Journal of the Marine Biological Association of the United Kingdom, 2008, 88(2), 331–339. ©2008 Marine Biological Association of the United Kingdom
doi:10.1017/S0025315408000659 Printed in the United Kingdom

Morphology of larvae of the family Mytilidae (Bivalvia) from the north-western part of the Sea of Japan

OLGA YA. SEMENIKHINA, NATALYA K. KOLOTUKHINA AND GEORGE A. EVSEEV

A.V. Zhirmunsky Institute of Marine Biology FEB RAS, 690041 Vladivostok, Russia

*The larval shell morphology of 10 bivalve species of the family Mytilidae (*Adula falcatoides, Crenella decussata, Crenomytilus grayanus, Modiolus kurilensis, Musculista senhousia, Mytilus coruscus, Mytilus galloprovincialis, Mytilus trossulus *and* Septifer keenae*, and an unidentified species Mytilidae indeterminate) from the Sea of Japan is described. The following morphological features were comparatively examined: larval shell outlines including shape and size of umbones, and anterior, posterior and ventral margins, hinge morphology, ligament location, sculpture, colour, and eye-spot outlines. Some dimensional parameters of larval shells are given. The time interval of occurrence of larvae in the plankton, water temperature in this period, and shell length of competent larvae are presented. It is demonstrated that, in spite of sometimes similar external morphological characters, identification of mytilid larvae creates no difficulties if all distinguishing characters are used.*

Keywords: larvae, Mytilidae, shell, hinge, morphology, identification, development, taxonomy

Submitted 17 May 2007; accepted 3 December 2007

INTRODUCTION

The family Mytilidae is one of the most widespread groups of bivalves which form the vast settlements in littoral and upper sublittoral zones of cold, boreal and subtropical waters of the World Ocean and often dominate in benthos communities (Seed, 1976; Scarlato, 1981; Lukanin *et al.*, 1985; Zaika *et al.*, 1990; Seed & Suchanek, 1992; Coan *et al.*, 2000). The mytilids are also common in biofouling communities on anthropogenic substrata as well as being important objects in harvesting and cultivation (Mason, 1976; Lutz, 1980; Suprunovich, 1988; Hickman, 1992).

On different data, from 13 to 16 mytilid species inhabit Peter the Great Bay in the Sea of Japan (Scarlato, 1981; Kafanov, 1991). Development of some mytilids is direct while in the life cycle of others there is a pelagic phase (Table 1). Although pelagic mytilid larvae have been intensively studied several species remained unidentified before our work began (Table 2). The purpose of the present study is to provide the most complete morphological descriptions of pelagic larvae of all Mytilidae species inhabiting the north-western part of the Sea of Japan in order to facilitate their identification in the plankton for population–biological studies including mariculture.

Larvae of 10 mytilid species from Peter the Great Bay in the Sea of Japan are described: *Adula falcatoides* Habe 1955; *Crenella decussata* (Montagu 1808); *Crenomytilus grayanus* (Dunker 1853); *Modiolus kurilensis* Bernard 1983; *Musculista senhousia* (Benson in Cantor 1842); *Mytilus coruscus* Gould 1861; *Mytilus galloprovincialis* Lamarck 1819; *Mytilus trossulus* Gould 1850; and *Septifer keenae* Nomura 1936 as well as an unidentified species Mytilidae indeterminate. The larval descriptions are based on both our own materials and literature data (Table 2).

Corresponding author:
O.Y. Semenikhina
Email: oja@mail.primorye.ru

MATERIALS AND METHODS

Bivalve larvae of the family Mytilidae from Vostok Bay and Possjet Bay of Peter the Great Bay in the Sea of Japan were used in this study. Larvae were sampled using a 96 μm plankton net every 5–10 d from water surface to the bottom in June–September, 2002–2005 in Vostok Bay and in June–September, 2002 in Possjet Bay.

Larvae were preserved in 96% ethanol. Shell morphology was studied by light microscopy and scanning electron microscopy (SEM). Specimens were cleaned with a 5–10% solution of sodium hypochlorite to remove the soft tissues (Rees, 1950). The shells were thoroughly rinsed with distilled water and then embedded in glycerine jelly for light microscopy. For SEM the shells were dehydrated in 96% ethanol and sputter-coated with gold.

For the taxonomic identification of unknown mytilid larvae, planktonic specimens were kept in aquaria for some weeks up to identifiable postlarval or definitive stages. Also, the larval morphological features of the mytilid species from other parts of the World Ocean (Rees, 1950; Loosanoff *et al.*, 1966; Chanley & Andrews, 1971; Zakhvatkina, 1972; Booth, 1977; Le Pennec, 1980; Redfearn *et al.*, 1986; Fuller & Lutz, 1989) were comparatively studied. Furthermore, our own knowledge of planktonic larval periods, gonad maturity of adult molluscs, water temperature in the areas investigated as well as the biogeographical characteristics of the species (Scarlato, 1981) and data on life cycles of other mytilids (Table 1) were used for the specific identification.

https://doi.org/10.1017/S0025315408000659 Published online by Cambridge University Press

Table 1. Developmental type in bivalve molluscs of the family Mytilidae from the north-western part of the Sea of Japan.

