Development, Temperature Tolerance, and Settlement Preference of Embryos and Larvae of the Articulate Brachiopod Laqueus californianus

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Abstract. Populations of the articulate brachiopod Laqueus californianus occur in dense single-species aggregations near the continental shelf/slope break (100-200 m) in Monterey Bay, California. The development of embryos and larvae of L. californianus has been examined by scanning electron microscopy. Fertilizable eggs are 130-140 μm in diameter, and sperm are unmodified. Cleavage is holoblastic and radial. At 10°C an up-swimming blastula develops by 18-h, and gastrulation occurs within 24-38 h. The embryo elongates on a new larval axis and the blastopore closes by 72 h. A trilobed articulate brachiopod larva forms by day 3-4, and a metamorphically competent larva with attachment disk is attained in 7 days. Competent larvae swim downwards.

Effects of temperature on larval survival and development rate have also been examined. Larvae die within 1 day at 25°C. At 20°C, development appears normal but results in spontaneous abnormal settlement of larvae 5-6 days old. At 15°, 10°, and 5°C, most larvae achieve competence in 5, 7, and 9 days, respectively. Many larvae survive for 71 days at 10° and 15°C.

Patterns of larval settlement vary among substrates, but larvae show strong preference for shells of living conspecific adults. Settlement and metamorphosis can occur within 24 h upon exposure of larvae to substrate.

Introduction

The Brachiopoda compose a major part of the fossil record (~30,000 described species), yet the biology of extant brachiopods (~280 species) is understood poorly relative to that of other macrofaunal invertebrates (Rudwick, 1970; James et al., 1992). This lack of knowledge exists in part because brachiopods often inhabit cryptic or inaccessible habitats and are rarely conspicuous members of communities that attract the attention of zoologists and ecologists. The dense communities of epifaunal brachiopods that dominated level-bottom, shallow-water habitats prior to the Permo-Triassic extinction are largely absent from recent seas (reviewed by Thayer, 1986; Rudwick, 1970), and numerous attempts have been made to explain this shift in abundance and diversity (Stanley, 1977; Vermeij, 1977; Gould and Calloway, 1980; Gilmour, 1981; Thayer, 1981, 1985, 1986; Valentine and Jablonski, 1983a; Law and Thayer, 1991; Rhodes and Thayer, 1991; Thayer and Allmon, 1991; Rhodes and Thompson, 1993). The present-day Brachiopoda are typically regarded as a relic phylum, with extant species living in relic or marginal habitats (James et al., 1992; Rhodes and Thompson, 1993).

A striking exception to this pattern occurs in Monterey Bay, California, where populations of the articulate brachiopod Laqueus californianus (Koch 1848, Terebratellacea) are found as dense epifaunal ‘beds’ at the outer margin of the continental shelf (100-200 m; Fig. 1A-B). These aggregations occur near rock outcrops associated with the San Gregorio fault zone, but the brachiopods are also abundant on nearby mud bottoms where individuals are attached to both living and dead shells of conspecifics (Fig. 1C). Research on L. californianus is limited, and little information is available concerning its reproductive biology.

This paper presents (1) a description of L. californianus embryos and larvae as examined by scanning electron microscopy (SEM), (2) data from assays of the effects of temperature on larval survival and development rate, and (3) results of experiments on substrate preference during larval settlement. The work constitutes part of an ongoing investigation of the biology and community ecology of the L.
califomianus beds in Monterey Bay—assemblages that are reminiscent of the fossil brachiopod ‘reefs’ described in the paleontological literature.

## Materials and Methods

### Collection

Adult *Laqueus califomianus* were collected at a depth of 104 m by the R/V *Point Lobos* and the remotely operated vehicle (ROV) *Ventana* at the head of Cabrillo Canyon at the continental shelf/slope break in northern Monterey Bay, California (Fig. 1A). Collections were obtained with a suction sampler because most animals were attached to living or dead brachiopod shells (Fig. 1B) and were readily dislodged from the seafloor. Upon recovery of the ROV, brachiopods were placed in coolers and transported to the Monterey Bay Aquarium Research Institute (MBARI) at Moss Landing, California (Fig. 1A), and placed in a recirculating seawater system at 10°C. Adults are hardy and have been held unfed for many months prior to use in embryological work.

