Marine Biology (1997) 128: 107–114

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Spawning and larval development of the black turban snail *Tegula funebralis* (Prosobranchia: Trochidae)

Received: 7 October 1996 / Accepted: 17 October 1996

Abstract An understanding of spawning and larval development can be fundamental to interpreting the abundance, distribution, and population structure of marine invertebrate taxa. *Tegula funebralis* (A. Adams, 1855), the black turban snail, has been the focus of numerous ecological studies on the Pacific coast of North America. To date, there are only conflicting and anecdotal reports of spawning, and there is no information on larval or juvenile development for this conspicuous and abundant species. On 19 September 1995, two individuals of *T. funebralis* were observed free-spawning gametes into seawater in tanks at the Oregon Institute of Marine Biology. Embryos and larvae were subsequently reared to metamorphosis and beyond. Development was pelagic and similar to development described for other trochids, and larvae were observed not to feed at any stage. Larvae began to metamorphose at 5.7 to 6.7 d and settled at 260 μm shell length. Juveniles grew $\simeq 10$ μm in shell length per day and appeared to feed on detritus. Juveniles lacked some adult diagnostic shell characters, including two columellar nodes and a closed umbilicus. In the field, small (<3 mm) juveniles occurred in the adult habitat on all sampling dates between October and March. Small juveniles were found only under rocks and were most abundant under rocks partially buried in coarse sand, suggesting that juveniles may utilize a specific microhabitat within the adult *T. funebralis* habitat.

Introduction

Spawning and mode of larval development are important factors influencing the abundance and distribution of marine invertebrate taxa (Thorson 1950; Perron and Kohn 1985; Levitan et al. 1992; Emlet 1995). Early stages in the life-histories of marine organisms also affect the genetic structure of adult populations (Roughgarden et al. 1988; Grosberg and Levitan 1992; Babcock et al. 1994) and the evolutionary persistence of marine taxa (Hansen 1978, 1980; Jablonski and Lutz 1983). The spawning and larval development of numerous species have been described in detail (e.g. Kumé and Dan 1968; Strathmann 1987; Smith et al. 1989) yet, surprisingly, the reproduction and development of some conspicuous and intensively studied intertidal organisms remain unknown. *Tegula funebralis* (A. Adams, 1855) is one such common, intensively-studied gastropod species. Despite the substantial literature documenting the ecology, behavior and physiology of the adults of this common gastropod of the Pacific coast of North America (see Abbott and Haderlie 1980 for review), spawning behavior and larval development are poorly known for this species and most members of the genus.

Tegula funebralis is a member of a geographically widespread and well-known genus containing more than 40 living species (M. Hellberg personal communication). In general, accounts of spawning, larval development and time in the plankton are scarce for the genus *Tegula*. Five *Tegula* species have been described as broadcast-spawners: *T. excavata* (Lamarck, 1822) (Lewis 1960), *T. brunnea* Philippi, 1848 (Belcik 1965), *T. argyrostoma* (Gmelin, 1791) and *T. rustica* (Gmelin, 1791) (Sasaki 1985), and *T. funebralis* (P. Frank: cited in Belcik 1965). However, *T. funebralis* also has been reported to exhibit internal fertilization, with females producing benthic egg masses (Hewatt 1934). Larval periods of 4 d have been reported for *T. argyrostoma* and *T. rustica* (Sasaki 1985), and 14 d for *T. funebralis* (Hewatt 1934), although developmental times can vary greatly with temperature (e.g. Strathmann 1987).

The present study describes a laboratory spawning event, larval development to metamorphosis, and aspects of early juvenile development and growth in *Tegula funebralis*. Prior to this study there have been

Communicated by M.F. Strathmann, Friday Harbor

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only anecdotal and conflicting descriptions of spawning for this species, and little information on other species in the genus or subfamily to which it belongs. This description of spawning and larval and early juvenile development will provide a foundation for interpreting ongoing and future studies of the ecology, phylogeny, life-history and evolution of this species, which has figured prominently in marine intertidal research on the west coast of North America.