Species	Type of development and/or brood care	Source
Adula falcatoides Habe 1955	Pelagic period	Kasyanov *et al.*, 1983; Kulikova & Kolotukhina, 1989
Dacrydium vitreum (Möller 1842)	Pelagic period short or absent; probably lecithotrophic development	Ockelmann, 1958, 1965
	Probably direct development	Naumov *et al.*, 1987
	Without brooding	Salas & Gofas, 1997
Crenella decussata (Montagu 1808)	Pelagic period short or absent; probably lecithotrophic development	Ockelmann, 1958, 1965
	Spheric clutch; pelagic period short	Rusanova, 1963; Naumov *et al.*, 1987
	Pelagic period short; lecithotrophic development	Own data
Crenomytilus grayanus (Dunker 1853)	Pelagic period; planktotrophic development	Drozdov & Kulikova, 1979; Drozdov *et al.*, 1983; Kasyanov *et al.*, 1983; Kulikova & Kolotukhina, 1989; Kalashnikova & Aizdaicher, 1993
Modiolus kurilensis Bernard 1983	Pelagic period; planktotrophic development	Kulikova & Kolotukhina, 1989; Kasyanov *et al.*, 1998
Musculista senhousia (Benson in Cantor 1842)	Egg-strings; pelagic period	Matveeva, 1979
	Clutch absent; pelagic period	Cheung *et al.*, 1962 [cited after Morton, 1974]
	Pelagic period; planktotrophic development	Kulikova, 1978; Kasyanov *et al.*, 1983; Kulikova & Kolotukhina, 1989; Kimura & Sekiguchi, 1994
Musculus corrugatus (Stimpson 1851)	Probably direct development	Naumov *et al.*, 1987
Musculus discors (Linnaeus 1767)	Egg-strings; direct development	Thorson, 1935, 1936; Jorgensen, 1946; Rusanova, 1963; Ockelmann, 1965; Kaufman, 1977; Matveeva, 1979; Naumov *et al.*, 1987
Musculus laevigatus (Gray 1824)	Egg-strings; direct development	Ockelmann, 1958; Rusanova, 1963; Kaufman, 1977; Matveeva, 1979; Naumov *et al.*, 1987
Musculus niger (Gray 1824)	Egg-strings; direct development	Thorson, 1935, 1936; Jorgensen, 1946; Ockelmann, 1958, 1965
	Probably direct development	Naumov *et al.*, 1987
Mytilus coruscus Gould 1861	Pelagic period; planktotrophic development	Yoo, 1969; Hur & Hur, 2000; Semenikhina & Kolotukhina, 2001
Mytilus galloprovincialis Lamarck 1819	Pelagic period; planktotrophic development	Zakhvatkina, 1972; Le Pennec & Masson, 1976; Satuito *et al.*, 1994*
Mytilus trossulus Gould 1850	Pelagic period; planktotrophic development	Kasyanov *et al.*, 1983; Kulikova & Kolotukhina, 1989
Septifer keenae Nomura 1936	Pelagic period short; lecithotrophic development	Own data
Vilasina pillula Bartsch in Scarlato 1960	Spheric clutch; direct development or pelagic period short	Guida & Rakov, 1979; Matveeva, 1979

*As *Mytilus edulis galloprovincialis*.

Approximately 10–20 specimens of every species were used for studying the larval shell morphology. Since early developmental stages of bivalve larvae are hardly distinguished we here concentrate on pediveligers. Larval shell terminology is the same as in works of Rees (1950) and Chanley & Andrews (1971). Provinculum length represented the linear distance between the lateral extremes of the hinge. Shell length was the greatest dimension along any axis of the shell. Shell height was the greatest measurement perpendicular to the hinge line (Lutz & Hidu, 1979; Fuller & Lutz, 1989).

RESULTS

In the family Mytilidae the larval shell is equivalve; its length is always more than its height. The shell shape varies from egg-shaped and triangular–oval to semicircular and D-shaped. Most of the examined species are non-equilateral, and the anterior shoulder is longer than the posterior one but in some species the shell is almost equilateral. In most species the anterior end is slightly pointed and the posterior end is more rounded. In some

Table 2. List of studied pelagic bivalve larvae of the family Mytilidae inhabiting the north-western part of the Sea of Japan.

Species	Source
Adula falcatoides Habe 1955	Kasyanov *et al.*, 1983; Kulikova & Kolotukhina, 1989; Evseev, 2005
Crenomytilus grayanus (Dunker 1853)	Drozdov & Kulikova, 1979; Kasyanov *et al.*, 1983; Kulikova & Kolotukhina, 1989; Kalashnikova & Aizdaicher, 1993; Evseev *et al.*, 2006
Modiolus kurilensis Bernard 1983	Kulikova & Kolotukhina, 1989; Kasyanov *et al.*, 1998; Evseev *et al.*, 2005
Musculista senhousia (Benson in Cantor 1842)	Kulikova, 1978; Tanaka, 1979b; Kasyanov *et al.*, 1983; Kulikova & Kolotukhina, 1989; Sakai & Sekiguchi, 1992; Kimura & Sekiguchi, 1994
Mytilus coruscus Gould 1861	Tanaka, 1979a; Hur & Hur, 2000; Semenikhina & Kolotukhina, 2001
Mytilus galloprovincialis Lamarck 1819	Le Pennec & Masson, 1976; Zakhvatkina, 1972
Mytilus trossulus Gould 1850	Kasyanov *et al.*, 1983; Kulikova & Kolotukhina, 1989; Evseev *et al.*, 2006
Septifer keenae Nomura 1936	Evseev *et al.*, 2004; Evseev *et al.*, 2005

https://doi.org/10.1017/S0025315408000659 Published online by Cambridge University Press

mytilids both ends are rounded and the anterior end is more obtuse. The ventral margin is mostly rounded but in some species it is almost straight. Umbones are usually well-marked and rounded, low, broad, massive or knob-shaped. In some species umbones are not pronounced or very low and hardly clear.

In most mytilids the larval shell surface is covered by more or less prominent co-marginal growth lines but in some species they are absent and the microsculpture is fine-grained. A dark eye-spot is either small and a dot, or large and in the form of a paint-brush stroke. The colour of preserved larva of different species varies from grey to yellow-brown and brown. Shell valves are thin and transparent or convex, massive and relatively non-transparent.

The larval hinge consists of large regular rectangular denticles of taxodont type located in both sides of provinculum and small denticles in its central part. The hinge line is straight or curved. In most species its length significantly exceeds an umbo length. The ligament is located in the central part of the provinculum and somewhat posteriorly displaced; the ligament pit is distinct.

Most mytilid larvae attain a size between 280 and 350 μm before settling, while in several species length of competent larvae does not exceed 190–200 μm.

Adula falcatoides (Figure 1A). The shell is triangular–oval, almost equilateral. The anterior end is raised in contrast to the posterior one; both ends are slightly pointed. The ventral margin is almost straight. The shell is low; a ratio of height to length is 0.75–0.77. Umbones are well-developed, broad and slightly inclined towards the anterior end. The shell is thick, convex and feebly transparent. Larvae are brown but umbones are more intensely coloured. The sculpture consists of distinct, almost regular co-marginal growth lines. The small eye-spot is well-marked.

The hinge is significantly curved and long. Its length amounting to 160–170 μm is considerably greater than umbo length. There are 11–13 large rectangular denticles in both anterior and posterior parts of the provinculum. In contrast to the other species the hinge lacks small denticles. The anterior margin of the umbo is located over the 6th–8th anterior provincular denticle. The ligament is placed in the central part of provinculum.

Larvae settle at a shell length of about 280 μm. Planktonic larvae occur from August to September in Vostok Bay and from July to September in Possjet Bay at water temperatures of 18–22°C and 17–21°C, respectively.

Musculista senhousia (Figure 1B). The shell is non-equilateral, triangular–egg-shaped. The anterior end is slightly pointed and somewhat raised; the posterior and ventral margins are rounded. The shell is high; a ratio of height to length is 0.89–0.92. Umbones are high, rounded and well-developed. The outer shell surface is covered by clearly marked co-marginal lines of growth. The valves are greatly convex and feebly transparent. Larvae are dark brown and umbones are more intensely coloured. The distinct eye-spot is small.