### Gametes and rearing

Culture methods were adapted from those in Reed (1987) as developed by Long (1964) for other articulate brachiopods. All embryological and larval work was performed in filtered (5 μm) seawater obtained from surface waters in mid-Monterey Bay; embryos and larvae did not survive in recirculated seawater.

Oocytes were obtained by pressing and washing dissected ovaries through 0.5-mm nylon mesh. Oocyte suspensions were washed several times in seawater and allowed to stand overnight to undergo germinal vesicle breakdown and to shed follicle cells prior to fertilization. Sperm were stripped from testes as above and induced to swim by addition of 0.5 M Trisma base buffer solution to the sperm suspension (20% Trisma base:sperm suspension; pH 9; 5-30 min). Once sperm were verified motile under the microscope, oocytes were fertilized by adding ~1% by volume of faintly milky sperm suspension. Excess sperm was washed from cultures after 30 min.

Embryos and larvae were cultured in unstirred glass
beakers or gallon jars at densities of 1-10 larvae/ml. Sea-
water was changed daily for the first 3 days and every other
day thereafter. After one day, healthy up-swimming em-
bryos were decanted from unfertilized eggs and poorly
swimming embryos at the bottom of culture vessels.

Microscopy

Aliquots of gametes, embryos, larvae, and juveniles were
examined with an ISI WB-6 scanning electron microscope
at 10 K v. The samples were prepared using Karnovsky’s
fixative (Gold, 1976), postfixation in 1% seawater-buff-
ered osmium, dehydration through an acetone series, crit-
ical point drying, and sputter coating with gold/palla-
dium.

Temperature effects

Two experiments were conducted to determine survivor-
ship and development rate as a function of temperature. Sur-
vival of larvae as a function of temperature was evalu-
ated in assays exposing 2-day-old gastrulae to five tempera-
tures. Capped vials containing embryos were placed in
water baths at 5°, 10°, 15°, 20°, and 25°C, ±0.5°C (three
replicate vials for each temperature, each vial containing 10
gastrulae and 10 ml of filtered seawater). Surviving larvae
were counted daily. To minimize handling errors, culture
water was not changed. The effect of temperature on develop-
ment rate of larvae was assessed by rearing several hun-
thred 2-day-old gastrulae in beakers held at the above tem-
peratures. These larvae were scored daily for developmental
stage, behavior, and general health, but were not counted.
Culture water in these beakers was changed every other day.

Settlement substrate preference

Two experiments were performed to evaluate the settle-
ment preferences of competent larvae. One experiment pro-
vided eight settlement substrates to larvae: (1) carbonate
rock, (2) frosted microscope slide, (3) unidentified sedimen-
tary rock collected from the Monterey Submarine Canyon,
(4) clam shell (Tresus nuttallii), (5) dead, air-dried (>1
month) L. californianus shell, (6) dead, air-dried L. califor-
нийус shell, (7) dead, air-dried L. californianus shell
subsequently “conditioned” in seawater for several days
prior to the experiment, and (8) small (~1 cm length) live
L. californianus. Shells in treatment (7) presumably devel-
opd a living microflora during conditioning. In this experi-
ment, 150 competent larvae (7 days old; 10°C culture) were
pipetted into each of forty-two 10-ml polystyrene wells. Substrates
were added (three wells for each substrate type), and the wells
were held in the coldroom for 24 h, after which any settled larvae were counted.

Counts in each experiment were square-root transformed
to satisfy assumptions of normality and equal variance, and
subsequently analyzed by ANOVA and Bonferroni t-tests
(SigmaStat). Data from treatments in which no larvae set-
tled were lumped into one group; because assumptions of
normality and variance could not be satisfied, these data
were analyzed by nonparametric ANOVA and Dunn’s test
(SigmaStat).

