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0300-9629(94)00211-8

MINI REVIEW

Feeding and digestive adaptations of bivalve molluscs to sulphide-rich habitats

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From the standpoint of sulphide availability, marine bivalves are divided into three categories: Type 1, external environment and pallial cavities low in sulphides while submerged; Type 2, external environment containing sulphides but pallial cavity normoxic and low in sulphides due to irrigation via siphons; and Type 3, external habitat variably rich in sulphides and pallial cavity with some oxygen and also suphides, due to lack of siphons. This review presents the known anatomical and physiological adaptations associated with feeding and digestion in Type 3 bivalves, compared with Types 1 and 2. The principal anatomical adaptations of Type 3 bivalves to habitats of increasing sulphide availability are, in order of occurrence and degree: reduction of labial palps; reduction in length and volume of intestine; reduction in stomach volume; disappearance of crystalline style and style sac; reduction in digestive tubule volume; disappearance of digestive gland secretory cells; and total disappearance of the digestive system. In parallel with the above adaptations, an increasing physiological reliance on endosymbiotic bacteria is observed, as evidenced from $\delta^{13}C$ values. We conclude that, under similar conditions of environmental sulphide availability, similar adaptations are found in the feeding/digestive system, irrespective of taxon, depth or geographic location. The convergence between littoral and deep-sea vent and seep inhabitants is particularly striking.

Key words: Feeding; Digestion; Bivalves; Sulphide; Adaptations; Littoral; Hydrothermal; Bacteria; Endosymbionts.

Comp. Biochem. Physiol. 111A, 183–189, 1995.

Introduction

Marine bivalves inhabit a wide variety of environments characterized not only by their physical location (epibenthic, endobenthic), but also by the chemical characteristics of these environments. In the past 15 years, considerable research has focussed on bivalves from the spectacular deep-sea hydrothermal sulphide vents and seeps; more recently, bivalves inhabit-

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ing sulphide-rich littoral sediments have also been studied (Cavanaugh *et al.*, 1981; Felbeck *et al.*, 1981; Fisher and Hand, 1984; Cavanaugh, 1985; Morton, 1986; Reid and Brand, 1986; Le Pennec, 1988; Le Pennec *et al.*, 1990; Tunnicliffe, 1991). These organisms present diverse physiological mechanisms which enable them to inhabit such environments (Cavanaugh, 1983; Childress *et al.*, 1984; Arp *et al.*, 1987; Brooks *et al.*, 1987; Doeller *et al.*, 1988; Vismann, 1991). Although many aspects of their biology are poorly understood (e.g. larval biology, detoxification, site colonization), the process of nutrition has been intensively studied since the first deep-sea vent animals were sampled

(see Childress and Fisher, 1992; Kennish and Lutz, 1992 for review and references). The principal characteristics of the trophic strategies have thus been determined for a number of species (Felbeck *et al.*, 1981; Cavanaugh, 1983; Schweimanns and Felbeck, 1985; Spiro *et al.*, 1986; Southward, 1986; Morton, 1986; Rau and Hedges, 1987; Le Pennec *et al.*, 1990). Recently, a deep-sea mytilid inhabiting methane seeps has also been discovered, and some aspects of its feeding have been determined (Page *et al.*, 1990).

The present review focusses on the feeding and digestive adaptations of bivalves inhabiting sulphide-rich environments. In their paper on the evolution of sulphide-sediment bivalves, Reid and Brand (1986) distinguished between endobenthic bivalves on the basis of the presence or absence of a siphon; this attribute determined the extent of exposure to reducing substances in the pallial cavity. More generally, from the standpoint of sulphide availability, bivalves may be divided into three categories: those whose external environment and pallial cavities lack sulphides (Type 1), those whose external environment contains some sulphides but whose pallial cavities are devoid of sulphides due to irrigation via the siphons (Type 2), and those whose external environment contains variable concentrations of sulphides and whose pallial cavities contain some oxygen as well as sulphides, due to a lack of siphons (Type 3). The following discussion will focus on littoral and deep-sea Type 3 bivalves, with reference to Types 1 and 2 for comparison.