Each side of the provinculum bears 5–7 high rectangular denticles. In the central part of the hinge there are 10–12 denticles, which are smaller but well-marked, too. The hinge line about 100–110 μm long is arched and almost equal to umbo length. The anterior margin of the umbo is located over the first provincular denticle. The ligament is slightly shifted to the end of the central part of the hinge.

Larvae are relatively small; a shell length before settling is approximately 280 μm. In plankton of Vostok Bay and Possjet Bay larvae occur from July to September at water temperatures of 15–22°C and 17–21°C, respectively.

Crenella decussata (Figure 1C). The shell is equilateral, in the form of an almost regular semicircle. The anterior and posterior ends are rounded; the anterior end is more obtuse. The ventral margin is rounded. Umbones are absent. The shell is relatively low; a ratio of height to length is 0.78–0.79. The outer shell surface is fine-grained; the growth lines are absent. The inner broad marginal ridge is clearly visible from the outside of the shell. The larval valves are thin; larvae are dark-grey. The eye-spot is imperceptible.

The very narrow straight provinculum 120–125 μm long bears 8–10 anterior and posterior denticles; in the centre of the hinge line denticles are not distinct. The ligament is located in the central part of the provinculum nearer to its posterior end.

Larvae are small; they undergo metamorphosis at a shell length of 190–200 μm. In plankton of Vostok Bay larvae occur from August to September at a water temperature of 18–22°C.

Septifer keenae (Figure 1D). The shell is slightly non-equilateral, in the form of a semicircle. The anterior end is smoothly rounded; the posterior end is slightly pointed. The posterior margin is somewhat straightened when changing to the rounded ventral margin. The shell is very low; a ratio of height to length is 0.7–0.71. Umbones are absent. The outer shell surface is fine-grained; the growth lines are absent. There is a broad marginal ridge inside the valves. The shell is relatively thick; larvae are grey and slightly violet. The eye-spot is a dot.

The hinge line is straight; its length is about 125–130 μm. The hinge is represented by 4–5 large denticles on the provinculum ends and 18–22 small central denticles. Unlike other species of the family, in *S. keenae* the large denticles do not considerably differ from small ones by their height and width. The ligament is located in the central hinge part but displaced to the posterior provincular end.

Larvae are small; a shell length before metamorphosis is 180–190 μm. In plankton of Vostok Bay larvae occur from August to September at a water temperature of 18–22°C.

Mytilus coruscus (Figure 1E). The shell is non-equilateral, round–egg-shaped. The posterior shoulder is shorter than the anterior one; the obtuse and rounded posterior end is slightly oblique ventrally. The anterior end is somewhat pointed and slightly raised. The ventral margin is rounded. The shell is high; height/length ratio is 0.89–0.92. Umbones are rounded and small. The shell is relatively thin; larvae are greyish. The outer shell surface is covered by well-marked co-marginal lines of growth. The small eye-spot is clearly distinct.

The provinculum consists of 5–6 large denticles located on each side of the hinge and 15–21 small central denticles. The latter are broad in their bases and easily observed. The curved hinge line reaching 115–125 μm is somewhat longer than umbo length. The anterior margin of the umbo is located over the second or third provincular denticle. The ligament is placed at the end of the central provincular part.

Larvae are relatively large; larval shell length is 330–350 μm before settling. In Vostok Bay planktonic larvae occur from August to September at a water temperature of 18–22°C; in Possjet Bay they are common from July to September at a water temperature of 17–21°C.

https://doi.org/10.1017/S0025315408000659 Published online by Cambridge University Press

Mytilus galloprovincialis (Figure 1F). The shell is non-equilateral, round–egg-shaped. The anterior shoulder is longer than the posterior one. The anterior end is slightly pointed and somewhat raised; the posterior end is broader but both ends are rounded. The ventral margin is also rounded. The shell is relatively high; a ratio of height to length is 0.86–0.88. Umbones are rounded and low. The shell is thick and larvae are yellowy-brownish. The shell surface is covered by regular co-marginal growth lines. The eye-spot is large and clear.

The hinge consists of 7–8 large denticles on each side of the provinculum and 16–18 small denticles in the centre. The hinge line 135–145 μm long is slightly curved and exceeds umbo length. The anterior umbo margin is placed over the 5th–6th provincular denticle. The ligament is located at the end of the central hinge part nearer to the posterior provincular denticles.

Larvae are relatively large; they settle at a shell length of approximately 330–350 μm. In plankton of Vostok Bay larvae occur from July to September and in Possjet Bay from June to August at water temperatures of 15–22°C.

Mytilus trossulus (Figure 1G). The shell is non-equilateral, triangular–egg-shaped. The anterior shoulder is slightly longer than the posterior one. The anterior end is pointed and slightly raised. The posterior and ventral margins are rounded. The shell is relatively high; height/length ratio is 0.84–0.87. Umbones are knob-shaped, rounded and narrow. The shell sculpture is represented by thin co-marginal lines of growth. The valves are relatively thin; larvae are yellowish. The distinct eye-spot is small.

The hinge consists of 8–10 large denticles on both sides of the provinculum and 17–20 small denticles in its central part. The hinge line is slightly curved; its length exceeding umbo length reaches 130–140 μm. The anterior margin of the umbo is located over the 6th–7th provincular denticle. The ligament is placed at the end of the central part of the provinculum.

Metamorphosis begins at a shell length of 300–330 μm. In plankton of Vostok Bay larvae occur from June to August at a water temperature of 15–22°C.

Crenomytilus grayanus (Figure 1H). The shell is non-equilateral, oval–elongated. The anterior shoulder is longer than the posterior one; the anterior end is slightly pointed and somewhat raised. The rounded posterior end is slightly drawn ventrally and smoothly changes to rounded ventral margin. The shell is not high; height/length ratio is approximately 0.83. Umbones are broad, rounded and low. The shell is transparent and thin. Larvae are yellowy-greyish, while umbones are more intensely coloured. The sculpture consists of fine co-marginal growth lines. The clearly distinct eye-spot is small.

The hinge line is slightly curved; its length exceeds the umbo length and reaches 130–135 μm. The hinge consists of 8–9 large denticles on both sides of the hinge and 21–25 small central denticles. The anterior margin of the umbo is located over the 4th or 5th provincular denticle. The ligament is placed behind the centre of provinculum at the end of the row of the small denticles.