Results

Obtaining gametes

Gonads were almost always present in animals >20-25
mm in length (maximum size is ~45 mm long). Sex was not
distinguishable externally, but was noted for 67 dissected
adults. Of these, 44% were female, which is not signifi-
cantly different than 50% (Z-test, P = 0.4). No hermaph-
roditism or brooding was observed. Season of reproduction
remains uncertain since collections have been sporadic and
few (n = 5). Both ovaries and testes typically appear plump
and were decanted from unfertilized eggs and poorly
swimming embryos at the bottom of culture vessels.

A second experiment was conducted to replicate por-
tions of the above experiment and to assess the effect of
rugosity (grooves; cf. Wisely, 1969) and surface-bound
conspecific chemical cues in larval substrate preference.
Treatments in this experiment included conditioned sub-
strates (as described above) and substrates “painted” with
brachiopod extract. Painted substrates were coated five
times with a solvent extract of whole L. californianus
(five adult L. californianus extracted in 300 ml 100%
acetic acid for 1 month) and allowed to air-dry > 1 week
before use. Substrate treatments were (1) no substrate
added, (2) painted rugose cockle shell (Clinocardium
nuttallii), (3) unpainted rugose cockle shell, (4) painted
smooth clam shell (Tresus nuttallii), (5) unpainted
smooth clam shell, (6) painted frosted microscope slide,
(7) unpainted frosted microscope slide, (8) painted
smooth microscope slide, (9) unpainted smooth micro-
scope slide, (10) conditioned smooth microscope slide,
(11) conditioned rugose cockle shell, (12) dead air-dried
bryozoan test (Membranipora membranacea), (13) dead
air-dried L. californianus pedicle, and (14) living L.
californianus. Thirty competent larvae (7 day-old; 10°C
culture) were counted into each of forty-two 10-ml poly-
ethylene wells. Substrates were added (three wells for each
substrate type), and the wells were held in the coldroom
for 24 h, after which any settled larvae were counted.

Counts in each experiment were square-root transformed
to satisfy assumptions of normality and equal variance, and
subsequently analyzed by ANOVA and Bonferroni t-tests
(SigmaStat). Data from treatments in which no larvae set-
tled were lumped into one group; because assumptions of
normality and variance could not be satisfied, these data
were analyzed by nonparametric ANOVA and Dunn’s test
(SigmaStat).
germinal vesicle (visible as a translucent area in the salmon-colored egg cytoplasm; Fig. 2A; see Stricker and Folsom, 1997) disappeared overnight, as did follicle cells. Unfertilizable immature oocytes were more firmly attached to the ovary and when stripped were usually recognizable by a large surface dimple that probably marks the site of attachment to the ovarian wall.

Sperm heads and midpiece together are 2 μm long with...
head and midpiece visible (Fig. 2B); their tails are 40-45 μm long.

Development

Embryos. A developmental schedule for L. californianus at 10°C is presented in Table I. Cleavage is holoblastic, equal, and radial (Fig. 2C-E). First cleavage occurs at 3 h post-fertilization, and subsequent cleavages follow at 1-h intervals until cell counts become problematic after the fourth cleavage. Polar bodies were looked for but not recognized (cf. Freeman, 1993a). A thick egg membrane (~2 μm; visible in Fig. 2A, C, E) appears to press blastomeres into the furrows of underlying cells in later cleavage stages (Fig. 2F).

A hollow blastula forms by 12 h (Fig. 3A) and becomes ciliated by 18 h post-fertilization. Over the next several hours, embryos swim to the surface of cultures, spiraling with a clockwise rotation (anterior view). Blastulae occasionally stop swimming when they contact the water surface. Over 20-34 h, embryos gastrulate. The blastopore opens widely at the posterior, as defined by direction of swimming (Fig. 3B-C). By 48 h, embryos flatten and elongate (“wedge” embryos; Fig. 3D-E) and the swimming axis shifts such that, relative to swimming direction (arrows in Fig. 3B, D-F), the blastopore becomes ventrolateral. At this time an apical tuft of cilia appears (Fig. 3D, but not visible in Fig. 3E-F) on the thicker and new anterior end of the wedge embryo. During this time the blastopore also elongates and begins to fill with cells (Fig. 3D) from the posterior forwards. By 72 h the blastopore is closed.

