the Bivalvia (Berg, 1985; Grassle, 1986; Fustec et al., 1987). Considerable progress has been made in the understanding of the feeding and digestive physiology of these organisms, which present varying degrees of association with symbiotic oxidizing bacteria (e.g. Rau and Hedges

1979; Jannasch 1985; Smith 1985; Morton 1986; Reid and Brand, 1986; Distel and Felbeck 1987; Diouris et al. 1989; Tunnicliffe 1991; Le Pennec et al., 1995a). In contrast, general principles of the reproductive biology of reducing-system bivalves are poorly understood, despite a spate of recent studies on individual species (Alatalo et al., 1984; Berg and Alatalo, 1984; Fisher and Hand 1984; Le Pennec et al., 1984, 1995b; Berg 1985; Dando et al., 1985, 1986; Frenkiel and Mouëza, 1985; Giere, 1985; Schweimanns and Felbeck, 1985; Reid and Brand, 1986; Southward, 1986; Distel and Felbeck, 1987; Gustafson et al., 1987; Herry and Le Pennec, 1987; Le Pennec, 1988; Distel and Wood, 1992; Johnson and Le Pennec, 1994; Frenkiel and Mouëza, 1995; Johnson and Le Pen-

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nec, 1995; Mullineaux and France, 1995; Frenkiel et al., 1996, 1997; Gros et al., 1996, 1997, 1998a,b; Beninger and Le Pennec, 1997; Le Pennec and Beninger, 1997; Eckelbarger and Young, 1999; see also Eckelbarger and Watling, 1995; Tyler and Young, 1999 for reviews).

To this point, several hypotheses have been formulated concerning different aspects of reproductive biology in the deep-sea environment. In a review of bivalve reproduction, depth was ascribed a major role in stable habitats (Mackie, 1984). However, deep-sea reducing systems are the result of intense geologic activity, and the vent environment is highly variable, the instability occurring at various temporal scales ranging from the minute to the decade (Lalou et al., 1984). This habitat instability led to the proposal of an r-type reproductive strategy (Desbruyères and Laubier, 1983). It was subsequently suggested that the organisms inhabiting these sites possess reproductive strategies dominated by their internal biology rather than by their environment (Turner et al., 1985; McHugh, 1989).

Paradigms of the reproductive biology of bivalves inhabiting coastal reducing systems are even less well-developed than the general considerations for deep-sea bivalves. Most coastal reducing system bivalves such as the Lucinidae and Thyasiridae are small (1–2 cm), and present no economic value, so they have been largely ignored by most contemporary malacologists wishing to engage in funded research. The early studies of Allen (1958) stood virtually alone, until the renewed interest in bivalves of coastal reducing systems generated by the deep-sea vents (Alatalo et al., 1984; Berg and Alatalo, 1984; Fisher and Hand 1984; Dando et al., 1985, 1986; Frenkiel and Mouëza, 1985, 1995; Giere, 1985; Schweimanns and Felbeck, 1985; Reid and Brand, 1986; Southward, 1986; Distel and Felbeck, 1987; Herry and Le Pennec, 1987; Le Pennec, 1988; Distel and Wood, 1992; Johnson and Le Pennec, 1994, 1995; Frenkiel et al., 1996, 1997; Gros et al., 1996, 1997, 1998a,b).

In this review, we present a synthesis of the available data concerning the reproductive biology of reducing-system bivalves, with an emphasis on the roles of internal biology, environmental variables, and the degree of association with symbiotic oxidizing bacteria.

2. Data base

Bivalves have previously been divided into three categories from the standpoint of sulphide availability within their pallial cavities: Type 1 species inhabit well-oxygenated environments (e.g. epibenthic forms), Type 2 species inhabit variably-reducing environments, but maintain aerobic conditions in their pallial cavities via siphons or tubes, and Type 3 species inhabit reducing environments with a mixture of aerobic and reducing conditions in their pallial cavities (Le Pennec et al., 1995a). In this review we extend this classification to reducing substances in general, and restrict coverage to Type 3 bivalves.

In addition to the work cited in the text, data for this review are derived from the literature cited in Table 1; some unpublished original data are also presented.