Metamorphosis begins at a shell length of about 280–300 μm. In plankton of Vostok Bay and Possjet Bay larvae are common in July–September at a water temperature of 15–22°C and 17–21°C, respectively.

Modiolus kurilensis (Figure 1I). The shell is non-equilateral, oblong–egg-shaped. The anterior shoulder is longer than the posterior one; the pointed anterior end is slightly raised. The postero-ventral margin is clearly drawn ventrally; the ventral margin is rounded. The shell is relatively high; a ratio of height to length is 0.85–0.89. Umbones are large, broad and low. The shell is thick and convex resulting in very sharp shell outlines. The outer shell surface is covered by clear co-marginal lines of growth. Larvae are yellow-brownish. The large eye-spot has a distinguishing shape of paint-brush stroke.

The hinge consists of 8–9 large denticles on each side of the hinge row and 18–21 small denticles in its centre. The hinge line is slightly curved; its length reaching 150–155 μm is somewhat greater than the length of the umbo. The anterior margin of the umbo is located over the 5th–6th provincular denticle. The ligament is displaced to the end of the central part of the provinculum.

Larvae are relatively large; they settle at a shell length of 300–330 μm. In Vostok Bay planktonic larvae occur from August to September at a water temperature of 18–22°C; in Possjet Bay larvae are common in July–September at a water temperature of 17–21°C.

Mytilidae indeterminate (Figure 1J). The shell is non-equilateral, triangular–egg-shaped. The posterior shoulder is shorter than the anterior one; the broad rounded posterior end is greatly drawn ventrally. The anterior end is pointed and considerably raised. The ventral margin is somewhat bulging. The shell is not high; a ratio of height to length is 0.79–0.82. Umbones are very low, flat and broad. The shell is thin. Larvae are greyish; their postero-ventral parts are yellowish. The sculpture is represented by fine co-marginal growth lines. The small eye-spot is well-marked.

The hinge consists of 5–7 large denticles on each side of the provinculum and 22–26 very small central denticles. The hinge line is little curved; its length reaching 145–155 μm is greater than umbo length. The anterior margin of the umbo is placed over the 4th–5th provincular denticle. The ligament is located in the central part of the hinge but somewhat displaced towards its posterior end.

A shell length is approximately 280–300 μm before settling. In plankton of Vostok Bay larvae occur from July to September at a water temperature of 17–22°C.

DISCUSSION

Pelagic larvae of the family Mytilidae can be distinguished by their shell outlines; dimensional parameters including length of the anterior and posterior shoulders; shell height to length ratio; outlines and size of umbones; sculpture; colour, and shape and size of an eye-spot. The hinge of the taxodont type consists of large regular rectangular denticles located on each end of the hinge line and, in most cases, small denticles in the central part of the provinculum that is invariably a common internal feature of larvae of all mytilid species. Also in all mytilid larvae studied the ligament is placed in the central part of the provinculum but its closeness to the posterior provincular part varies in different species.

The larval shells of *A. falcatoides* and *M. senhousia* (Figure 1A & B) are characterized by well-developed large umbones. In both species shells are thick, convex, feebly

https://doi.org/10.1017/S0025315408000659 Published online by Cambridge University Press

transparent and dark with more intensely coloured umbones. The co-marginal growth lines are distinct. At the same time in *A. falcatoides* unlike other mytilid larvae the ventral margin is almost straight and a shell height is considerably less than its length. Larvae of *M. senhousia* are relatively small. In both species the hinge line is more curved than in other species of the family, and in *M. senhousia* it is almost equal to the umbo length but in *A. falcatoides* hinge length considerably exceeds umbo length. *Adula falcatoides* also develops more large provincular denticles than other mytilids and lacks central denticles. The anterior umbo margin is located over the 6th–8th anterior denticles but in *M. senhousia* it is placed almost over the beginning of the provinculum.

Larvae of *C. decussata* and *S. keenae* (Figure 1C & D) distinctly differ from other mytilid larvae by D-shaped shell, absence of umbo, the straight hinge margin, and homogeneous fine-grained sculpture without co-marginal lines of growth. These shell characters indicate lecithotrophic development (Ockelmann, 1965; O'Foighil, 1986; Jablonsky & Lutz, 1980; Lutz & Kennish, 1992; Table 1). Larvae of *S. keenae* are smaller and their shells are lower, thicker and more antero-posteriorly extended than those of *C. decussata*. The hinge of *C. decussata* consists of a larger number of marginal provincular denticles and the central denticles are not so clear. In *S. keenae* the posterior, anterior and central provincular denticles do not greatly differ in shape and size.

In *M. coruscus* (Figure 1E) a ratio of shell height to its length is larger than in other species of the family. The anterior shell end is less pointed than in *M. trossulus*. The shell is thinner; the larva is lighter coloured. The shell sculpture is represented by more distinct co-marginal lines of growth. Quantity of the anterior and posterior provincular denticles is considerably less than in *M. trossulus* and *M. galloprovincialis* and its hinge line is shorter. The anterior margin of the umbo is located closer to the beginning of the provinculum.

Larvae of *M. galloprovincialis* and *M. trossulus* are superfacially similar (Figure 1F & G). But in *M. galloprovincialis* the larval shell is higher and its umbones are broader. The shell is thicker; the larva is darker. There are fewer large denticles than in *M. trossulus* and the anterior margin of the umbo is closer to the beginning of the hinge line. The ligament is placed closer to the posterior part of provinculum.

Unlike larvae of *M. trossulus*, larvae of *M. kurilensis* (Figure 1I) are larger and their umbones are also larger and broader. The anterior shell end is more pointed and the postero-ventral margin is distinctly drawn out ventrally.