Larvae. From 80-96 h (day 3-4) the swimming embryos differentiate into larvae 150 μm long, with apical, mantle, and pedicle lobes (Figs. 3F, 4A). The apical tuft is prominent (Fig. 4A), and dorsal and ventrolateral pairs of setal bundles develop from the posterior margin of the mantle lobe (Fig. 4C). The mantle lobe is ciliated sparsely, but ciliation of the apical and pedicle lobes remains uniform. From 96-128 h (day 4-5; Fig. 4B) the setae lengthen, ciliation is lost from the pedicle lobe, and cilia at the margin of the apical lobe form a well-defined locomotory band. Viewed from anterior, swimming larvae rotate slowly clockwise while metachronal waves pass counterclockwise through cilia of the locomotory band. As viewed through a dissecting microscope in culture bowls, larvae swim ~1 mm/s. They remain near the surface, and if disturbed can stop swimming, spread their setae, and sink; they do not swim backwards. Side, top, or bottom illumination produces no obvious photobehavior, and no pigment or eyespots are visible by light microscopy or SEM. Near the end of this period (120-128 h; day 5), the apical tuft disappears (Fig. 4B). By 145 h (day 6), the pedicle lobe begins to appear conical, and the ventral side of the mantle lobe begins to grow posteriorly to partially cover the pedicle lobe. At this time a small percentage of larvae begin to swim downwards, and many display distinctive, apparently muscular lateral flexions of the apical lobe while swimming. By 168 h (day 7; Fig. 4D-E), the ventral margin of the mantle lobe has become extended as a prominent skirt partly covering the pedicle lobe, a posteriorly directed ventral band of cilia develops on the mantle lobe, and a concave depression (the “attachment disk”) forms at the terminus of the pedicle lobe (Fig. 4E). Most larvae leave the surface of cultures by 168 h and are found swimming obliquely downwards at the bottom of culture bowls. Such larvae swim, without rotating, and press the anteroventral surface of the apical lobe against the substrate. We used the presence of an attachment disk (Fig. 4E) to indicate metamorphic competence in the temperature and settlement substrate preference experiments described below.

Metamorphosis. Several hundred larvae successfully metamorphosed in culture, although most did not settle. Many larvae also underwent abnormal or incomplete metamorphoses. Complete metamorphosis includes cementation of the pedicle lobe attachment disk to the substrate, reversal of the mantle lobe anteriorly (Fig. 5A) so that it encloses the apical lobe (Fig. 5B), and growth of adult shell valves on the now exterior surfaces of the mantle lobe (Fig. 5B). Metamorphosis of individual larvae has not been directly followed but occurs within 24 h of addition of appropriate substrate. Larval setae are not shed immediately. Juveniles that metamorphosed normally have survived to 115 days in culture, reaching a shell diameter of ~400 μm before death.

Temperature

In an assay of survival over a range of temperature (results not figured), no embryos or larvae survived 1 day at 25°C; about 15% survived to day 7 at 20° and 15°C, when