3. Discussion

3.1. Sexual maturity

Data on age at sexual maturity in reducing-system bivalves are singularly lacking. To our knowledge, no age determinations have yet been performed on any Type 3 species, although the limited data available for littoral species suggests a lifespan of only 2–3 years (Monnat, 1970). Even size-at-maturity data are extremely sparse, being limited to cursory observations in the deep-sea genera *Calyptogena* and *Bathymodiolus*, and in the tropical littoral *Lucina pectinata* (= *Phacoides pectinatus*). In a study of 154 *Calyptogena magnifica* up to 24.1 cm in length from the Galapagos and 21°N vent fields, Berg (1985) reported that mature gonads appeared at a minimum size of approximately 11 cm. In the same study, Berg (1985) examined 227 *Bathymodiolus thermophilus* from 20 to 167 mm in length, and placed the size at maturity at 40 mm for males, and 60 mm for females. The minimum size for sexual maturity in *L. pectinata* was determined by biopsy to be 20–24 mm in samples comprising a total of several thousand individuals with a maximum size of 80 mm (Frenkiel and Mouëza, 1985).

3.2. Sexuality

The data concerning the sexuality of reducing-system bivalves is as scanty as that concerning

Table 1
Representative Type 3 bivalves their reproductive characteristics, and larval/postlarval sizes^a

Species	Site	Depth (m)	Environmental timing cues (+/-)	Sexuality	Gameto-genesis (c/d)	Spawning (a/sa/ma)	Gamete size (µm)			Larva/Post-larva (µm)	References
							♀	♂ Head	Total		
<i>Loripes lucinalis</i>	Temperate regions	0-99									Johnson and Le Penneec (1994) Johnson et al. (1996)
	e.g. Bay of Brest, France	0-1	+	s	d	sa	14-95		10.5		
<i>Codakia orbicularis</i>	Tropical regions										Berg and Alatalo (1984) Mouëza and Frenkiel (1995), Gros (1997)
	e.g. Grand Bahamas Island	0-99	+	s	d	sa	108-112			PI: 150-174 PII: 170-224	
	Guadeloupe		+	s	d	sa	92-108		18-20	PI: 160-170 PII: 190-200	
<i>Solemya reidi</i>	California to Alaska	40-600									Gustafson and Reid (1986, 1988)
	e.g. Albertini canal (Canada)	40	+	s	c	ma?	271		55	No distinction PI/PII: 360/440	
<i>Bathypecten vulcani</i>	EPR: 12°59', 103°56'W	2630	+	s	c?	ma?	100				Le Penneec (unpublished)
<i>Bathymodiolus azoricus</i>	MAR:	850-1700	+	s	d	a?					Comtet (1998)
	Menez Gwenn and Lucky Strike vents										PII: 472-604
<i>Bathymodiolus elongatus</i>	North Fiji Basin: 18°49'S, 173°29'W	2000		s	d				3.6		Le Penneec and Beninger (1997)

Table 1 (Continued)

Species	Site	Depth (m)	Environmental timing cues (+/-)	Sexuality	Gameto-genesis (c/d)	Spawning (a/sa/ma)	Gamete size (μm)		Total	Larva/Post-larva (μm)	References	
							♀	♂ Head				
<i>Bathymodiolus childressi</i>	Gulf of Mexico: 27°43'N, 91°16'W	710			d?	a?	80 max.	3.9			Eckelbarger and Young (1999)	
<i>Bathymodiolus thermophilus</i>	Galapagos rift: 0°48'N, 86°90'W	2495		s	c		53.9			PI: 95	Lutz et al. (1980)	
	EPR: 12°80', 103°56'W	2630		s	c		55.9			PI: 108 PII: 470	Berg (1985)	
<i>Bathymodiolus puteoserpentis</i>	MAR: Snake Pit vents	3480		s	d			3.2			Le Penneç (1988), Le Penneç and Beninger (1997)	
								3.7		PI: 120	Le Penneç and Beninger (1997), Comtet (1998)	
<i>Acharax alinae</i>	Lau basin	1890		s							No distinction	Métivier and Von Cosel (1993)
	(Fiji islands): 22°32'S 176°43'W				c		600	28		PI/PII: 1350		Beninger and Le Penneç (1997)
<i>Calyptogena kilmeri</i>	Guaymas Basin: Monterey Canyon	900	+	s	d	a/sa?	58–80					Lisin et al. (1997)
<i>Calyptogena pacifica</i>	Monterey Canyon	600	+	s	d	a/sa?	68–74					Lisin et al. (1997)
	EPR/Juan de Fuca			s	c		110	3.5				Le Penneç (unpublished)