Bivalves constitute a major component of sulphide-rich ecosystems. In the deep-sea vent and seep systems, species of the Vesicomyidae, Mytilidae, Solemyidae and Pectinidae families are found, whereas littoral hypoxic or reducing habitats are abundantly colonized by a number of bivalve families. The chemical characteristics of these habitats are not, however, homogeneous; rather, heterogeneity is a function of the availability of oxygen and sulphur-rich reducing substances. In the case of hydrothermal vents, for example, a gradient of decreasing oxygen and increasing sulphides is observed toward the vent origin; this gradient may be affected by current hydrology (Edmond and Von Damm, 1983). Similarly, littoral habitats vary widely in their degree of sulphide availability, from salt marshes and mud flats to eutrophic harbours and pulp-mill effluent sites (Schweimanns and Felbeck, 1985; Southward, 1986; Diouris *et al.*, 1989). The purpose of the present review is to draw together knowledge of the feeding and digestive system adaptations in bivalves inhabiting environments of varying sulphide availability, and to relate this to the characteristics of each habitat type. It will be shown that convergent adaptations are found in habitats as superficially different as deep-sea vents and shallow-water littoral systems, and that adaptations to these habitats correspond to the degree of sulphide availability, regardless of depth or geographic separation of the species considered.

Data base

Most of the data for this review are derived from existing literature sources; these are listed in Table 1. Additional original data is presented where appropriate.

Discussion

Type 1 bivalves have variously-developed labial palps, even within the same species. This has been linked to habitat particle load (Kiørboe and Møhlenberg, 1981) and also to intrinsic differences in pallial organ specialization for the regulation of ingestion volume regulation (Beninger *et al.*, in prep.). The stomach contents of *Placopecten magellanicus* and *Mytilus edulis* have been examined and shown to contain abundant planctonic organisms, and their digestive glands possess functioning secretory and absorptive cell types (Robinson *et al.*, 1981; Shumway *et al.*, 1987; Beninger and Le Pennec, 1993). The gills of several species have been examined thoroughly, and bacteriocytes have never been observed (e.g. Le Pennec *et al.*, 1988c; Beninger *et al.*, 1993). Examination of the only such report in the gill of *Spisula subtruncata* (Bouvy *et al.*, 1986) shows an erroneous interpretation of rickettsia-like nodules (very common in bivalve gill filaments) as bacteriocytes.

Type 2 species, such as *Tapes decussatus* and *Abra tenuis* which may be found in both sulphide-containing and sulphide-absent sediments, are characterized by well-developed labial palps, abundant stomach contents, and functioning digestive gland cells (Grassé, 1960; Henry, 1987). No gill bacteriocytes are present (Grassé, 1960), and the $\delta^{13}C$ values for these species, -18.1% to -20.1%, are consistent with a phytoplankton-based food source (Le Pennec *et al.*, 1994).

Type 3 bivalves which colonize sulphide-containing habitats as varied as deep-sea hydrothermal vents, subduction zones, ports, reducing-chemical effluent zones and salt marshes all present striking modifications of their gills: a considerable increase in volume, accompanied by the transformation of most epithelial cells to bacteriocytes (Cavanaugh *et al.*, 1981; Felbeck *et al.*, 1981; Cavanaugh,