Table I

| Developmental schedule of Laqueus californianus at 10°C. |
|--------------------------------------------------------|
| **Event** | **Event** | **Event** |
| 0 (0) Insemination | 48 (2) Wedge larva; apical tuft; blastopore elongating |
| 3 (0) 1st cleavage (2-cell) | 72 (3) Blastopore closed |
| 4 (0) 2nd cleavage (4-cell) | 80 (3) Lobe differentiation begins; setae appear |
| 6 (0) 4th cleavage (16-cell) | 128 (5) Full trilobed larva; apical tuft lost |
| 12 (0) Unciliated blastula; upswimming begins | 154 (6) Pedicle lobe conical; some downswimming |
| 18 (0) Ciliated blastula; Gastrulation begins | 168 (7) Competent larva; attachment disk complete; downswimming |
| 26 (1) Gastrula; large open blastopore | | |
Figure 3. Late embryos and early larva of Laqueus californianus. (A) Broken 18-h-old blastula. Blastomeres are rounded, not yet ciliated, and ~1 layer thick beneath the egg membrane. Blastocoel is spacious and hollow. Scale bar, 50 μm; A-F to same scale. (B-C) Lateral and posterior views of 34-h-old gastrulae. Embryos are ciliated and swim to the surface of cultures with blastopore ("BP") trailing (arrows ‘sd’ indicate swimming direction). Blastopore open to archenteron. (D-E) Oblique ventral and lateral views of 48-h-old ‘wedge’ embryos. Blastopore fills with cells and closes by the first larval stage. Swimming direction changes (arrows ‘sd’) such that the blastopore becomes ventrolateral. An apical tuft develops (visible in D but not E-F) at the new anterior of the embryo. (F) Dorsolateral view of 80-h-old (3-day) early larva, with apical (top), mantle (middle), and pedicle (bottom) lobes differentiating. Pair of short dorsal setal bundles in foreground, and longer ventrolateral bundles to left and behind larva. Mantle lobe unciliated.
Figure 4. Larvae of *Laqueus californianus*. (A) Dorsal view of 96-h-old early larva. Apical lobe ('AL') uniformly ciliated except for prominent apical tuft ('AT'), mantle lobe ('ML') unciliated with short dorsal setal bundles and the left ventrolateral bundle visible, and pedicle lobe ('PL') rounded and ciliated. Scale bar, 50 μm. (B) Dorsal view of 128-h-old larva. Band of locomotory cilia differentiating on margins of apical lobe; the balls at tips of many cilia are probably fixation artifacts. Apical tuft cilia are present at this stage but not preserved on this specimen. Setae of mantle lobe erected, as when swimming larva is disturbed. Pedicle lobe has lost its cilia but is still rounded. Scale as in A. (C) Posterior view of 4-day-old larva as in A. Pedicle lobe rounded and sparsely ciliated, ventrolateral ('VLS') and dorsal ('DS') setal bundles pairs on mantle lobe, and cilia on apical lobe. Scale as in A. (D) Lateral view of 168-h-old metamorphically competent larva. Locomotory ciliated band ('LCB') on apical lobe; the apical tuft of cilia is absent in competent larvae. Ventral ciliated band ('VCB') now present on mantle lobe. Pedicle lobe partially enclosed by mantle lobe; the attachment disk has formed on its distal tip. Scale bar, 45 μm. (E) Oblique ventral view of mantle and pedicle lobes of competent larva, showing ventral ciliated band and attachment disk. Scale bar, 20 μm.

these treatments were terminated; and about 80% of embryos or larvae held at 10° and 5°C survived to day 11 of the experiment. Most mortality occurred in the first 24-48 h, suggesting that either (a) late embryos (gastrulae and wedge embryos) were more sensitive to higher temperatures than larvae, or (b) lack of water changes produced the observed mortality at higher temperatures.

In a second assay, development rate increased with tem-
Temperature within survival limits (Table II). Embryos held at 25°C did not develop and swam near the bottom of dishes on day 1 of the experiment. All were dead by day 2. Embryos moved from 25° to 10°C on day 1 survived for several days but did not develop. At 20°C, embryos developed into early larvae by day 1 but swam abnormally at the bottom of dishes, and by day 2 appeared competent to metamorphose. On day 3-4, most larvae cemented to the bottom of the glass culture dish but did not metamorphose (larvae 5-6 days old). Instead the mantle and pedicle lobes

**Table II**

Temperature effects on development rate and swimming behavior of *Laqueus californianus*.