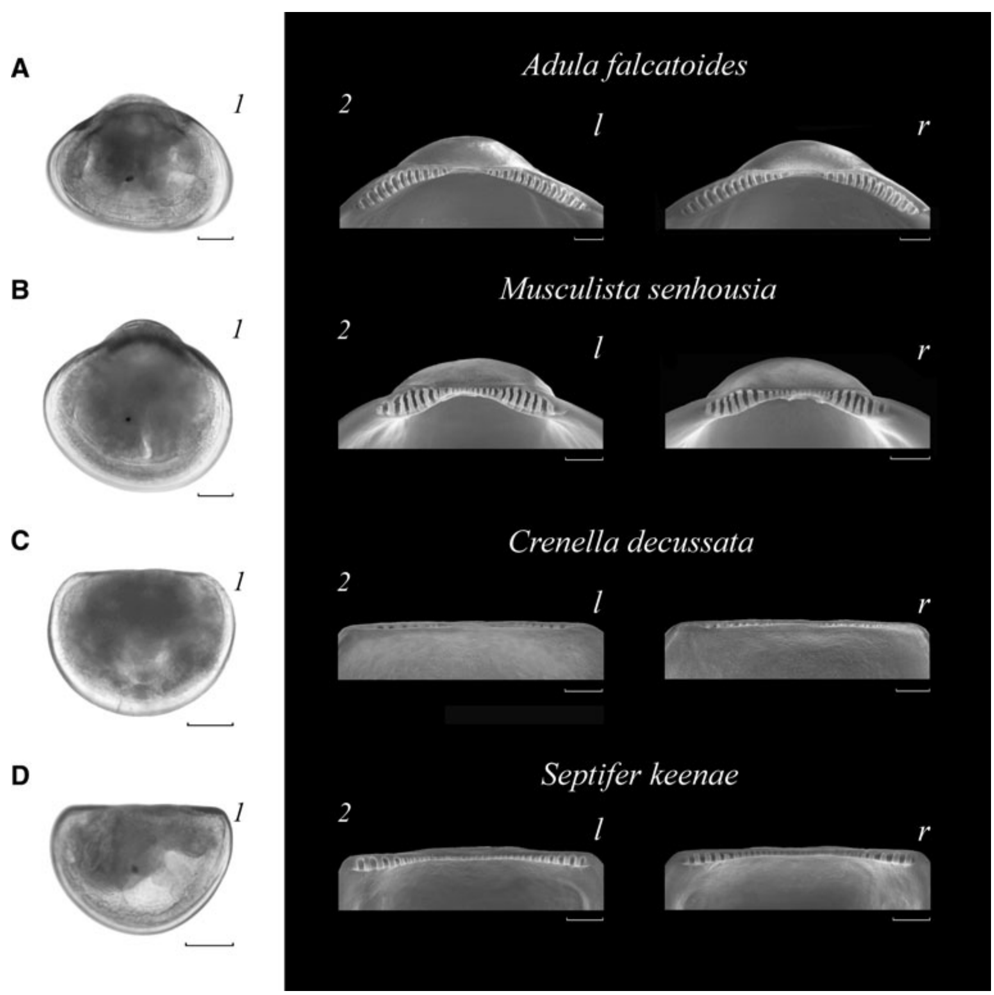

Fig. 1. Morphology of larvae of the family Mytilidae: (A) *Adula falcatoides*; (B) *Musculista senhousia*; (C) *Crenella decussata*; (D) *Septifer keenae*; (E) *Mytilus coruscus*; (F) *Mytilus galloprovincialis*; (G) *Mytilus trossulus*; (H) *Crenomytilus grayanus*; (I) *Modiolus kurilensis*; and (J) Mytilidae indeterminate: 1, general view, scale bar: 50 µm; 2, hinge, scanning electron microscopy, scale bar: 20 µm (l, left valve; r, right valve).

https://doi.org/10.1017/S0025315408000659 Published online by Cambridge University Press

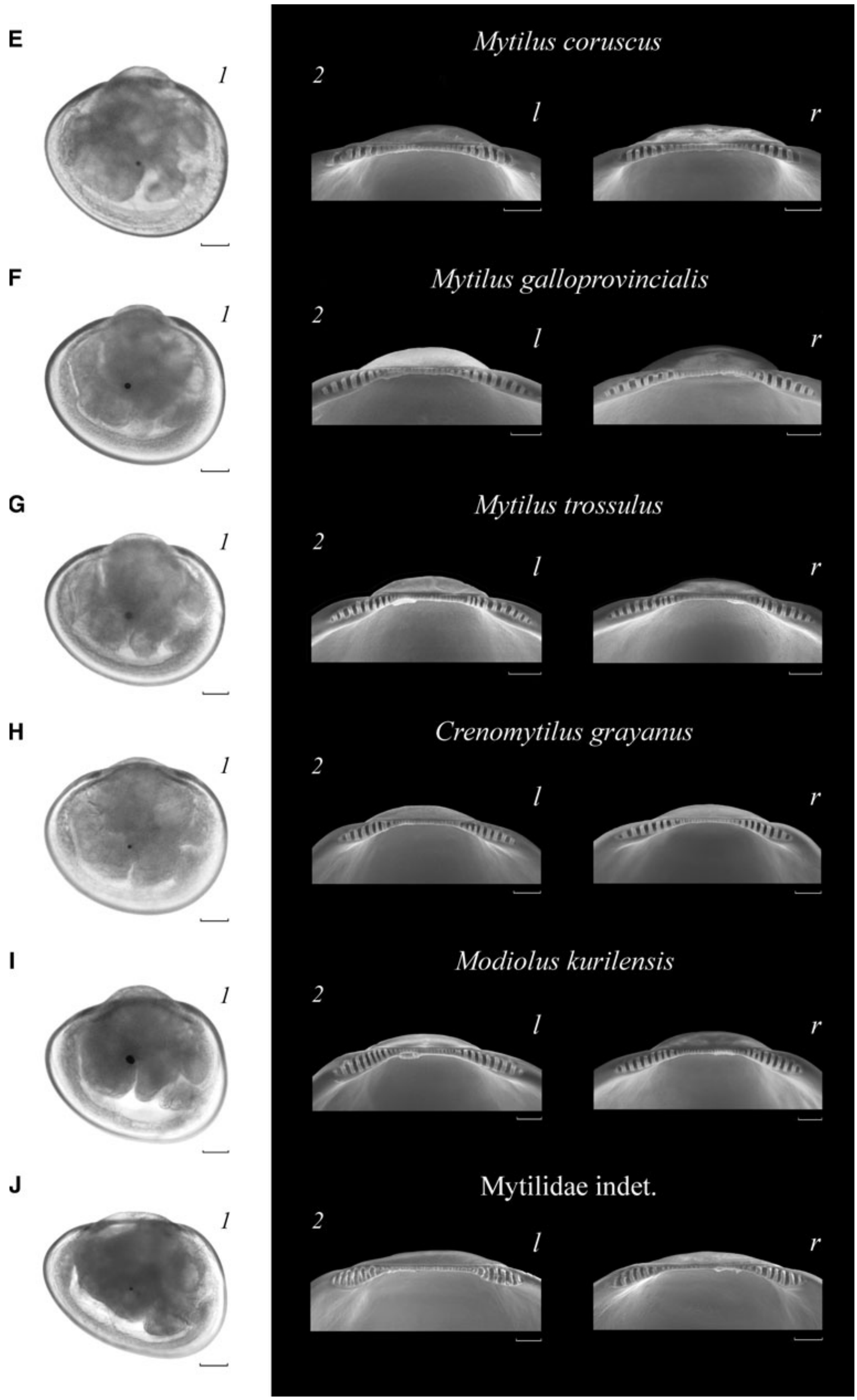

Fig. 1. Continued.