Table 1. Sampling sites and references concerning data of bivalves studied

Bivalve type	Habitat	Site	Reference
Type 1			
Mytilus edulis	Epibenthic	44°35′N, 64°12′W	Robinson *et al.* (1981); Beninger and Le Pennec (1993)
Placapecten magnellanicus	Epibenthic	45°06′N, 67°02′W	Shumway *et al.* (1987); Beninger *et al.* (1990a,b)
Crassostrea virginica	Epibenthic	/ 46°10′N, 64°20′W	Galtsoff (1964); Beninger *et al.* (1991 and in preparation); Robinson *et al.* (1981)
Type 2			
Tapes decussatus	Endobethic	48°33′N, 4°25′W	Le Pennec (unpublished data)
Abra tenuis	Endobethic	48°23′N, 4°25′W	Le Pennec (unpublished data)
Type 3 littoral			
Lucinella divaricata	Endobethic	48°13′N, 4°30′W	Herry and Le Pennec (1987)
Loripes lucinalis	Endobethic	48°23′N, 4°25′W	Le Pennec *et al.* (1994)
Thyasira flexuosa	Endobethic	48°23′N, 4°25′W	Le Pennec *et al.* (1988a); Reid and Brand (1986); Bernard (1972)
Solemya velum	Endobethic	41°32′N, 70°39′W	Conway and Capuzzo (1990); Krueger *et al.* (1992)
Solemya reidi	Endobethic	49°23′N, 123°06′W	Reid (1980); Fisher and Childress (1986)
Type 3 deep sea			
Bathypecten vulcani	Vent fringe epibenthic	12°49′N, 103°56′W	Le Pennec *et al.* (1988b)
Bathypecten sp.	Vent fringe epibenthic	00°48′N, 86°13′W	Le Pennec *et al.* (1988b)
Bathymodiolus thermophilus	Vent ubiquitous epibenthic	12°80′N, 103°56′W 00°50′N, 86°08′W	Le Pennec *et al.* (1988c); Smith (1985)
Calyptogena magnifica	Vent fissures epibenthic	9°50′N, 109°17′W	Le Pennec (unpublished data)
Calyptogena laubieri	Seep hemibenthic	33°36′N, 137°32′E	Le Pennec and Fiala-Médioni (1988)
Calyptogena phaseoliformis	Seep hemibenthic	35°54′N, 142°30′E	Le Pennec and Fiala-Médioni (1988)
Acharax alinae	Seep endobenthic	22°32′N, 176°43′W	Métivier and Von Cosel (1993)

/ Data unavailable.

1983, 1985; Le Pennec and Hily, 1984; Schweimanns and Felbeck, 1985; Fiala-Médioni *et al.*, 1986; Southward, 1986; Herry and Le Pennec, 1987; Le Pennec *et al.*, 1987). Chemoautotrophic bacteria, usually Gram-negative, are progressively degraded by lysosomal enzymes, and the resulting metabolites are distributed throughout the host bivalve (Rau and Hedges 1979; Fry and Sherr, 1984; Le Pennec *et al.*, 1988a; Diouris *et al.*, 1989; Herry *et al.*, 1988). The prevailing view of bivalve digestive system adaptations to hydrothermal habitats is that they possess a reduced stomach and intestine, and obtain their carbon and energy requirements from the sulphide-oxidizing symbiotic bacteria (Cavanaugh, 1985; Vismann, 1991). Comparative study of Type 3 species shows, however, that there is no single set of digestive system adaptations to these habitats; rather, from coastal hypoxic and reducing sites to the deepest waters having yielded endosymbiotic bacteria in bivalves (−5901 m at the foot of the landward wall of the Japan Trench; Fujioka *et al.*, 1988), these organisms present a range of digestive system modifications which are related to the availability of sulphides in their habitat and pallial cavity. The salient features of these modifications are presented in Table 2, and may be compared with the corresponding features of Type 1 and Type 2 species.