Table 1 (Continued)

Species	Site	Depth (m)	Environmental timing cues (+/–)	Sexuality	Gametogenesis (c/d)	Spawning (a/sa/ma)	Gamete size (µm)			Larva/Post-larva (µm)	References
							♀	♂ Head	Total		
<i>Calyptogena soyoae</i>	Sagami Bay (Japan)	1160		s	c						Endow and Ohta (1990)
<i>Calyptogena magnifica</i>	Galapagos rift: 0°48'N, 86°90'W	2450		s	c		173.8				Berg and Turner (1980); Berg (1985)
	EPR: 20°50'N, 109°06'W	2600		s	c		160		PI:240/PII: 450		Berg (1985)
	EPR: 20°50'N, 109°06'W	2600		s	c		105–195				Boss and Turner (1980)
	EPR: 9°50'N, 109°17'W	2515	–	s	c		110–200	3			Le Pennec (unpublished)
<i>Calyptogena phaseoliformis</i>	Japan Trench: 35°54'N, 142°30'E	5695		s	c		180	4.8			Le Pennec (unpublished)

^a +/–, presence or absence of environmental timing cues; a/sa/ma, annual, semi-annual, multi-annual spawning; c/d, continuous or discontinuous gametogenesis; s, sexes separate or successive hermaphrodite; blank spaces, data unavailable;?, data does not allow confirmation of inferred reproductive pattern/activity.

sexual maturity. The available results indicate that simultaneous hermaphroditism is not common (Table 1). No simultaneous hermaphrodites were observed in the *B. thermophilus* specimens studied by Berg (1985), while only 2 of 20 specimens of *B. thermophilus*, and only 1 of 5 specimens of *Calypptogena phaseoliformis* were observed to be simultaneous hermaphrodites (Le Pennec, unpublished). The limited data rarely allow to distinguish between the dioecious and the successive hermaphrodite modes; *C. magnifica* appears to present one or the other (or both) of these modes, since no simultaneous hermaphrodites were observed in the specimens studied by Berg (1985). A protandric hermaphroditism was suggested for *Bathypecten elongatus* (Le Pennec and Beninger, 1997), and for *B. azoricus* (Comtet, 1998). Quantitative size-class data establish a protandric hermaphroditism for the tropical lucinid *L. pectinata*, with considerable variation among samples (Frenkiel and Mouëza, 1985). To this point, then, it seems that the dominant mode of sexuality in the above species is either dioecious or successive hermaphrodite; much more data will be required to refine this conclusion.

3.3. Reproductive cycle

Published reports of the reproductive activity of bivalves in general, and of reducing-system bivalves in particular, are rather ambiguous. One source of ambiguity is the scale of reference: the individual organism or the population. An individual organism may present a particular reproductive pattern, but within a population there may be several concurrent patterns (Hadfield and Strathmann 1996), such that reproductive activity may be labelled 'continuous' for the population, but may be discontinuous for many individuals (Gustafson et al. 1987). Second, the terms 'continuous' and 'discontinuous' themselves are imprecise, since reproductive activity comprises several processes which are not strictly cotemporaneous, such as gametogenesis and gamete emission. Third, the techniques for evaluating the various aspects of reproductive activity are quite heterogeneous, ranging from reporting the simple presence of gamete types (e.g. for *Acharax alinae*, where only one specimen of each sex was available — Beninger and Le Pennec, 1997), the measurement of oocyte diameters (Gustafson et al. 1987; Lisin

et al., 1997), and stereological scoring of the gonad tissue types (Lisin et al., 1997). Fourth, spawning pattern cannot be concluded based solely on mature oocyte presence, since oocytes may be stored in the gonad; time-series observations are necessary to determine when the proportion of mature oocytes declines. Such ambiguity concerning 'reproductive activity' may be at least partly responsible for the seemingly contradictory results for species of similar habitats and life histories (see Frenkiel et al., 1997; Lisin et al., 1997).