Materials and methods

Spawning and collection of gametes

On the afternoon of 19 September 1995, numerous grass-green eggs were seen surrounding a female *Tegula funebralis* (A. Adams, 1855) in a flow-through seawater table at the Oregon Institute of Marine Biology (OIMB), Charleston, Oregon. A spawning male was also found in the same sea table. These adults had been collected several months earlier at Gregory Point, Cape Arago, Oregon, and had been allowed to graze freely in the water table. Of seven *T. funebralis* in the same water table, only two were releasing gametes. Spawning occurred immediately after the water table had been emptied, cleaned and refilled, subjecting snails to turbulence and a noticeable drop in water temperature. Gametes from the two spawning snails were collected by pipette over the duration of release and transferred to 0.45 μm-filtered seawater. Eggs and sperm were collected separately, and eggs which had not undergone fertilization or which were not developing normally were removed from culture.

Eggs, embryos and larvae were examined frequently and measured to the nearest 5 μm by means of a compound microscope equipped with an ocular micrometer. To measure the diameter of the clear, colorless jelly coat, eggs or embryos were placed in a suspension of Japanese "Sumi" ink in seawater (Schroeder 1980).

Larval rearing

Development was not synchronous, as eggs were fertilized over a 2 h spawning period. The times of 12 developmental events were recorded as the times when the majority of embryos were at a given stage. Qualitative observations of the larvae were also made.

Embryos and larvae were maintained in 1000 ml beakers at ambient seawater temperature (13 to 15 °C) at initial concentrations of 1 larva ml^{-1}. Cultures were gently and constantly stirred at 12 swings min^{-1} by means of swinging paddles on a rack (as described in Strathmann 1971). The seawater in the beakers was replaced with fresh 0.45 μm-filtered seawater once per day.

Larvae that began to exhibit swimming/crawling behavior and appeared competent to metamorphose were placed in small numbers in glass dishes containing filtered seawater and small rocks collected from the adult habitat (north side of Sunset Bay, Charleston). To test whether metamorphosis would occur without a natural cue, some larvae were also maintained in clean dishes without rocks. Dishes were kept at 13 to 15 °C and checked after 24 h for metamorphosing individuals. Additional larvae from clean cultures were provided with rocks after 10 and 13 d to determine if larvae were still metamorphically competent (no older larvae were tested for competence).

Approximately 10 early (pretorsional) and 10 late (fully developed) veligers were placed in cultures containing single-celled algae (Tahitian strain *Isochrysis galbani*, *Rhodomonas lens* and *Dunaliella tertiolecta*) for 2 h. Treated larvae were immediately examined under a fluorescence microscope to determine whether their guts contained chlorophyll, which fluoresces red under blue light. Larvae were first examined whole, then crushed under a coverslip and reexamined.

Juvenile rearing

Newly metamorphosed laboratory-reared juveniles were placed on small rocks collected from adult *Tegula funebralis* habitat (similar to rocks used to test for metamorphosis). All large grazers such as limpets, chitons, and other snails were removed from the rocks before juveniles were added. Potential predators were also removed. Bowls were partially immersed in running seawater at ambient temperature (13 to 15 °C), and the seawater in the bowls was replaced weekly with freshly-filtered seawater. Juveniles were measured and photographed approximately every 7 d. For photography, juveniles were briefly narcotized with a 1:1 solution of 7.5% MgCl and filtered seawater. Juveniles were handled with eyelash-tipped wands, and for transfer between containers they were brushed gently off the substrate and moved with a suction pipet.

To observe juvenile diet, the gut contents of live juveniles were visually examined with transmitted light under a dissecting microscope at 50×. Juvenile guts were also checked for the presence of algae by examining live juveniles under blue light for gut-fluorescence.

Juveniles in the field

For comparison with laboratory-reared specimens and to estimate when and where *Tegula funebralis* recruit in the field, small juveniles were collected in the field at low tides on four dates, 15 October and 21 November 1995, and 19 January and 20 March 1996. The search was concentrated in sections of the intertidal where adults were found, but areas of the intertidal above adult habitat were also examined. Sampling was not quantitative. The tops, sides and undersides of intertidal cobbles were examined in the field, and pebbles and samples of coarse shell were collected and examined under a dissecting microscope in the laboratory. Juveniles of <3.0 mm shell length were collected and measured across the longest diameter by means of an ocular micrometer (± 20 μm). Larger juveniles were not collected or measured.