Because the larval shell of *M. kurilensis* is more convex and thicker the shell outline is better defined and the larva is less transparent. The co-marginal lines are clearer and more distinct than in *M. trossulus*. The larva of *M. kurilensis* is darker and its eye-spot is larger being in the form of a paint-brush stroke. In *M. trossulus* the anterior umbo margin is located somewhat farther from the beginning of the provinculum as compared to the provinculum of *M. kurilensis*.

https://doi.org/10.1017/S0025315408000659 Published online by Cambridge University Press

Larvae of *C. grayanus* (Figure 1H) differ from larvae of *M. trossulus* and *M. kurilensis* by a lower shell, broader umbones and a more rounded anterior margin. The postero-ventral shell margin is considerably less drawn out ventrally than in *M. kurilensis*. The shell is thinner; the larva is light-brown. The co-marginal lines are less distinct. The eye-spot is smaller than in *M. trossulus*. The provinculum of *C. grayanus* bears more central denticles. The anterior umbo margin is located over the 4th–5th anterior provincular denticle, while in *M. trossulus* and *M. kurilensis* the anterior margin of the umbo is placed over the 6th–7th and the 5th–6th denticle, respectively.

An unidentified species Mytilidae indeterminate (Figure 1J) was found to belong to the family Mytilidae due to the comparative study of the larval morphological features in the mytilid species inhabiting the north-western part of the Sea of Japan (Table 2) and other areas of the World Ocean (Rees, 1950; Loosanoff *et al.*, 1966; Chanley & Andrews, 1971; Zakhvatkina, 1972; Booth, 1977; Le Pennec, 1980; Redfearn *et al.*, 1986; Fuller & Lutz, 1989). Larvae of Mytilidae indeterminate are characterized by the morphological features peculiar to the mytilid larvae, namely shell outlines, its dimensional ratios, hinge of the taxodont type, location of ligament, sculpture, and presence of an eye-spot. Larvae of species examined mainly differ from other mytilid larvae, particularly *M. kurilensis*, by a more oblong and almost triangular shell, greatly drawn out postero-ventral margin, more raised anterior end, almost straight ventral margin, and very low flat umbones. The shell of Mytilidae indeterminate is thinner; a larva is greyish. The hinge line is relatively long and slightly curved. The provinculum bears a larger number of very small central denticles than in *M. kurilensis*, while the quantity of large denticles on each side of the hinge is considerably less.

Since the pelagic larvae of all mytilid species inhabiting the north-western part of the Sea of Japan are identified, it might be supposed that larvae of Mytilidae indeterminate are brought into Peter the Great Bay from warmer areas of the Sea of Japan or over subtropical waters from the Yellow and East China Seas through the Korean Strait (Yurasov & Yarichin, 1991). Our observations carried out earlier would support this hypothesis. So, larvae of Mytilidae indeterminate settling on hard substrata do not survive during the cold seasons. The maximum length of juvenile specimens of this species, which were collected in different biotopes, does not exceed 400–450 μm. Nevertheless, no descriptions of larvae with similar morphological features, which inhabit other areas of the Asian part of the Pacific Ocean, were found in the literature (Miyazaki, 1962; Hayashi & Terai, 1964; Tanaka, 1979b; Sakai & Sekiguchi, 1992; Ozawa & Sekiguchi, 2002).

The hinge morphology is one of the most important criteria in taxonomy both of adult bivalves and their larvae (Rees, 1950; Cox, 1969; Turner & Boyle, 1975; Lutz & Hidu, 1979; Le Pennec, 1980; Lutz *et al.*, 1982). The larval hinge as the most invariable and determinant character permits not only identification of the larvae but also defining the taxonomic status of the species. So, Coan & Scott (1997) and Coan *et al.* (2000) recently ascertained that *M. kurilensis* is a synonym for *M. modiolus*, which is widely distributed in the Atlantic Ocean and the Pacific waters off the American coast. However, the comparative study of the larval morphological features in *M. kurilensis* from the Sea of Japan and *M. modiolus* from the Atlantic waters (Lutz & Hidu, 1979; Fuller & Lutz, 1989) showed significant differences exceeding the specific level. In *M. modiolus* there are no more than 5–6 large denticles on each side of provinculum of late veliconch larvae, whereas the hinge of *M. kurilensis* bears 8–9 anterior and posterior provincular denticles. The anterior margin of the umbo is located over the 5th–6th denticle in *M. kurilensis* and over the first or second denticle in *M. modiolus*. In addition, in the latter the hinge line is appreciably longer than in *M. kurilensis*. Externally, the shell of *M. kurilensis* is less dorso-ventrally extended. Thus, based on the comparative study of the larval shell morphological features, particularly the provinculum morphology, it appears that Coan's revision of the specific status of *M. kurilensis* from the Sea of Japan is erroneous.

ACKNOWLEDGEMENTS

We are very grateful to Dr Valery A. Brykov (A.V. Zhirmunsky Institute of Marine Biology, Vladivostok) who provided us with plankton samples from Possjet Bay in the Sea of Japan. We greatly appreciate Dr Valentina A. Kulikova (A.V. Zhirmunsky Institute of Marine Biology, Vladivostok), Dr Nikolaus Malchus (Universitat Autònoma de Barcelona, Barcelona) and anonymous referees for their critical reading of the manuscript and very helpful comments. We are also very grateful to Dr Nikolaus Malchus for his thorough correction of the English.

This study was partially funded by grant 06-III-A-06-161 from the Presidium of the Far Eastern Branch of the Russian Academy of Science.

REFERENCES

Booth J.D. (1977) Common bivalve larvae from New Zealand: Mytilacea. *New Zealand Journal of Marine and Freshwater Research* 11, 407–440.

Chanley P.E. and Andrews J.D. (1971) Aids for identification of bivalve larvae of Virginia. *Malacologia* 11, 45–119.

Coan E.V. and Scott P.H. (1997) *Checklist of the marine bivalves of the Northeastern Pacific Ocean*. Santa Barbara Museum of Natural History. Contributions in Science 1.

Coan E.V., Scott P.H. and Bernard F.R. (2000) *Bivalve seashells of Western North America. Marine bivalve mollusks from Arctic Alaska to Baja California*. Santa Barbara Museum of Natural History.

Cox L.R. (1969) General features of Bivalvia. In R.C. Moore (ed.) *Treatise on invertebrate paleontology*. Part N, Vol. 1. *Mollusca* 6. *Bivalvia*, Geological Society of America Inc., University of Kansas, pp. 2–129.