Among the littoral Type 3 species, *Lucinella divaricata* inhabits fine sand substrates which are slightly muddy, on the fringes of marsh grass beds. It has a complete and functional digestive system, characterized by abundant stomach contents, a gastric shield and crystalline style, well-developed digestive tubules lined with both secretory and absorptive cells, and highly degraded intestinal contents (Herry and Le Pennec, 1987). Although the gill is greatly modified and comprises bacteriocytes containing endosymbiotic bacteria whose degradation supplies metabolites to the host, it nevertheless conserves functional ciliated tracts which transfer captured particles to the oral region via a ventral particle groove. The polyvalent nutritional strategy of this species has been outlined by Herry and Le Pennec (1987) and by Le Pennec *et al.* (1988a); this has been confirmed by δ^{13}C measurements as shown in Table 2 (Felbeck, 1983; Le Pennec *et al.*, 1994; Rau et Hedges, 1979; Spiro *et al.*, 1986). Spiro *et al.* (1986) concluded that δ^{13}C values of −23.4 to −22.8‰ in the tissues of animals with endosymbiotic gill bacteria indicated that approximately half of their carbon was of bacterial origin; more extreme negative values are found when this proportion increases. Using this guideline, it may be estimated that *L. divaricata* obtains approximately 40% of its metabolic require-

Table 2. Feeding/digestive tract characteristics, bacteriocyte presence and $\delta^{13}C$ values of bivalves studied

Bivalve type	Species	Labial palps	Digestive gland Absorptive cells	Secretory cells	Stomach contents	Bacteriocytes	$\delta^{13}C$ (‰)
Type 1	*Mytilus edulis*	+ +(+)	+ + +	+ + +	+ + +	—	/
	Placopecten magellanicus	+ +	+ + +	+ + +	+ + +	—	/
	Crassostrea virginica	+ + +	+ + +	+ + +	+ + +	—	/
Type 2	*Tapes decussatus*	+ +	+ + +	+ + +	+ + +	—	−20(1)
	Abra tenuis	+ + +	+ + +	+ + +			−20(1)
	Lucinella divaricata	+ +	+ + +	+ + +	+ + +	+	−28.1(1)
Type 3 (littoral)	*Loripes lucinalis*	+	+	+	+ +	+	−32.7
	Thyasira flexuosa	+	+	+	+ +	+	−30(1)
	Solemya velum	+	/	/	+	+ + +	−33.9 to −32.4(1) −32.1 to −30.9(5)
	Solemya reidi	+	—	—	—	+ + +	−30(2)
Type 3 (deep sea)	*Bathypecten vulcani* & *Bathypecten* sp.	+ +	/	/	+ + +	+	/
	Bathymodiolu thermophilus	+ +	+ +	+ +	+ + +	+ + +	−32.7 to −33.9(3)
	Calyptogen magnifica	+	+	+	+ + +	+ + +	−32.6 to −32.7(4)
	Calyptogena laubieri	+	/	/	+ + +	+ + +	/
	Calyptogena phaseoliformis	+	*	—	+	+ + +	/
	Acharax alinae	+	—	—	—	+ + +	/

+ + + well developed or abundant; + +(+) variably well developed; + + normally developed or present; + reduced or rare; — absent; / no data; * bacteriocytes. $\delta^{13}C$ values expressed as ‰: (1) gill (Conway and Capuzzo, 1990; Le Pennec et al., 1994); (2) all tissues (Felbeck, 1983); (3) foot and mantle (Rau and Hedges, 1979); (4) mantle (Rau, 1981); (5) foot (Conway and Capuzzo, 1990).

ments from gill endosymbionts (Le Pennec et al., 1994). *Thyasira flexuosa* also possesses a fully functional digestive tract (Allen, 1959; Herry and Le Pennec, 1987); however, its $\delta^{13}C$ value of −30‰ indicates that it relies more heavily on metabolites provided by its endosymbionts (between 60 and 80% of total metabolites—Le Pennec et al., 1994), which are located within "bacteriosomes" of storage epithelial cells (Reid and Brand, 1986). Ultrastructural studies have shown that digestive activity has a highly seasonal component in this species (Le Pennec et al., 1988a), with reduced activity in the winter months. *Thyasira flexuosa* presumably relies most on its endosymbionts during this period. Such plasticity in carbon source utilization may be typical of the genus *Thyasira*, as has been shown for populations of *T. sarsi* and *T. equalis* in a 4-year study (Dando and Spiro, 1993).