Results

Gametes and spawning behavior

The female *Tegula funebralis* extruded eggs singly or in clumps of 5 to 10 held together by a soft gel which dispersed quickly. Eggs were negatively buoyant, but were easily suspended by slight water movement; single eggs were observed suspended in the water up to 0.5 m away from the female. Eggs were spherical, 160 to 165 μm in diameter, and surrounded by an egg envelope 200 μm in diameter. The egg envelope was surrounded by an unstriated jelly coat, 450 to 460 μm in diameter (Fig. 1a), which was not visible without a suspension of "Sumi" ink particles. The eggs were green over approximately half their surface and yellowish over the other half.

The male extruded sperm in short puffs from the mantle cavity, forming a quickly-dispersing cloud. Sperm heads were 9 μm long, tails ~40 μm long, and sperm appeared to burrow into the jelly coat surrounding the eggs. Sperm were seen among eggs collected immediately under the spawning female, although the male and female *Tegula funebralis* were ≃ 1 m apart during spawning. Both snails released gametes sporadically for ≃ 2 h. Neither snail made an effort to approach the other during spawning.

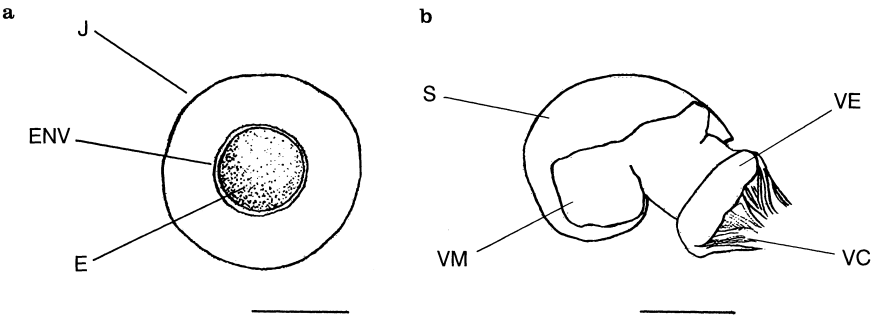

Fig. 1 *Tegula funebralis*. **a** Egg (*E*), egg envelope or egg membrane (*ENV*), and jelly coat (*J*) (*scale bar* = 200 μm); **b** newly hatched veliger (1.75 d old), side view, optical section (*S* shell; *VC* velar cilia; *VE* velum; *VM* visceral mass) (*scale bar* = 100 μm)

Development

The first two cleavages were equal, and cleavage followed the typical spiralian pattern described by Robert (1902) for *Gibbula magus* (as *Trochus magus* Linnaeus, 1758). Early development was similar to that of other trochids such as *Callistoma ligatum* (Gould, 1849) (Strathmann 1987; Holyoak 1988a) and *Gibbula cineraria* Linnaeus, 1758 (Robert 1902; Underwood 1972). Eggs contained green pigment that was concentrated near the vegetal pole of the 2 to 4 cell embryo, and at the vegetal end of the macromeres at later cleavage stages. Green pigment later appeared in the gut area and prototrochal cells of the trochophore, as reported by McGee (1964) for *Tegula brunnea*, and in the prototrochal cells and visceral mass of the veliger. The gut area was bluish-green and the prototrochal cells were yellow- or grass-green (brightness and shade varied greatly among larvae). Development of *T. funebralis* at 13 to 15 °C followed the approximate schedule given in Table 1.

At 18 h, embryos were ciliated gastrulae that rotated slowly in the egg envelope. After 1 d, embryos were well-formed trochophore larvae, 190 μm long with a stomadeum and shell-gland invagination, very similar in appearance to the stereotypical trochid trochophore (see Hickman 1992, her Fig. 2H). The prototroch consisted of a single row of large cells with long (30 μm) compound cilia based near the midline of each cell. Green pigment was concentrated inside the larval body and anteriorly in the prototrochal cells. At the trochophore stage, the egg envelope had stretched to ≃215 μm in diameter and the jelly coat appeared to have dissipated.