Drozdov A.L. and Kulikova V.A. (1979) Development of *Crenomytilus grayanus* Dunker. The life-time examination. In *Fisheries bivalve mollusks and mussels and their role in ecosystems*. Leningrad: Zoological Institute of Academy of Sciences of the USSR, pp. 54–56.

Drozdov A.L., Zavarzina E.G. and Kulikova V.A. (1983) The embryonic and larval development of *Crenomytilus grayanus*. In Sveshnikov V.A. (ed.) *Biology of* Crenomytilus grayanus. Moscow: Nauka, pp. 35–41.

Evseev G.A. (2005) Early stage morphogenesis of *Adula falcatoides* (Bivalvia: Mytilidae) and problems of taxonomy and phylogeny of rock-boring mytilids of the West Pacific. *Bulletin of the Russian Far East Malacological Society* 9, 137–154.

Evseev G.A., Kolotukhina N.K. and Brykov V.A. (2006) Early stage morphogenesis of *Mytilus trossulus* and *Crenomytilus grayanus* and

https://doi.org/10.1017/S0025315408000659 Published online by Cambridge University Press

problems of taxonomy of Mytilinae (Bivalvia, Mytilidae). *Bulletin of the Russian Far East Malacological Society* 10, 67–87.

Evseev G.A., Semenikhina O.Ya. and Kolotukhina N.K. (2004) Larval and juvenile morphogenesis of *Septifer keenae* (Bivalvia, Mytiloidea, Septiferidae) and problems of recapitulative phylogeny of mytilids. *Zoologichesky Zhurnal* 83, 1317–1329.

Evseev G.A., Semenikhina O.Ya. and Kolotukhina N.K. (2005) Early stage morphogenesis: an approach to problems of taxonomy, phylogeny and evolution in the Mytilidae (Mollusca: Bivalvia). *Acta Zoologica Sinica* 51, 1130–1140.

Fuller S.C. and Lutz R.A. (1989) Shell morphology of larval and post-larval mytilids from the north-western Atlantic. *Journal of the Marine Biological Association of the United Kingdom* 69, 181–218.

Guida G.M. and Rakov V.A. (1979) Methods of identification and classification of bivalve larvae of the families Pectinidae, Mytilidae and Ostreidae from the Possjet Bay (the Sea of Japan). In Likharev I.M. (ed.) *Mollusks. The main results of their studying*. Leningrad: Nauka, pp. 105–107.

Hayashi T. and Terai K. (1964) Study on the larvae and young of Japanese surf clam, *Spisula (S.) sachalinensis* (Schrenk), at Shikuzu, Muroran City. 1. Taxonomy of the Pelecypoda's veliger larvae in plankton. *Scientific Reports of the Hokkaido Fisheries Experimental Station* 2, 7–38.

Hickman R.W. (1992) Mussel cultivation. In E.M. Gosling (ed.) *The mussel* Mytilus*: ecology, physiology, genetics and culture*. Amsterdam: Elsevier, pp. 465–510.

Hur Y.B. and Hur S.B. (2000) Development and growth of larvae of four bivalve species. *Journal of Aquaculture* 13, 119–128.

Jablonski D. and Lutz R.A. (1980) Molluscan larval shell morphology: ecological and paleontological applications. In D.C. Rhoads and R.A. Lutz (eds) *Skeletal growth of aquatic organisms*. New York: Plenum Press, pp. 323–377.

Jorgensen C.B. (1946) Lamellibranchiata. In Thorson G. (ed.) *Reproduction and larval development of Danish marines bottom invertebrates*. Meddelelser fra Kommissionen for Danmarks Fiskeri-og Havundersøgelser. Series Plankton 4, 277–311.

Kafanov A.I. (1991) *Shelf and continental slope bivalve molluscs of the Northern Pacific Ocean: a check-list*. Vladivostok: Far Eastern Branch of the Academy of Sciences of the USSR.

Kalashnikova S.A. and Aizdaicher N.A. (1993) On larval development of *Spisula sachalinensis* (Cardiida, Mactridae), *Ruditapes philippinarum* (Cardiida, Veneridae) and *Crenomytilus grayanus* (Mytilida, Mytilidae) in culture. *Zoological Zhurnal* 72, 13–19.

Kasyanov V.L., Kryuchkova G.A., Kulikova V.A. and Medvedeva L.A. (1983) *Larvae of marine bivalves and echinoderms*. Moscow: Nauka.

Kasyanov V.L., Kryuchkova G.A., Kulikova V.A. and Medvedeva L.A. (1998) *Larvae of marine bivalves and echinoderms*. New Delhi: Amerind Publishing Co. PVT. Ltd.

Kaufman Z.S. (1977) *Peculiarities of sexual cycles of the White Sea invertebrates*. Leningrad: Nauka.

Kimura T. and Sekiguchi H. (1994) Larval and post-larval shell morphology of two mytilid species *Musculista senhousia* (Benson) and *Limnoperna fortunei kikuchii* Habe. *Venus* 53, 307–318.

Kulikova V.A. (1978) Morphology, seasonal dynamics of number and settling of the larvae of the bivalve *Musculista senshousia* in Busse Lagoon (South Sakhalin). *Biologia Morya* 4, 133–135.

Kulikova V.A. and Kolotukhina N.K. (1989) *Pelagic larvae of the bivalve mollusks from the Sea of Japan. Methods, morphology, identification*. Vladivostok: Far Eastern Branch of the Academy of Science of the USSR.

Le Pennec M. (1980) The larval and postlarval hinge of some families of bivalve molluscs. *Journal of the Marine Biological Association of the United Kingdom* 60, 601–617.

Le Pennec M. and Masson M. (1976) Morphogenese de la coquille de *Mytilus galloprovincialis* (Lmk.) eleve au laboratoire. *Cahiers de Biologie Marine* 17, 113–118.

Loosanoff V.L., Davis H.C. and Chanley P.E. (1966) Dimensions and shapes of some marine bivalve mollusks. *Malacologia* 4, 351–435.

Lukanin V.V., Naumov A.D. and Fedyakov V.V. (1985) On characteristic features of mussel biocenosises in the White Sea. In Lukanin V.V. (ed.) *Research of the White Sea mussel*. Leningrad: Zoological Institute of the Academy of Science of the USSR, pp. 59–69.

Lutz R., Goodsell J., Castagna M., Chapman S., Newell C. *et al.* (1982) Preliminary observations on the usefulness of hinge structures for identification of bivalve larvae. *Journal of Shellfish Research* 2, 65–70.