In the present paper, we attempt to reduce ambiguity by first distinguishing between gametogenesis and spawning, since mature gametes may be present (stored) without being destined for imminent spawning. The relative amount of connective acinal or inter-acinal tissue constitutes a measure of gametogenic activity which indicates the state of reserves used for gametogenesis (Loosanoff, 1937; Coe, 1943; Reddiah, 1962; Kennedy and Battle, 1964; Loosanoff, 1965; Naidu, 1970; Beninger, 1987; Frenkiel et al., 1997). A decrease in the relative amount of connective acinal or inter-acinal tissue indicates active gametogenesis and not storage; a large amount of acinal or inter-acinal tissue, with mature gametes, indicates storage. Gametogenesis may therefore be designated as continuous when the amount of inter-acinal tissue or the thickness of the acinal wall remains small throughout the year, and discontinuous when the amount of such tissue varies markedly within the year. Unfortunately, very few studies present such data, and we must largely rely on observations of gamete presence and maturity (Table 1); future work should include this important aspect.

The second criterion of reproductive activity is spawning. Although this does not provide information on the dynamics of reproductive activity between spawning periods, continuous spawning can indicate continuous gametogenesis. While the data on successive hermaphroditism (see above) indicates that at least some of the larger Type 3 bivalves are iteroparous, virtually no reliable data are available for the smaller species. We must therefore limit our discussion to the three iteroparous patterns generally observed in bivalves, with allowances for scales (see above) and reproductive flexibility (Hadfield and Strath-

mann, 1996): annual spawning for species which emit their gametes once per year, semiannual spawning for species which emit their gametes twice per year, and continuous (dribble) spawning for species which emit small numbers of gametes throughout the year or throughout the period between annual and semiannual emissions.

Cyclic environmental events are present in almost all littoral habitats, and may function as reproductive timing cues. The principal known environmental timing factors are temperature (Sastry, 1963; Caddy, 1967; Sastry, 1979; Alatalo et al., 1984; MacDonald and Thompson, 1986; Beukema, 1992; Minchin, 1993; Olive, 1995), photoperiod (Sastry, 1970; Olive 1995), tidal rhythm (Korringa, 1955; Gillmor, 1982; Borrero, 1987; Gouletquer et al., 1987; Walker and Heffernan, 1994; Honkoop and Van Der Meer, 1997), phytoplankton density and quality (Lubet, 1976; Sastry, 1979; Newell et al., 1982; Lubet, 1986; MacDonald and Thompson, 1986; Barber et al., 1988; Hilbish and Zimmerman 1988; Paulet and Boucher, 1991; Mathieu and Lubet, 1993; Olive, 1995), and salinity (Le Dantec, 1968; Lubet and Choquet, 1971; Lubet, 1981; Cox and Mann, 1992). In Type 3 littoral species, the limited data available suggest that the pattern of reproductive activity depends on the degree of trophic dependence on endosymbionts (Table 1). The mixotrophic lucinid *Loripes lucinalis* presents a peak in oocyte acinal occupancy in the Bay of Brest in May which coincides with the spring phytoplankton bloom and is more intense than the peak in October (Johnson and Le Pennec, 1994; Le Pennec et al., 1995b). This species also presents marked seasonal variations in acinal wall thickness, which varies inversely to the amount of mature gametes in the gonad (Johnson and Le Pennec, 1994). Conversely, the obligate symbiont *Solemya reidi* displays continuous gametogenesis and spawning (Gustafson et al., 1987).

Although conventional wisdom is that tropical littoral habitats lack cyclic environmental factors, this is not the case for the vast majority of the littoral regions which span 60° about the equator. Virtually every tropical littoral habitat presents either a detectable tidal cycle, seasonal differences (e.g. rainy and dry), small photoperiod differences, or cyclic changes in seston composition (e.g. Frenkiel et al., 1997; see also review by Eckelbarger and Watling, 1995). Distinct reproductive cycles are observed in the tropical Type 3

mixotrophic littoral species *Codakia orbicularis*: the gonads are mature from May to September (Gros, 1997), but gamete emission occurs essentially during August and September (Berg and Alatalo, 1984). Similarly, the mixotrophic Type 3 tropical lucinid *L. pectinata* displays discontinuous reproductive gametogenesis (validated by variations in acinal wall thickness), but the small number and near-uniform maturity of the oocytes indicates storage for spawning at any time throughout the year (Frenkiel et al. 1997). Taken together, these fragmentary data therefore indicate that mixotrophic littoral Type 3 species possess discontinuous reproductive activity, regulated by environmental timing cues, whereas obligate symbionts, whose trophic input is independent of environmental events, present continuous reproductive activity.