Table 1 *Tegula funebralis*. Development schedule at 13 to 15 °C

Time	Developmental stage
2 h	2-cell stage
3 h	4-cell stage
3 h 30 min	8-cell stage
4 h	16-cell stage
18 h	ciliated gastrulae
25 h 30 min	trochophores
40 h	hatched pre-torsional veligers
48 h	first 90° of torsion
53 h	retraction into shell
4 d	eyespots, propodium
5.7 d	swimming/crawling veligers
6.7 d	metamorphosis

After 40 h, larvae hatched as actively swimming, pretorsional veligers (Fig. 1b). Hatching larvae were 220 μm in length and had a well-formed shell and velum, but lacked a foot, operculum, eyespots or tentacles. Larvae swam to the surface in still water. At 2 d, veligers had completed the first 90° of torsion and had a foot, operculum and cilia 70 μm in length; 5 h later, veligers were able to retract fully into their shells. Four days after inferred fertilization, veligers had two dark-red eyespots, a small propodium, and prototrochal cilia ≃90 μm long (Fig. 2). The larval shell was unpigmented, coiled, slightly striated and had faint lines of spiral sculpturing running from apex to aperture (Fig. 3).

At 5.7 d, larvae were swimming–crawling veligers with large, active propodia. When they came in contact with a surface, larvae at this stage would cease swimming, retract the velum, and begin to crawl. Larvae crawling on clean glass extended the velum and swam off again after 1 to 5 min, while some larvae that settled on algae-encrusted rocks did not swim off again during 30 min of periodic observation. By the following morning (6.7 d), some (~25) larvae had metamorphosed on algae-encrusted rocks. No larvae kept in clean culture had metamorphosed by 6.7 d, but 3 to 4 had metamorphosed on glass by Day 10. Some larvae from clean culture metamorphosed on Day 10 when added to dishes containing small rocks, and others metamorphosed on Day 13 when this procedure was repeated. Newly metamorphosed juveniles had a green digestive gland, unpigmented translucent shells 260 μm long, and a velum that was reduced to small buds on either side of the head (Fig. 4a). Velar cilia, but not velar cells, sloughed off early in metamorphosis. Juveniles crawled very actively over coralline red algae and encrusting red and brown algae, but did not appear to grow or feed for several days. Older juveniles (>2 wk) had golden-brown gut contents that did not fluoresce under blue light. Post settlement mortality was very high; only 3 juveniles out of ≃50 settlers survived to 7 d post-metamorphosis.

Fifteen days after metamorphosis, the three surviving juveniles had lost all green pigment in the digestive gland and had added a considerable amount of new shell. The teleoconch had raised parallel ribs extending from the

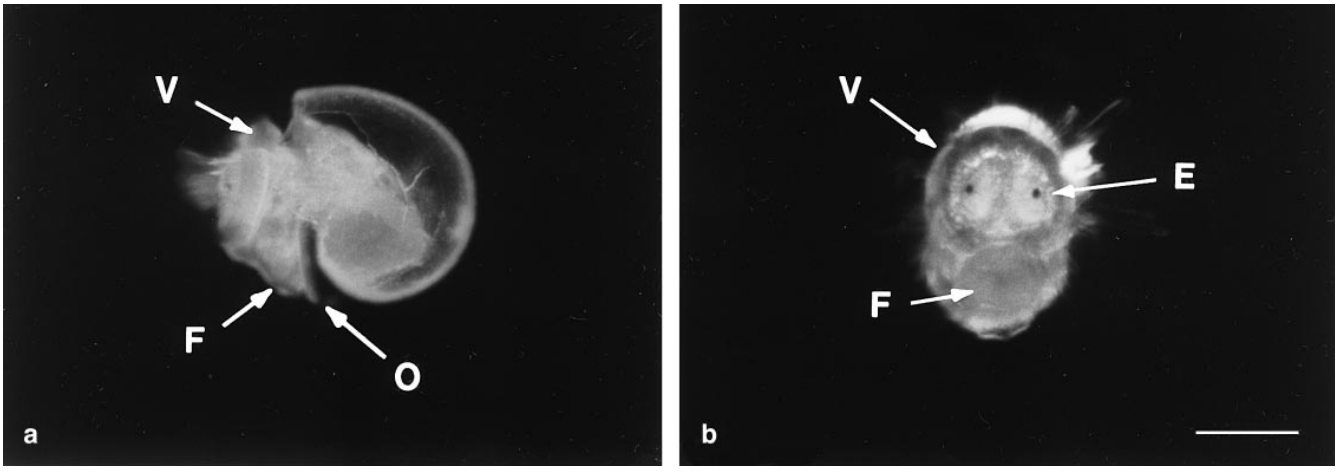

Fig. 2 *Tegula funebralis.* Four d-old veliger. **a** Side view (*F* foot; *O* operculum; *V* velum); **b** frontal view of larva (*E* eyespots; *F* foot; *V* velum) (*scale bar* = 100 μm)

