21    Larval Transport, Food Limitation, Ontogenetic Plasticity, and the Recruitment of Sabellariid Polychaetes

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ABSTRACT Sabellariid polychaetes have long-term planktotrophic larvae whose dispersal is likely to be greatly influenced by hydrodynamic transport processes. Adult distributions of gregarious species, and distributions of nongregarious species that form aggregations under some circumstances, suggest that oceanic and smaller-scale, near-shore circulation patterns strongly influence patterns of larval supply. During offshore transport, larvae may be advected into areas of low phytoplankton abundance. Previous laboratory studies on five species of sabellariids of the genera *Phragmatopoma* and *Sabellaria* indicate that the rate of larval development for these polychaetes is highly dependent on food concentration. In this study, competent (i.e., ready to metamorphose) larvae of *Phragmatopoma lapidosa californica* are demonstrated to undergo a reversible reversion to a precompetent condition in response to starvation. This response occurred rapidly: metamorphosis of larvae sampled from cultures denied food for 4 days dropped from 76 percent to 20 percent. Larvae starved for 6 days regained competence after two days of feeding; those starved for 20 days regained competence after 8 days of feeding. Changes in competence in response to food availability were coincident with changes in larval morphology. Starvation resulted in decreases in body length and energy content, and larval tentacles became shorter and lost cilia associated with putative sensory organs that are potentially involved in substratum selection. Larval morphology returned to normal when feeding was reinitiated, with regeneration paralleling regained competence. Ontogenetic plasticity, coupled with physical defenses against planktonic predation, may help sabellariid larvae survive long periods of larval transport in oligotrophic offshore waters. Plasticity may also prevent metamorphosis when food is scarce and juvenile survivorship would likely be low.

## Introduction

Marine invertebrate zooplankton live in an environment that is nutritionally dilute (Conover, 1968) and where the food supply of phytoplankton is temporally and spatially patchy (Steele, 1978; Mackas et al., 1985). For holoplankton, such as copepods, food limitation is more likely to occur offshore than near-shore (Checkley, 1980), with some species displaying greater tolerances for lower food availability than others (Dagg, 1977). For planktotrophic invertebrate larvae, the importance of food supply on larval survival and subsequent recruitment has been the subject of some debate (reviewed in Day and McEdward, 1984; Olson and Olson, 1989). In general (i.e., for

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the few species that have been investigated), crustacean larvae appear to have little starvation tolerance, while molluscan and echinoderm larvae endure low phytoplankton abundances with a concomitant decrease in growth rate. Little is known of the responses of polychaete larvae to food limitation (see Table 1 of Olson and Olson, 1989).

Marine polychaetes of the family Sabellariidae inhabit tubes made of cemented grains of sand. Found in all seas, there are some fifty species belonging to at least six genera (reviewed in Pawlik and Faulkner, 1988). The group is remarkably cohesive in terms of adult and larval morphology. Moreover, all species that have been studied are dioecious, broadcast spawners with long-term planktotrophic larvae (Eckelbarger, 1978). Approximately twenty species (mostly in the genera *Phragmatopoma*, *Sabellaria*, and *Gunnerea*) settle gregariously to form colonies and reefs in lower intertidal and shallow subtidal environments around the world (see Fig. 1 of Pawlik and Faulkner, 1988); the remainder are mostly or entirely nongregarious, found on shells or rocks at depths ranging from the intertidal to the deep sea.

Sabellariid larvae have long been popular study organisms, particularly for investigations of larval behavior at the time of settlement (e.g., Wilson, 1968; Eckelbarger, 1978; Smith and Chia, 1985; Pawlik, 1986, 1988a,b; Amieva et al., 1987). Research on settlement specificity has explained much about the observed recruitment patterns of the adult worms. Laboratory experiments conducted in still-water have revealed that, while gregarious species preferentially settle on the tube sand of adult conspecifics, nongregarious species settle just as readily on control sand, and both gregarious and nongregarious species delay metamorphosis indefinitely in the absence of substrata (Pawlik, 1986, 1988a,b; Pawlik and Chia, 1991). A near-absolute substratum specificity has been confirmed for the gregarious species *Phragmatopoma lapidosa californica* in choice experiments conducted in laboratory flumes under hydrodynamic conditions similar to those of subtidal environments, with the additional discovery that larval behavior in different flow regimes can alter larval delivery to the substratum (Pawlik et al., 1991; Pawlik and Butman, 1993). Much of the foregoing work, however, has concentrated on the behavior of competent larvae (i.e., mature larvae that are poised to settle) that have come into proximity of the substratum; yet, the precompetent larval life span of sabellariids is estimated at weeks to months (Barry, 1989; see later discussion) and may constitute a significant portion of their lives in the plankton.