Lutz R.A. and Hidu H. (1979) Hinge morphogenesis in the shell of larval and early post-larval mussels *Mytilus edulis* L. and *Modiolus modiolus* (L.). *Journal of the Marine Biological Association of the United Kingdom* 59, 111–121.

Lutz R.A. and Kennish M.J. (1992) Ecology and morphology of larval and early postlarval mussels. In E.M. Gosling (ed.) *The mussel* Mytilus*: ecology, physiology, genetics and culture*. Amsterdam: Elsevier, pp. 53–85.

Lutz R.A. (ed.) (1980) *Mussel culture and harvest: a North American perspective*. Amsterdam: Elsevier.

Mason J. (1976) Cultivation. In B.L. Bayne (ed.) *Marine mussels: their ecology and physiology*. Cambridge: Cambridge University Press, pp. 385–410.

Matveeva T.A. (1979) Adaptations to bearing of eggs in some marine bivalves. In *Morphology, systematics and phylogeny of mollusks*. Proceedings of the Zoological Institute, 80. Leningrad: Academy of Science of the USSR, pp. 39–43.

Miyazaki I. (1962) On the identification of lamellibranch larvae. *Bulletin of the Japanese Society of Scientific Fisheries* 28, 955–966.

Morton B. (1974) Some aspects of the biology, population dynamics and functional morphology of *Musculista senhousia* Benson (Bivalvia, Mytilidae). *Pacific Science* 28, 19–33.

Naumov A.D., Scarlato O.A. and Fedyakov V.V. (1987) Class Bivalvia. In Scarlato O.A. (ed.) *Mollusks of the White Sea*. Leningrad: Nauka, pp. 205–257.

O'Foighil D. (1986) Prodissoconch morphology is environmentally modified in the brooding bivalve *Lasaea subviridis*. *Marine Biology* 92, 517–524.

Ockelmann K.W. (1958) The zoology of East Greenland. Marine Lamellibranchia. *Meddelelser om Grønland* 122, 1–256.

Ockelmann K.W. (1965) Developmental types in marine bivalves and their distribution along the Atlantic coast of Europe. In L.R. Cox and J.F. Peake (eds) *Proceedings of the First European Malacological Congress, London, 1962*. London: Conchological Society of the Great Britain and Ireland, Malacological Society of London, pp. 25–37.

Ozawa H. and Sekiguchi H. (2002) Shell morphology of larvae and post-larvae of the two tropical *Modiolus* species, *Modiolus auriculatus* and *Modiolus philippinarum* (Bivalvia: Mytilidae). *Venus* 61, 25–39.

Redfearn P., Chanley P. and Chanley M. (1986) Larval shell development of four species of New Zealand mussels (Bivalvia, Mytilidae). *New Zealand Journal of Marine and Freshwater Research* 20, 157–172.

Rees C.B. (1950) The identification and classification of lamellibranch larvae. *Hull Bulletin of Marine Ecology* 3, 72–104.

https://doi.org/10.1017/S0025315408000659 Published online by Cambridge University Press

Rusanova M.N. (1963) The brief data on biology of some common invertebrate species from the Cape Kartesh area. In Palenichko Z.G. (ed.) *Materials on integrated research of the White Sea*, 2. Moscow–Leningrad: Academy of Science of the USSR, pp. 53–65.

Sakai A. and Sekiguchi H. (1992) Identification of planktonic late-stage larval and settled bivalves in a tidal flat. *Bulletin of the Japanese Society of Fishery and Oceanography* 56, 410–425.

Salas C. and Gofas S. (1997) Brooding and non-brooding *Dacrydium* (Bivalvia: Mytilidae): a review of the Atlantic species. *Journal of Molluscan Studies* 63, 261–283.

Satuito C.G., Natoyama K., Yamazaki M. and Fusetani N. (1994) Larval development of the mussel *Mytilus edulis galloprovincialis* cultured under laboratory conditions. *Fisheries Science* 60, 65–68.

Scarlato O.A. (1981) *Bivalve molluscs from temperate latitudes of the western part of the Pacific Ocean*. Leningrad: Nauka.

Seed R. (1976) Ecology. In B.L. Bayne (ed.) *Marine mussels, their ecology and physiology*. Cambridge: Cambridge University Press, pp. 13–65.

Seed R. and Suchanek T.H. (1992) Population and community ecology of *Mytilus*. In E.M. Gosling (ed.) *The mussel* Mytilus*: ecology, physiology, genetics and culture*. Amsterdam: Elsevier, pp. 87–157.

Semenikhina O.Ya. and Kolotukhina N.K. (2001) Morphology of *Mytilus coruscus* larvae (Bivalvia: Mytilidae). *Zoologichesky Zhurnal* 80, 1518–1521.

Suprunovich A.V. (1988) *Invertebrate aquaculture*. Kiev: Naukova Dumka.

Tanaka Y. (1979a) Identification of bivalve larvae—2. *Aquabiology* 1, 43–50.

Tanaka Y. (1979b) Identification of bivalve larvae—3. *Aquabiology* 1, 23–29.

Thorson G. (1935) Biologische studien über die Lamellibranchier *Modiolaria discor* L. and *Modiolaria nigra* Gray in Ostgrönland. *Zoologische Anzeiger* 111, 297–304.

Thorson G. (1936) The larval development, growth and metabolism of Arctic marine bottom invertebrates. *Meddelelser om Grønland* 100, 1–155.

Turner R.D. and Boyle P.J. (1975) Studies of bivalve larvae using the scanning electron microscope and critical point drying. *Bulletin of the American Malacological Union* 40, 59–65.

Yoo S.K. (1969) Food and growth of larvae of certain important bivalves. *Bulletin of Pusan Fisheries College* 9, 65–87.

Yurasov G.I. and Yarichin V.G. (1991) *Currents in the Sea of Japan*. Vladivostok: Far Eastern Branch of the Academy of Sciences of the USSR.

Zaika V.E., Valovaya N.A., Povchun A.S. and Revkov N.K. (1990) *Mytilids of the Black Sea*. Kiev: Naukova Dumka.

and

Zakhvatkina K.A. (1972) Larvae of bivalve mollusks—Bivalvia. In Vadyanitsky V.A. *Determinant book of fauna of the Black and Azov Seas*, 3. Kiev: Naukova Dumka, pp. 250–270.

Correspondence should be addressed to:
Olga Ya. Semenikhina
A.V. Zhirmunsky Institute of Marine Biology FEB RAS
690041 Vladivostok
Russia
email: oja@mail.primorye.ru

https://doi.org/10.1017/S0025315408000659 Published online by Cambridge University Press