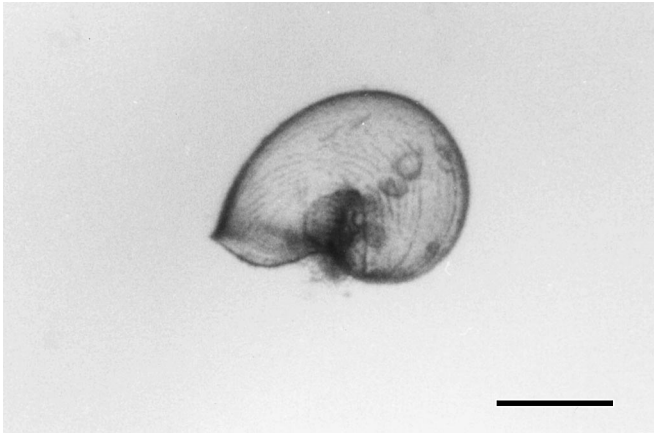

Fig. 3 *Tegula funebralis.* Shell of 5 d-old veliger larva, 260 μm long (*scale bar* = 118 μm)

protoconch to the shell aperture (Fig. 4b), and shell-coiling was dextral. The shell was unpigmented until the seventh week after metamorphosis, when dark purple pigment began to color the growing lip of the shell, particularly on the ribs. Juveniles had no apparent skin pigmentation for the first 2 mo, after which small amounts of purple pigment appeared on the food and head. Juveniles crawled actively and appeared to prefer the topsides of rocks for the first 2 wk of development, after which they were found primarily on the undersides. Juveniles grew an average of 10.4 μm d^{-1} in shell length for the first 6 mo (Fig. 5).

Larval feeding

Tegula funebralis larvae lacked a visible post-oral ciliary band (metatroch) that functions in particle capture in planktotrophic caenogastropod and opisthobranch veligers. No chlorophyll was detected in the guts of whole or crushed *T. funebralis* veligers by fluorescence microscopy after a 2 h exposure to unicellular algal cultures. Neither pre- nor post-torsional larvae had visible algal cells or other material in their guts.

Juveniles in the field

Juvenile *Tegula funebralis* of <1.3 mm shell length were found intertidally at Sunset Bay and Middle Cove, Cape Arago, at each of four sampling dates between October and March. The smallest juvenile of *T. funebralis* found on any sampling date was 0.95 mm in shell length. Juveniles were confidently identified as *T. funebralis* for the following reasons; (1) field juveniles were identical in appearance to laboratory-reared juveniles, except for greater shell wear on field specimens; (2) adults were very abundant, and were the only *Tegula* species found at the two sites; and (3) patterns of shell ribbing, a low spire and the size and shape of the protoconch readily distinguished juvenile *T. funebralis* from juveniles of the other common trochid gastropod at the site, *Lirularia succincta* (Carpenter, 1864). Small juveniles (between 0.95 and 3.0 mm in shell length (Fig. 6)) were locally abundant (1 to 7 juveniles per cobble) on the underside of cobble partially buried in coarse sand in the adult *T. funebralis* habitat. Juveniles were pale purple with purplish-black pigment at the growing lip of the aperture, except for the smallest (<1 mm) snails, which were unpigmented. Pigment occurred mainly on the ribs, giving some juveniles a striped appearance. Small juveniles had an open umbilicus and appeared to lack the two columellar nodes used to distinguish adult *T. funebralis* from other local *Tegula* species (Kozloff 1987). Larger *T. funebralis* were also found, ranging from 3.0 mm in shell length to fully grown adult snails (2 to 3 cm shell height).