Loripes lucinalis has reduced labial palps and digestive gland, although it still has considerable particulate matter in its intestine, where some digestion probably occurs (Le Pennec, unpublished data). Its $\delta^{13}C$ value of −32.7‰ (Le Pennec et al., 1994) confirms its greater degree of dependence on endosymbiotic bacterial metabolites, compared with either of the preceeding littoral Type 3 species (81%— M. Diouris, Laboratoire de Physiologie Végétale, Université de Bretagne Occidentale, Brest, France, Pers. Comm.).

Solema velum has a very reduced digestive system and hypertrophied gills containing high densities of endosymbiotic bacteria (Conway and Capuzzo, 1990). Although its $\delta^{13}C$ values (−33.9 to −30.9‰; Conway and Capuzzo, 1990) indicate that it may rely on bacterial carbon to the same extent as *Loripes lucinalis*, this species has been shown to ingest suspended algae (Krueger et al. 1992). Although the Solemyidae are protobranchs, *S. velum* is a crude suspension-feeder (Levinton, 1977), ingesting about half that of a type 2 bivalve (*Mya arenaria*), and it is suggested that the majority of its metabolic needs are met via endosymbiotic bacteria (Krueger et al., 1992).

Solemya reidi inhabits an extreme sulphide-rich habitat in littoral waters receiving effluent from paper mills in Alberni Canal near Vancouver, Canada. This species totally lacks a digestive system, such that its metabolic requirements must be met by direct absorption of organic matter and by its gill endosymbionts (Reid, 1980; Fisher and Childress, 1986). Its $\delta^{13}C$ value of −30‰ (Felbeck, 1983) indicates that 60–80% of its metabolites are derived from bacterial endosymbionts; the remainder must therefore originate in dissolved organic matter. Five species of the endobenthic littoral Type 3 genus *Solemya* and the deep-sea endobenthic Type 3 genus *Acharax* are the only known bivalves to have reduced their digestive system to complete absence in the face

of extreme sulphide availability (Métivier and Von Cosel, 1993). Nevertheless, in *Acharax alinae*, labial palps are present and better-developed than those of *Solemya atacama* and *Acharax eremita* (Métivier and Von Cosel, 1993), and a vestigial oral cavity has been observed (Le Pennec, unpublished data). In the deep-sea Type 3 genus *Calyptogena*, two species (*C. laubieri* and *C. phaseoliformis*) live half-buried in the sediment, and this rare bivalve habit is here termed "hemibenthic." *C. phaseoliformis* has a vestigial digestive tract (Le Pennec and Fiala-Médioni, 1988). Digestive tubules are present but extremely reduced; this bivalve is also unique in that its digestive gland absorptive cells (secretory cells absent) are, in reality, bacteriocytes; scanning electron micrographs show degradation of the endosymbionts, suggesting that some metabolites are provided to the host from these cells (Le Pennec, unpublished data). *Calyptogena laubieri* presents a great degree of reduction in its labial palps, intestine, and digestive tubule volume (Table 2), indicative of a nutritional strategy more dependent on its abundant gill bacteriocytes and their endosymbionts. *C. laubieri* appears to continue using its digestive organs (as shown by its heterogeneous stomach contents—Le Pennec and Fiala-Médioni, 1988). *Calyptogena magnifica*, on the other hand, was considered to have a non-functional digestive tract, despite presenting the same modifications as *C. laubieri* (Boss and Turner, 1980). This question was revisited by Morton (1986), who stated that the cytology of its digestive gland allowed it to function. Moreover, recent studies conducted on samples of *C. magnifica* from the 9°N site (Table 1) revealed that the stomachs were filled with various particles and the digestive gland possessed absorptive and secretive cells (Table 2; Le Pennec *et al.*, in preparation). It would thus appear that the digestive system of *C. magnifica* is at least partly functional. Heavy dependence on bacteria endosymbionts may, none the less, be characteristic of the genus, as evidenced by the

$\delta^{13}C$ depletion of $-37‰$ in a new species from the Juan de Fuca ridge vents (Southward *et al.*, 1994).