In this chapter, we will focus on presettlement factors that may play important roles in the dispersal and ultimately the recruitment of sabellariid larvae. We will summarize available evidence that transport of sabellariid larvae by currents and eddies greatly influences the distribution and gregarious settlement of several species. We will also discuss nutrition-dependent plasticity in the development of sabellariid larvae and the potential importance of this flexibility in extending the larval life span.

## Materials and Methods

The ontogenetic plasticity of *Phragmatopoma lapidosa californica* was examined in five laboratory time-course experiments in which three batches of larvae of *P. l. californica* were alternately fed or starved. Subsamples of each batch were assessed for metamorphic competence, body length, tentacle length, and energy content. Results from only two experiments (time courses A and B) are presented because the other experiments were prematurely terminated when cultures became contaminated and large numbers of larvae died. Experiments were conducted at Friday Harbor Laboratories, University of Washington, using larvae from animals collected off Point Loma, San Diego, California (see Pawlik, 1986). Time course A was conducted September to November 1989; time course B ran May to July 1990. Larvae were cultured, measured, and

assayed for metamorphic competence as detailed in Pawlik (1986, 1988a). Three batches of larvae, derived from a single spawn of multiple male and female worms, were followed for each time course. Each batch consisted of two 3-l jars each containing about 6000 larvae. Both jars of each batch were sampled for each experiment. As the time course progressed, and the number of larvae dwindled, the two jars were pooled into one. Prior to the onset of a starvation sequence, data were pooled for all batches (see Fig. 21.1 and Table 21.1).

Metamorphic competency was assayed by placing 20–30 larvae from each batch (subsampling from the jars) into each of three dishes containing sand from tubes of adult *P. l. californica* (made from "Ottawa sand") and scoring the number of metamorphosed juveniles and swimming larvae after 24 h (see Pawlik, 1986, 1988a). Body lengths and tentacle lengths were measured on ten narcotized larvae from each batch (subsampling from both jars). Energy content of larvae was periodically determined, using the dichromate oxidation microtechnique of McEdward and Carson (1987) with glucose as the standard. Energy content assays were performed on 100 larvae (time course A) or 50 larvae (time course B) per assay tube, with three to four replicates per batch (subsampling from both jars). Larvae were given several hours to void their digestive tracts prior to oxidation with dichromate, so as not to include the gut contents in energy content determinations. Larvae were washed in three changes of 0.33 $M$ solution of $MgSO_4$ to remove chloride.

Scanning electron micrographs were taken of representative larvae of *Phragmatopoma lapidosa californica* sampled during time course A. Techniques employed in narcotization, fixation, embedding, and microscopy were those of Amieva and Reed (1987).

## Results and Discussion

### Larval Transport

The distribution of most benthic marine invertebrates can ultimately be traced to the settlement of their larvae. Prior to settlement, larval distributions are influenced by a host of physical and biological factors (Young and Chia, 1987; Pawlik, 1992), with physical transport processes likely dominating over much of the larval life span (Butman, 1987). Oceanic currents can drive long-range larval transport (review in Scheltema, 1986), while in estuarine habitats, larval distributions are influenced by exchange rates, circulation patterns (Boicort, 1982), tides, and stratification due to temperature and salinity differences (Stancyk and Feller, 1986; Young and Chia, 1987). Along continental margins, a variety of physical factors may affect transport, including wind drift (Efford, 1970; Denny, 1987), upwelling (Yoshioka, 1986), internal waves (Shanks, 1986), tidal bores (Pineda, 1991), and meanders and filaments (Bane et al., 1981). Recent models of marine invertebrate recruitment consider larval supply entirely the result of physical transport of passive larvae (e.g., Possingham and Roughgarden, 1990), an assumption that has drawn some criticism in light of the evidence for behavioral responses at the time of settlement (review in Pawlik, 1992; Pawlik and Butman, 1993).