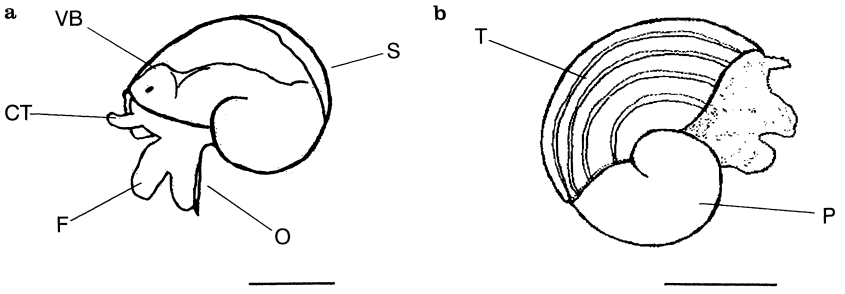

Fig. 4 *Tegula funebralis*. **a** Newly metamorphosed juvenile, 6.7 d after inferred fertilization (*CT* cephalic tentacle; *F* foot; *O* operculum; *S* shell; *VB* remaining buds of velum) (*scale bar* = 100 μm); **b** juvenile, 15 d post-settlement, showing ribbed teleoconch growth [*P* protoconch (larval shell); *T* teleoconch; *scale bar* = 200 μm]

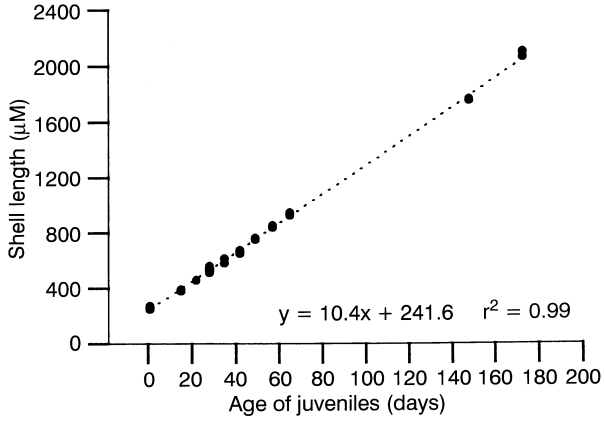

Fig. 5 *Tegula funebralis*. Post-metamorphic growth of juveniles. Shell length measured as greatest distance across shell with umbilicus down; 15 individuals were measured at settlement (Day 0), 3 for first month and 2 thereafter

Discussion

The family Trochidae contains both species that deposit benthic egg masses and species that broadcast-spawn their gametes (Hickman 1992). In the present study, *Tegula funebralis* was found to belong to the second category, confirming unpublished observations by P. Frank (reported in Belcik 1965) and in contrast to Hewatt's (1934) description of benthic egg masses, cited later by Abbott and Haderlie (1980). Both developmental modes occur within some trochid genera, and it is possible that both benthic and dispersing egg masses could occur within a single species, although reports of this phenomenon are rare. An example is the keyhole limpet *Diodora aspersa* (Rathke, 1833), in which free-spawned eggs of two laboratory-kept specimens varied in their adhesive properties (Hadfield and Strathmann 1996). If this type of variation occurs in *T. funebralis*, some spawns might appear to be soft benthic masses while others could disperse freely; however, while *T. funebralis* has been the subject of numerous laboratory and field studies, none have reported benthic egg masses.

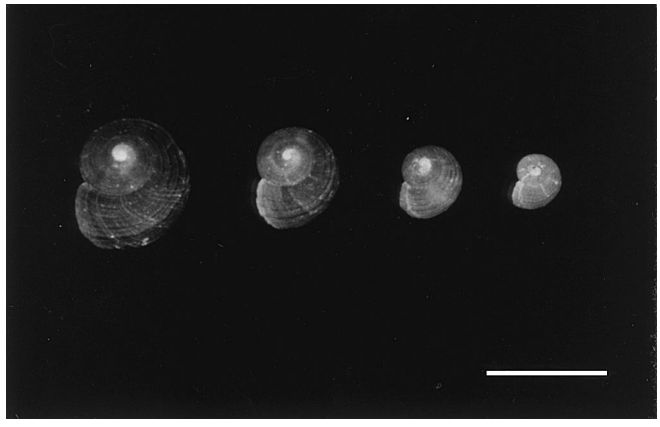

Fig. 6 *Tegula funebralis*. Field-collected juveniles, ranging in size from 1.0 to 2.5 mm measured across greatest diameter (*scale bar* = 2.2 mm)