| Temp (°C) | Observation      | Day of experiment (Age of larva) |
|----------|------------------|----------------------------------|
|          |                  | 1 (3)       | 2 (4)       | 3 (5)       | 4 (6)       | 5 (7)       | 6 (8)       | 7 (9)       |
| 5        | Stage            | Gastrula w/ AT | Early TL w/ AT | Early TL w/ AT | Full TL w/ AT | Full TL w/o AT | Full TL w/o AT | Competent |
|         | Swim             | ~All up      | ~All up      | ~50% up      | ~50% up      | Most near bottom | Most near bottom | Competent |
| 10       | Stage            | Gastrula w/ AT | Full TL w/ AT | Full TL w/o AT | Full TL w/ AT | Full TL w/ AT | Competent |
|         | Swim             | ~All up      | ~All up      | ~50% up      | ~30% up      | ~20% up      | Most near bottom | Competent |
| 15       | Stage            | Early TL w/ AT | Full TL w/o AT | Competent |
|         | Swim             | ~All up      | ~50% up      | ~30% up      | Competent |
| 20       | Stage            | Early TL w/ AT | Competent |
|         | Swim             | Most near bottom | Most near bottom | Most near bottom | Most near bottom | Most near bottom |
| 25       | Stage            | Gastrula w/o AT | Dead-Terminate |
|         | Swim             | Most near bottom | Most near bottom | Most near bottom | Most near bottom | Most near bottom |

Abbreviations: AT, apical ciliary tuft; Competent, metamorphically competent larva; TL, trilobed larva.
became abnormally tall so that the apical lobe came to rest on a thin stalk \( \sim 300 \mu m \) off the bottom. This treatment was terminated on day 5. Embryos and larvae developed normally and with little mortality at 15\( ^\circ \), 10\( ^\circ \), and 5\( ^\circ \)C, with accelerated development at higher temperatures. Thus at 15\( ^\circ \)C, larvae became competent on day 3 of the experiment (larvae 5 days old), whereas larvae at 5\( ^\circ \)C did not become competent until day 7 (larvae 9 days old). Embryos and larvae at these temperatures swam normally at the surface of cultures, but at or near the time of attaining metamorphic competence they moved to the bottom of dishes. No larvae metamorphosed, but many survived at 10\( ^\circ \) and 15\( ^\circ \)C until day 69, when the experiment was terminated (larvae 71 days old). The higher survival of larvae in 15\( ^\circ \) and 20\( ^\circ \)C water compared to larvae in the temperature survival assay was probably due to frequent water changes in this experiment.

**Settlement substrate preference**

In the first larval settlement experiment very few larvae settled on carbonate rocks, microscope slides, rocks from brachiopod habitat in the Monterey Submarine Canyon, clam shells, and dead, air-dried *L. californianus* shells (Fig. 6A). A moderate but significantly \( (P < 0.05) \) higher percentage settled on dead, air-dried *L. californianus* pedicles and dead, air-dried but conditioned *L. californianus* shells. In addition, a number of larvae settled on pieces of dead, air-dried bryozoan test that were inadvertently included with two of the clam-shell treatments (these settlers were scored separately and the data treated as replicates). Nevertheless, by far the largest percentage \( (P < 0.05) \) settled on living *L. californianus* shells. These results indicate that significantly more larvae settled on conspecifics, and further, that shells of living brachiopods were most highly preferred.

Results from the second settlement experiment confirm that larvae preferred shells of live conspecific brachiopods (Fig. 6B; \( P < 0.05 \)), and indicate that larvae had a low preference for substrates that were conditioned or painted with brachiopod extract. These latter treatments received no settlement, and their counts were lumped in the ‘other’ category (Fig 6B).

Several additional experiments (data not presented) produced results consistent with those above. However, in many cases settled larvae, as scored in all settlement experiments, failed to undergo complete metamorphosis (see Metamorphosis, above).