Data concerning the reproductive cycles of deep-sea reducing-habitat species are even more sparse than those for littoral species (see Tyler and Young, 1999 for recent review). Due to sampling constraints, no complete study of the gametogenic activity of any deep-sea species has been performed. Nevertheless, the scattered data on various deep-sea symbiotic species and various sites allows a tentative framework to be constructed, along with working hypotheses concerning reproductive strategy.

The degree of cyclicity in the reproductive activity of deep-sea Type 3 species appears to be directly related to (1) the presence of environmental timing/conditioning cues, and (2) the degree of trophic dependence on endosymbionts. Environmental timing/conditioning cues in the deep-sea habitat include the downward flux of seasonally-produced particulate organic matter (Khripounoff and Albéric, 1991; see also Eckelbarger and Watling, 1995 for review), and thermal fluctuations created by tidal cycles (Chevaldonné, 1996). The mixotrophic species of the *Bathymodiolus* genus illustrate this point. Discontinuous spermatogenesis was strongly suggested for *B. puteoserpentis* and *B. elongatus* (Le Pennec and Beninger, 1997), and more recently for *Bathymodiolus azoricus* from the Lucky Strike and Menez Gwen mid-Atlantic ridge fields, which presents a complete gametogenic resting phase (Comtet, 1998). *B. puteoserpentis* and *B. azoricus* both inhabit the temperate mid-Atlantic Ridge, and could thus be subject to seasonal fluctuations in

the production of epipelagic organic matter, known to regulate life-cycles in the deep-sea (Tyler, 1988; Eckelbarger and Watling, 1995). The members of the *Bathymodiolus* genus are mixotrophic (Le Pennec, 1988; Le Pennec *et al.*, 1992), and inhabit the upper bathyal regions, where they would be exposed to such seasonal fluctuations in food availability. The relative shallowness of these sites also allow them to be affected by the semi-diurnal tidally-generated thermal fluctuations observed in the habitats of symbiotic species (Chevaldonné *et al.*, 1991; Zal *et al.*, 1995; Chevaldonné, 1996), which could also participate in the timing of reproductive activity as suggested for *Bathymodiolus* spp. (Comtet, 1998). The reports of 'continuous' ovogenesis in *B. thermophilus* (Lutz *et al.* 1980; Berg, 1985; Le Pennec, 1988) are not necessarily at variance with the idea of major spawning cycles in this mixotrophic genus, since these observations are based only on the simultaneous presence of all gamete stages in the gonad of specimens recovered at unique dates and sites rather than over a period of time from the same site, and may therefore simply indicate arrested gametogenesis or dribble spawning between major emissions. This uncertainty underscores the need for time-series data, particularly costly and difficult to obtain for these oceanic deep-sea species.

Deep-sea species which rely totally on endosymbionts and inhabit depths which present no cyclic environmental cues could be expected to present true continuous gametogenesis. However, once again the lack of time-series data does not allow firm conclusions to be drawn; although *A.alinae* displayed all gamete stages simultaneously (Beninger and Le Pennec, 1997), this observation is subject to the same caveat as the example above.

3.4. Gametes

Bivalve spermatozoa are generally small; the mean head and midpiece length for 44 species belonging to 17 families is 5.1 ± 3.7 μm (standard error), and the corresponding mean flagellum length is 34 ± 17.1 μm (Beninger and Le Pennec, 1997). In contrast, the spermatozoon lengths are much more diverse in Type 3 species. The vesicomimid spermatozoa are slightly smaller than the mean reported above, at 3–4.8 μm head + midpiece length (Le Pennec, unpublished); similarly,

symbiotic mytilids present a head + midpiece length of 3.6–3.7 μm . The corresponding lengths greatly exceed the mean in *L. lucinalis* (10.5 μm — Johnson *et al.*, 1996), *C. orbicularis* (18–20 μm — Mouëza and Frenkiel, 1995), and *A.alinae*, which holds the world bivalve record to date at 28 μm (Beninger and Le Pennec, 1997). This extraordinary spermatozoon size range among Type 3 species is probably in part a consequence of the wide range of oocyte size (see below), since the general rule appears to be that large oocytes necessitate large spermatozoa for effective fertilization (Beninger and Le Pennec, 1997, but see gamete sizes for Vesicomymidae (Table 1) and *Scrobicularia plana* in Beninger and Le Pennec, 1997).