The benthic egg masses in Hewatt's (1934) account were observed the day after two "copulating" specimens of *Tegula funebralis* had been observed in the laboratory, but it is not clear if *T. funebralis* were observed laying these egg masses or if there were other gastropod species in the tank that may have been responsible. Hewatt's description of copulation is unlikely to be accurate, because while "contact pairing" [external fertilization in which a male and a female spawn while in contact with each other, typically with the male perched on the female's shell (Hickman 1992)] has been reported for some trochaceans, trochacean gastropods generally lack morphological specializations for internal fertilization (with a possible exception in some deep-sea trochaceans: see Hickman 1992 for review). The egg-mass diameter reported for *T. funebralis* (3 mm) by Hewatt (1934) is also "improbably small" (Strathmann 1987, p. 236, based on Abbott and Haderlie 1980, who referenced Hewatt 1934), time to hatching differs considerably from this study (7 d compared to <2 d), and Hewatt's brief description provides no distinguishing characteristics of embryos or larvae. Hewatt's report must therefore be considered suspect unless additional evidence supports the presence of either cryptic species or two spawning modes within the nominal taxon *T. funebralis*.

Definitive information regarding the timing of spawning and settlement in *Tegula funebralis* is lacking. The spawning event described in this study occurred in mid-September, and P. Frank (cited in Belcik 1965) reported a spawning event in Oregon in August. Paine (1971) found that caloric values of female *T. funebralis* in Washington dropped abruptly in June to September, May to June and July to September of three consecutive

years, presumably due to gamete release. Frank (1975) found small (<7 mm) individuals from February through June in Oregon, but year-round at Pacific Grove, California, and inferred that spawning may be seasonal in the northern range of *T. funebralis* but year-round in the south. In the present study, which occurred in the same general locale as Frank's Oregon population, small (<1.3 mm) individuals were found in the field over a period of at least 5 mo (October to March). If juvenile growth rates were the same in the field as in the laboratory, then field juveniles of 1.3 mm shell length were ~3.3 mo old. These data suggest that settlement may have occurred from July through December (and possibly beyond), although it is possible that growth rates in the field differ significantly from the observed laboratory growth rates. Additional studies are necessary to determine when *T. funebralis* spawn, and if the timing of gamete release varies along the species' range.

Tegula funebralis larvae reared at 13 to 15 °C were competent to metamorphose at 5.7 d. This is consistent with the relatively short times to metamorphosis of other nonplanktotrophic temperate trochid gastropods with planktonic larvae [e.g. *Calliostoma ligatum* (Gould, 1849), 14 d (Strathmann 1987) or 12.2 d (Holyoak 1988a); *Cantharidus callichroa callichroa* (Philippi, 1850), 7 d (Son and Hong 1994); *Margarites marginatus* Dall, 1919, 14 d (Hadfield and Strathmann 1990) or 10.5 d (Holyoak 1988b); *Gibbula cineraria*, 8 to 9 d (Underwood 1972), *T. argyrostoma* and *T. rustica*, 4 d (Sasaki 1985)]. Larval developmental time can be highly dependent on temperature (e.g. Strathmann 1987), and warmer temperatures generally shorten developmental times. Temperatures as warm as 13 to 15 °C are somewhat unusual along the Oregon coast, although they do occur. Therefore, 5.7 d may represent the minimum time to metamorphosis that *T. funebralis* larvae would experience off the Oregon coast under normal conditions. Some larvae in this study retained metamorphic competence for at least 13 d after fertilization, and with cooler water temperatures the competent period might be lengthened beyond 13 d.

Nearshore ocean currents vary seasonally along the Oregon coast, and the timing of spawning will affect both direction and extent of the dispersal of gametes and larvae. Because *Tegula funebralis* has a minimum planktonic period of 5.7 to 6.7 d from free-spawned egg to competent larva, and because eggs and larvae may be in the plankton for ≥13 d, it seems likely that embryos and larvae have the potential for substantial dispersal in the field. Mean velocities of alongshore currents off the Oregon coast range from 10 cm s^{-1} in summer to 30 cm s^{-1} in winter (Allen et al. 1983), and maximum current velocities can reach 100 cm s^{-1} (Huyer et al. 1979). Therefore, a larva with a 5.7 d precompetent pelagic period might easily disperse ~50 km along the coast in summer or three times as far in winter. Nearshore currents are generally from the south in winter and from the north in summer (Hickey 1979), but both the direction and speed of currents over the continental shelf off Oregon can be highly variable (Huyer et al. 1975). The direction and extent of dispersal by *T. funebralis* gametes and larvae are likely to vary greatly with local hydrodynamic regimes at the time of spawning.