**Discussion**

**Environmental setting and adult habitat**

Adult *Laqueus californianus* occur in dense epifaunal beds near the outer margin of the continental shelf in northern Monterey Bay (100-200 m; Fig. 1A-C). These beds are near carbonate rock outcrops associated with the San Gregorio fault zone (Dan Orange, University of California at Santa Cruz, pers. comm.), but often extend over or occur on near-horizontal soft sediment (Fig. 1B) where individual brachiopods are attached to either living or dead brachiopod shells (Fig. 1C) lying on mud. Other aggregations of *L.
L. californianus have been observed on the continental shelf a few kilometers north of Monterey Bay, and Mattox (1955) dredged masses of adults from 60-240 m off Santa Catalina Island. Tunnicliffe and Wilson (1988) found abundant populations of L. californianus on vertical rock walls in British Columbia. L. californianus ranges from Alaska to southern California and also occurs in the Sea of Japan (Bernard, 1972; Tunnicliffe and Wilson, 1988). The species is typically found at depths <200 m (Hertlein and Grant, 1944), but is common in the intertidal zone of British Columbia (Bernard, 1972), and shell fragments have been dredged from 1570 m off the Monterey Peninsula (Dall, 1920). L. californianus is also common on rock walls in the Monterey Submarine Canyon to at least 800 m (Barry, unpubl), where it occurs as scattered individuals intermixed with the more ovate form Laugeus californianus var. vancouveriensis. The non-aggregated occurrence of L. californianus var. vancouveriensis reported by other authors (Hertlein and Grant, 1944; Mattox, 1955; Bernard, 1972; Tunnicliffe and Wilson, 1988). Terebratulina crossei also occurs in the Monterey Submarine Canyon, and the inarticulate Glottidia albida occurs in soft substrates on the continental shelves of Monterey Bay (Zimmer and Haderlie, 1980).

Development

Embryos and larvae. Development of L. californianus is similar to that of another north Pacific terebratellacean, Terebratulina transversa (Long, 1964; Stricker and Reed, 1985a,b,c; Long and Stricker, 1991; Freeman, 1993a,b). The eggs of L. californianus are smaller than those of T. transversa (135 vs. 150 μm diameter), and the sperm tails of L. californianus spermatozoa are longer (45 vs. 30 μm). Reed (1987) states that L. californianus eggs are 170 μm in diameter, larger than observed in this study. Cleavage and embryogenesis appear nearly identical, although we have not identified polar bodies in L. californianus embryos. Larvae of the two species are also similar, although L. californianus larvae are smaller (150 μm vs. 200 μm in length), do not develop pigmented eyespots, and lack vegetative cells at the posterior margin of the apical lobe.

The developmental schedule of L. californianus is slower than that of T. transversa. At 12°-13°C, T. transversa reaches metamorphic competence in 4 days (Freeman, 1993a), whereas L. californianus takes 7 days to achieve competence at 10°C and 5 days at 15°C (Table I). We have maintained L. californianus larvae in culture for 71 days, which to our knowledge, is the longest recorded for articulate brachiopod larvae (also see Peck and Robinson, 1994, for a description of 45-day-old larvae of Liothyrella uva in the Antarctic). We do not know over what portion of this period L. californianus larvae remain competent to settle and metamorphose.

Development among articulate brachiopods is highly conservative (reviewed by Chuang, 1990; Long and Stricker, 1991; James et al., 1992), and development in L. californianus is similar to that of other terebratellaceans and articulate brachiopods in general.

Metamorphosis. Metamorphosis in L. californianus is similar to that described for T. transversa and other articulate brachiopods (reviewed by Long and Stricker, 1991; Chuang, 1990). However, many larvae in our cultures metamorphosed incompletely and did not proceed to develop normally. The anterior end of the apical lobe of such animals developed an ectodermal invagination (not illustrated) that is strikingly similar to stomodeal invaginations reported for other species by previous authors (Percival, 1944, 1960; Mano, 1960; Franzen, 1969). We have not followed the fate of this invagination in these abnormal individuals. Incomplete metamorphosis appears to be fairly common among articulate larvae (Percival, 1960; Freeman, 1993b) and in our cultures is probably a laboratory artifact associated with quality of eggs, culture seawater, or substratum.