Littoral non-reducing system bivalve species present oocytes which range from 40 to 200 μm in size, equal to a range ratio of 1:5 (see Beninger and Le Pennec, 1997). Notwithstanding, littoral non-reducing system bivalves present a relatively homogeneous intraspecific oocyte size (Franc, 1960; Allen, 1961; Sastry, 1979; Lubet, 1986; Beninger and Le Pennec, 1997). The potential significance of egg sizes in relation to larval developmental strategies is discussed below.

The only data on variability in mature oocyte sizes in littoral reducing system bivalves was presented for the mixotrophic *L. lucinalis* (Johnson and Le Pennec, 1994; Le Pennec *et al.*, 1995b). The mature oocytes of this species present a surprising size range, from 14 to 95 μm diameter at different times of the year, although fertilization is only possible at sizes above 55 μm (Johnson and Le Pennec, 1994; Le Pennec *et al.*, 1995b). The increased size of *L. lucinalis* oocytes corresponds to an increase in both phytoplankton density and in the transfer of metabolites from symbiotic bacteria to the gonad during the spring phytoplankton bloom in May (Johnson and Le Pennec, 1994), demonstrating a good example of flexibility in oocyte sizes (Hadfield and Strathmann, 1996).

Deep-sea non-symbiotic bivalves possess oocytes of approximately 100–300 μm diameter, rich in vitelline reserves (Thorson, 1946; Scheltema, 1972; Mackie, 1984). The situation is much more complex for deep-sea reducing system bivalves, according to their degree of dependence on endosymbionts. The mixotrophic Mytilidae (*Bathymodiolus* spp.) possess the smallest oocytes of all the vent or seep species, at 40–50 μm from the 13°N site (Le Pennec *et al.* 1984) and 50–60

μm from the Galapagos rift (Berg, 1985), and up to 80 μm in *Bathymodiolus childressi* (Eckelbarger and Young, 1999), in the same range as the littoral *Mytilus edulis* which measure 68–70 μm (Bayne, 1976). The largest oocytes reported to date for any bivalve are those of the obligate symbiotic solemyid *A. alinae*, at approximately 600 μm (Beninger and Le Pennec, 1997); the Vesicomidae fall between these extremes at 150–200 μm (Table 1, Berg and Turner 1980; Boss and Turner 1980; Berg 1985; Le Pennec, unpublished). These sparse data suggest that mixotrophic deep-sea reducing environment species possess the smallest oocytes, while the obligate symbiotic species possess the largest oocytes. The consequences of this relationship are explored below.

Another characteristic of oocyte sizes in deep-sea reducing system bivalves is the large degree of intraspecific variability and/or polytypy (sensu Hadfield and Strathmann, 1996), as was also pointed out for littoral reducing system bivalves. This is well illustrated in *C. magnifica*, where reported diameters from the Galapagos rift are 150–195 μm (Boss and Turner, 1980), 173.8 μm mean diameter (Berg 1985), a maximum of 309 μm from a small sample (Berg and Turner, 1980), and 364–382 μm for seven oocytes found in the jar containing a single fixed female (Berg and Turner, 1980). Diameters reported from other sites are 160 μm at 21°N (Kennish and Lutz, 1992), and 100–200 μm at 9°N (Berg, 1985; Le Pennec, unpublished). The variability in mature oocyte sizes again suggests that they may be viable above a minimum threshold size, and that additional reserves are incorporated to the limits imposed by metabolite availability from either particulate + dissolved matter (mixotrophs) or endosymbionts (mixotrophs and obligate symbionts).

3.5. Symbiont acquisition

Two modes of symbiont acquisition may be envisaged: inter-generational transfer via gametes, or environmental contamination of the early developmental stages. These have been termed vertical and horizontal transmission, respectively (Endow and Ohta, 1990; Cary and Giovannoni, 1993; Cary 1994), although this nomenclature poses some borderline semantic problems. In effect, it is extremely difficult to demonstrate complete inter-generational transmission, since this

would require either identifying the symbionts in the gonad, or identifying bacterial gene sequences in individual gonad, both of which would be extremely difficult to execute. As shown below, in the few studies to date vertical transmission has been inferred from the presence of endosymbionts or their DNA in either later-stage gametes, inter-acinal tissue, or pooled gamete assemblages. Since it is so difficult to rule out environmental transmission (e.g. infection of gonad during gametogenesis), we propose a terminology based on medium of acquisition, rather than on the 'nature–nurture' notion. *Transgonadal* acquisition thus applies when the symbionts are acquired by the gametes within the gonad, whereas *postspawning* acquisition occurs when the symbionts are acquired following gamete release to the environment.