Marine species with long-lived planktotrophic larvae generally disperse more broadly and show much less population differentiation over large spatial scales than species that lack a planktonic larval stage, although there are exceptions (see Palumbi 1995 for review). It is not clear, however, what to expect from lecithotrophic species whose time in the plankton is of intermediate length and may vary considerably, e.g. from 5.7 d to at least 13 d for *Tegula funebralis*. The tropical trochid gastropod *Tectus coerulescens* Lamarck, 1822, inferred from its large, yolky eggs to have a short-lived lecithotrophic larva, exhibited significant genetic differentiation over several hundred kilometers (Borsa and Benzie 1996). In contrast, the sympatric trochid *Trochus niloticus* (Linnaeus, 1758), a lecithotroph whose planktonic larvae are competent to metamorphose from 3 to >8 d post-fertilization (Heslinga and Hillmann 1981), showed little genetic differentiation among populations over the same geographic scale (Borsa and Benzie 1996). If *Tectus coerulescens* and *Trochus niloticus* have equal potential for larval dispersal, these data suggest that ecological or historical factors can override the influence of planktonic period on patterns of genetic subdivision. However, if the larval planktonic period is not known for a given species (such as *Tectus coerulescens*), such data are difficult to interpret. An understanding of developmental mode and planktonic larval period is fundamental to interpreting ongoing and future population genetic analyses of *Tegula funebralis* and other marine taxa, such as *Tectus* and *Trochus*.

Like other archaeogastropod larvae studied to date, *Tegula funebralis* larvae appear to be nonfeeding and did not consume algal cells at any stage of development. Larvae are probably not capable of particle capture, since larvae of all stages lacked a visible metatrochal ciliary band, a structure that is implicated in particle capture by feeding gastropod larvae (Fretter 1967; Strathmann and Leise 1979). It has been suggested that trochacean larvae may feed at the swimming/crawling stage (Hickman 1992), but no algal cells or other material were seen in the guts of swimming/crawling *T. funebralis* larvae. However, guts of swimming/crawling larvae were highly opaque, so if present, small amounts of detritus may have been missed. Both early and late juveniles appeared to be detritus feeders (gut contents were golden-brown and did not fluoresce under blue light).

In the field, 0.95 to 3.0 mm juveniles were found in adult *Tegula funebralis* habitat on the undersides of cobbles partially buried in coarse sand. Small juveniles were found only in this habitat type and adults were generally lacking, suggesting that juveniles may utilize a specialized microhabitat within the adult habitat. Juveniles in this microhabitat may be exposed to different predators, food sources and environmental stresses than

adults, and the availability of juvenile microhabitat may be one of the factors shaping adult distribution and abundance. Small individuals (< 2 mm) have not been considered in ecological studies of *T. funebralis*, possibly because they are overlooked due to their small size or because juveniles have not previously been identifiable to species.

This study provides the first detailed description of the larval and juvenile development of *Tegula funebralis*, a member of a genus and subfamily for which such data are generally scarce (Hickman 1992). This study also confirms that gametes of *T. funebralis* are free-spawned, in contrast to Hewatt's (1934) description of benthic egg masses. Information on spawning and larval and juvenile development will be necessary to interpreting future and ongoing studies of the ecology, taxonomic relationships and population dynamics of *T. funebralis*, an historically important species in intertidal research on the west coast of North America.

Acknowledgements I thank R. Emlet (OIMB), P. Frank (University of Oregon), M. Hellberg (Scripps Institute of Oceanography), and C. Hickman (University of California at Berkeley) for valuable suggestions and encouragement. I am also indebted to P. Marko (University of California at Davis) for assistance in collecting specimens and comments on the manuscript, and to B. Butler (OIMB) for invaluable help with reference material. I also thank R. Collins, C. Hickman, M. Strathmann and an anonymous reviewer for comments that greatly improved the manuscript. This work was supported in part by NSF Grant OCE-9416590 to R. Emlet.

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