Larval and recruitment biology

Depth-regulatory behavior. Changes in swimming direction associated with larval stage observed for L. californianus are similar to that known for a number of other articulate larvae (Calloria inconspicua–Percival, 1944; Doherty, 1979; Chuang, 1996; Frenulina sanguinolenta–Mano, 1960; Terebratulina septentrionalis–Noble et al., 1976; Terebratulina retusa–James et al., 1992). Such behavior has been attributed to phototaxis (e.g., reviews by Long and Stricker, 1991; James et al., 1992), and late larvae of many species develop putative eyespots (reviewed by Chuang, 1990). L. californianus larvae, however, do not have eyespots and show no obvious photobehavior in response to vertically or horizontally directed lights; their vertical swimming behaviors are probably geotactic.

Most invertebrate larvae exhibit depth-regulatory swimming (see Mileikovsky, 1973; Chia et al., 1984), with young larvae typically swimming up in the water column and older larvae swimming or sinking downwards (Thorson, 1964; Young and Chia, 1988). Off central California where surface temperatures are <20°C (J.T. Pennington and F.P. Chavez, unpubl. data), L. californianus can develop at surface temperatures (Table II). At 1 mm/s (see Results), larvae might swim to the surface in ~28 h from brachiopod beds at 100 m. Such larvae could spend several days near the surface and could easily be dispersed dozens of kilometers by currents (see Breaker and Broenkow, 1994); the faster development at surface temperatures (Table II) should also be advantageous in terms of predation and other time-dependent sources of mortality (Rumrill, 1990). This see-
nario contradicts the notion that articulate larvae are so short-lived that they must have very limited dispersal (Rudwick, 1970; James et al., 1992), resulting in patchy meter-scale distributions of adults (especially brooding species; see Noble et al., 1976; reviewed by James et al., 1992). If L. californianus larvae can delay metamorphosis for long periods, as may be suggested by their 71-day survival in culture, widespread dispersal could occur, which could have implications for arguments concerning evolutionary rates (cf. Jablonski and Lutz, 1983; Valentine and Jablonski, 1983b). We plan to conduct field experiments to confirm the possibility that L. californianus larvae migrate to and from the surface during the course of their development, and to determine how long the larvae remain competent to settle and metamorphose.

Settlement. Late larvae of L. californianus swim to the bottom of cultures and engage in what may be a ‘searching’ behavior. In this behavior, the larvae swim, not rotating as do younger larvae, with the anteroventral surface of the apical lobe pressed against or in proximity (within micrometers) to the substrate. This anteroventral surface is at or near the leading edge of the site of blastopore closure (e.g., the possible site of the adult mouth; Long and Stricker, 1991), and it is possible that the larvae are ‘tastimg’ potential settlement sites. Similar behaviors occur among other articulate species (reviewed by Long and Stricker, 1991; James et al., 1992; Chuang, 1990, 1996). Percival (1960) additionally described late larvae of Notosaria (= Tegulorhyncha) nigricans ‘running about’ the substrate by means of the ventral ciliated band.

We have not observed larvae in the act of settlement (cementation to substrate), but substrate-choice experiments (Fig. 6A-B) indicate that larvae settle preferentially on shells of living L. californianus. They also settle in moderate numbers on nonliving brachiopod shell and pedicle, but prefer conditioned (biofilmed) shell. Gregarious settlement is not uncommon among articulates (reviewed by Long and Stricker, 1991; James et al., 1992), but has usually been inferred from distribution of juvenile recruits. Conditioned substrates, presumably colonized by microfauna, are also known to facilitate brachiopod settlement (Percival, 1960). The finding that the larvae strongly prefer living conspecific substrate, however, is new, though both Percival (1960) and Freeman (1993a) noted that live or freshly smashed conspecific shells were effective inducers of metamorphosis in N. nigricans and T. transversa, respectively. The settlement-inducing cues remain unknown—substrates treated with a brachiopod extract were apparently unattractive. Gregarious settlement would appear to be adaptive in Monterey Bay, where the brachiopod beds are largely composed of living animals cemented to each other and onto dead shell material imbedded in sediment underlying the beds (Fig. 1B-C). Larvae settling on live rather than dead shells should stand less chance of burial (but on gregariousness also see Doherty, 1979; James et al., 1992). Almost certainly, preferential settlement of larvae on living conspecifics is one factor that promotes formation and maintenance of the L. californianus beds in Monterey Bay.

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