To date, all examples of transgonadal acquisition have been transovarial. Such a mode of transfer has been proposed and confirmed for the obligate symbionts *S. reidi* and *S. velum* (Gustafson and Reid 1988; Cary and Giovannoni, 1993; Cary, 1994; Krueger et al., 1996), and several species of the *Calyptogena* genus: *C. soyoae* (Endow and Ohta 1990), *C. magnifica*, *C. phaseoliformis*, and *C. pacifica* (Cary and Giovannoni 1993). In the mixotrophic species studied to date, however, postspawning transmission seems to be the rule, as shown for four species of lucinid (Gros et al. 1998a), *C. orbicularis* (Gros et al. 1996, 1998b), and *B. thermophilus* (Herry and Le Pennec, 1987). The fundamental difference in mode of symbiont acquisition between obligate symbionts and mixotrophs, if confirmed by future studies, underscores the closeness of the host–symbiont relationship in the former.

3.6. Larval developmental strategies

The options available for larval development are influenced by oocyte size. It is tempting to consider species with small oocyte dimensions to present planktotrophic development, whereas those with the larger oocyte dimensions would present predominantly lecithotrophic or direct development (Ockelmann, 1965; Scheltema, 1972, 1977; Sastry, 1979; Franzén, 1983; Gustafson and Reid, 1986). However, egg size may also reflect developmental rate within a developmental type, such that for the same temperature planktotrophic species with large eggs may present a

faster developmental rate due to the availability of stored reserves, whereas planktotrophic species with smaller eggs may present a slower developmental rate (dependant on food availability) (Allen 1961). Littoral Type 1 and Type 2 bivalves present oocytes of this type, generally from 40 to 100 μm in diameter; the developmental strategy is initially endotrophic, rapidly evolving to mixotrophic and finally exotrophic (Lucas et al., 1986). Environmental factors being equal, and notwithstanding species-specific variability and polytypy (Hadfield and Strathmann, 1996), the size of the prodissoconch I (PI) in the developing veliger larva of a given species is directly related to oocyte size, while the size of the prodissoconch II (PII) indicates the duration of the planktonic larval life (Ockelmann, 1965; Mileikovsky, 1974; Jablonski and Lutz, 1980; Lutz et al., 1980).

Superimposed upon the oocyte size-dependent options for larval trophic strategy is the larval dispersal strategy, itself dependent on habitat constraints. Dispersive larval forms will be favoured in habitats which are geographically contiguous and temporally stable; this is the case for most Type 1 and Type 2 species. Dispersive larval forms may be either endotrophic or exotrophic, the chief characteristic of dispersal being transport over long distances. Dispersive larval forms will also be favoured in habitats which are geographically isolated and temporally unstable, since individuals in any given generation cannot predict the remaining habitat longevity; this is the case for deep-sea vents and seeps (Mullineaux and France, 1995). Retentive larval stages will be favoured in habitats which are geographically isolated and/or temporally stable (Allen, 1961; Boss and Merrill, 1965; Blacknell and Ansell, 1974; Runham, 1993; Hadfield and Strathmann, 1996); larval development will be short (limiting dispersal), as in *S. reidi* (Gustafson and Reid 1986). A large oocyte size may therefore indicate either rapid development tending to restrict dispersal, or slower development tending to favour dispersal. However, since slower development is the rule in cool waters (see Hadfield and Strathmann, 1996), and in particular the cool waters of the deep-sea environment (Mullineaux and France, 1995), it is likely that large oocytes encountered in such species indicate prolonged development during dispersal.