Among the Type 3 deep-sea bivalves, the epibenthic *Bathypecten vulcani* from the 13°N site and the undetermined epibenthic *Bathypecten* sp. collected at Roses Garden in the Galapagos ridge (Le Pennec *et al.*, 1988b) show the least degree of dependence on bacterial endosymbionts. The gill does not display the hypertrophy associated with reliance on endosymbionts; rather, it contains relatively few bacteriocytes (Le Pennec *et al.*, 1988b). This partial adaptation to sulphide availability may be associated with its distribution in the deep-sea habitat, which it shares with serpulid polychaetes on the fringes of active hydrothermal seeps. The epibenthic *Bathymodiolus thermophilus* also possesses a fully functional digestive tract (Le Pennec *et al.*, 1988c), but bacteriocytes occupy much more of its gill epithelium than either of the two preceding hydrothermal vent species. In addition, its digestive system presents a wide range of digestive enzymes (Le Pennec *et al.*, 1992). *Bathymodiolus thermophilus* is thus much more of a "generalist" in the hydrothermal habitat, being capable of exploiting both suspension-feeding and the production of its endosymbionts, depending on the availability of particulate organic matter and sulphides, respectively. This nutritional polyvalence is reflected in the extent of its epifaunal and epibenthic distribution in the vent zone, from vestimentiferan tubes to basaltic rocks (Smith, 1985). Not surprisingly, *Bathymodiolus thermophilus* is the last bivalve to persist after extinction of its hydrothermal vents (Hessler and Smithey, 1984; Desbruyères and Laubier, 1984).

The foregoing data and discussion show that a pattern of feeding and digestive system adaptations among bivalves is correlated with the sulphide availability of their habitat and pallial cavity, regardless of depth or geographic location (Fig. 1). These adaptations are evidenced in Type 3 species only. The increasing

Reduction of labial palps, appearance of endosymbionts
↓
Reduction in length and volume of the intestine, gill hypertrophy to accomodate endosymbionts
↓
Reduction in stomach volume
↓
Disappearance of the crystalline style and associated style sac
↓
Reduction in digestive tubule volume
↓
Disappearance of digestive gland secretory cells
↓
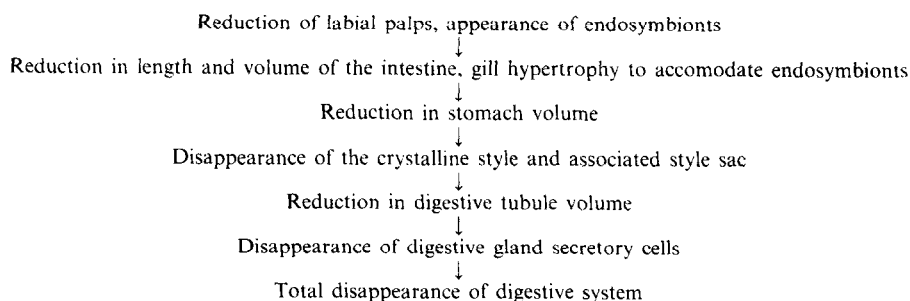Total disappearance of digestive system

Fig. 1. Progressive pattern of feeding and digestive system adaptive characters in Type 3 littoral and deep-sea bivalves, depending on reducer availability.

metabolic reliance on endosymbiotic bacteria parallels this pattern, and obviously constitutes a determining element in the adaptation of bivalves to these environments. Future research might well benefit from enzymatic studies of the digestive systems of Type 3 bivalves, as well as dissolved substance uptake, in order to refine understanding of carbon source utilization in these species.

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