The available data on larval development in Type 3 bivalves is still far too scanty to allow

reliable generalizations. However, as noted above, the genus *Bathymodiolus* presents the smallest oocytes of all the vent or seep species (Table 1), well within the range for Type 1 and Type 2 species; the small oocyte size argues strongly for an early exotrophic strategy (Ockelmann, 1965; Turner et al., 1985). The existence of such a strategy in this genus may reflect their limited reliance on endosymbionts relative to other Type 3 species (Le Pennec et al., 1995a), i.e. the adoption of a bivalent trophic strategy since their presumed origin in shallow seeps (Craddock et al., 1995), and also corresponds to their limited depth distribution compared to the other vent species (Table 1). Given the considerations outlined above, it is tempting to conclude that the large oocyte and prodissoconch sizes in many of the more obligate symbiont species (Table 1) are related to the geographic isolation and temporal instability of vent and seep habitats, which when combined with the low temperatures of the deep-sea waters favour a protracted larval dispersal, thus increasing the probability of finding another site. This suggestion is supported by the observation that the oocytes of the species *C. magnifica*, *C. pacifica*, and *C. kilmeri* are large and float (Cary and Giovannoni, 1993; Lisin et al., 1993). It is thus clear that in the absence of data on larval development times in reducing-habitat species, hypotheses must take into account not only egg and prodissoconch sizes, but also degree of habitat isolation and stability, as well as temperature. Attempts to definitively relate larval development and dispersal strategies to oocyte size await clear data on dispersal indicators such as gene flow, lipid biomarkers, and physiological tolerances (see Tyler and Young, 1999 for review). Firm conclusions must also await data on larval durations in each species, which will require a considerable research effort both in the field and in the laboratory, especially for vent and seep species.

4. Conclusion

Type 3 reducing-system bivalves present reproductive particularities associated with their habitat and with their degree of reliance on bacterial endosymbionts. The data on size-at-maturity and sexuality are far too limited to allow general patterns or conclusions to be drawn, and this is an aspect which requires much more extensive sampling and study.

In the assessment of reproductive activity, we suggest that gametogenesis and spawning each be considered as components of this process. The sparse data to this point indicate that both tropical and temperate species from littoral reducing habitats display patterns of reproductive activity related to their degree of trophic dependance on endosymbionts, with obligate symbionts presenting continuous gametogenesis and spawning, and mixotrophic species characterized by cyclic reproductive activity corresponding to environmental timing/conditioning cues present in littoral habitats. For deep-sea species, the degree of cyclicity appears to be related to both the presence or absence of environmental timing cues and the degree of trophic dependance on endosymbionts: discontinuous reproductive activity is observed in species subjected to environmental timing cues, whereas in habitats lacking such cues, mixotrophic species show cyclic activity but obligate symbionts display continuous activity.

The size range of spermatozoa is much greater in Type 3 species than in those whose pallial cavity is not exposed to reducing substances; this probably reflects the diversity of oocyte sizes. In littoral species, the great intraspecific range in oocyte sizes may correspond to a flexible response to phytoplankton availability. Most deep-sea species present a direct relationship between oocyte sizes and degree of dependence on endosymbionts, with a large measure of intraspecific variability and/or polytypy, indicating varying contributions from particulate matter (mixotrophs) or endosymbionts (obligate symbionts). A notable exception to this pattern is the genus *Bathymodiolus*, which possesses oocytes in the same size range as the exotrophic littoral Type 1 species. This could be a consequence of phylogenetic constraints (sensu Eckelbarger and Watling, 1995), or simply the adoption of a bivalent trophic strategy.

The terms 'vertical' and 'horizontal', commonly used to distinguish between parental and environmental transmission of endosymbionts, are inadequate, since it is presently impossible to demonstrate complete and exclusive inter-generational transmission. As noted for reproductive activity and gamete sizes, differences in the mode of symbiont acquisition also appear subject to the degree of trophic reliance on endosymbionts. Transgonadal acquisition appears to be the rule in obligate symbiont bivalves, whereas postspawning transmission is observed in mixotrophic species.

Larval development and dispersal strategies can be partially deduced from oocyte and prodissoconch sizes, and these again appear to be related to the degree of trophic reliance on endosymbionts. The data are too scanty to indicate whether this pattern is related to larval duration, trophic strategy, or dispersal strategy. Additional data on larval duration, obtained both in situ and in pressurized incubation vessels, as well as much more extensive information on larval dispersal, will be required in order to resolve this question. As in the case of the study of reproductive activity, the costs of in situ monitoring are prohibitive, so some aspects of the reproductive biology of deep-sea reducing-system bivalves may remain unresolved.

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