Nevertheless, there is good evidence that sabellariid distributions are strongly influenced by passive transport processes. For *Phragmatopoma*, a genus that is most likely monospecific with subspecies distributed along both Atlantic and Pacific coasts of the New World (Fig. 1 of Pawlik and Faulkner, 1988; Pawlik, 1988b), large reef formations are found adjacent to major oceanic boundary currents: along the coasts of California, Ecuador and Peru, Brazil, and East Florida. *Phragmatopoma* is present, but not abundant, between these locations along each coast. Its distribution, however, appears to have little to do with temperature because it is common in the tropics (Caribbean), as well as in cold temperate areas (southern Chile). *Phragmatopoma lapidosa lapidosa* is not found south of Brazil; this southern range limit coincides with the Subtropical
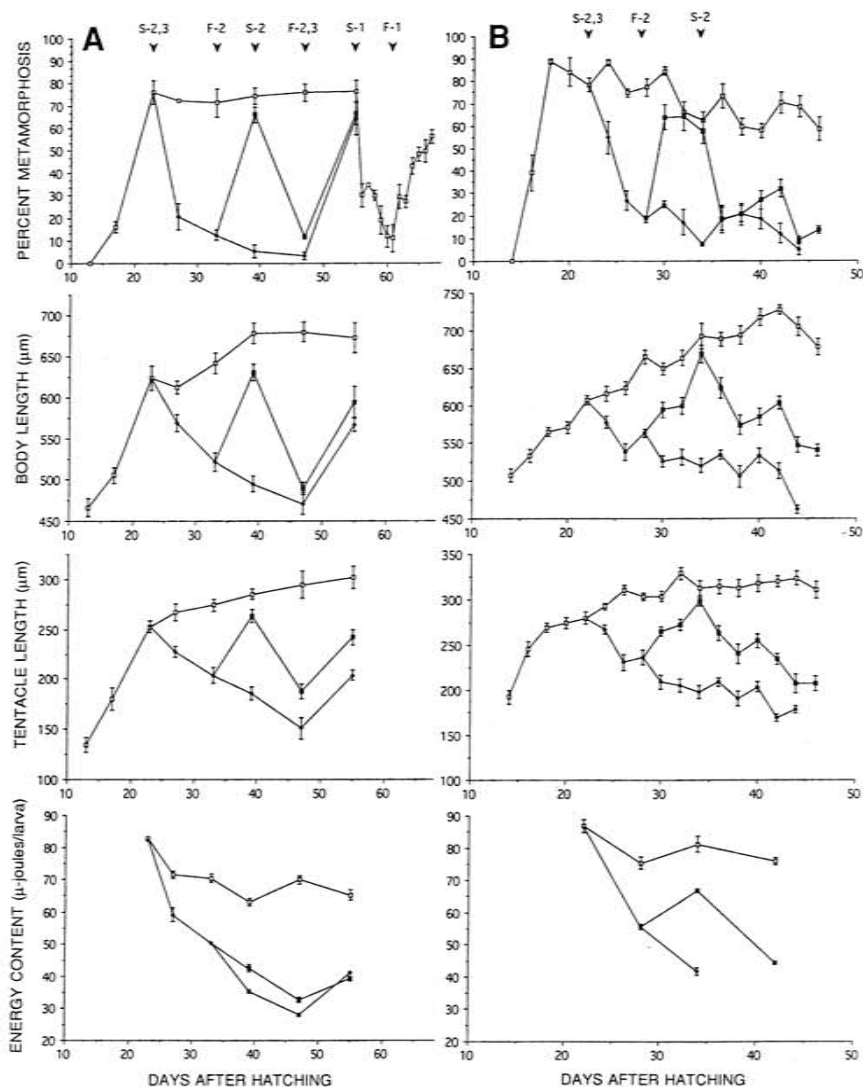
FIGURE 21.1. Ontogenetic plasticity of *Phragmatopoma lapidosa californica* in the laboratory. Two time-course experiments (A and B) in which three batches of larvae (□—□, ■—■, ◆—◆) of *P. l. californica* were alternately fed or starved. Subsamples of each batch were assayed for metamorphic competence, body length, tentacle length, and energy content. Standard errors of the mean are shown for each measurement. Changes in the feeding schedule are indicated above the figures (see Table 21.2); for example, *S-2,3* signifies that starvation began for batches 2 and 3 on that date, *F-2* means that feeding was resumed for batch 2, etc. Data recorded up to the beginning of the first starvation sequence (A: days 1–23; B: days 1–22) are pooled for all batches (all batches treated the same up to this time); from that day until the split between batch 2 and 3 (A: days 23–33; B: days 22–28), data are pooled for batches 2 and 3 (2 and 3 treated the same up to this point); from that day to the end of the time course, data are separate for each batch.

Table 21.1. Time required for development to metamorphic competence for sabellariid polychaetes cultured in the laboratory and for a field population

| Species (distribution) | Culture temperature (°C) | Time to maturity | Source |
|---|---|---|---|
| *Phragmatopoma lapidosa lapidosa* | 15 | 27 days | Pawlik, 1988b |
| (Florida to Brazil) | 20 | 16 days | Pawlik, 1988b |
| | 22–25 (?) | 3–4 weeks | Mauro, 1975 |
| | 21–23 | 14–30 days | Eckelbarger, 1976 |
| *Phragmatopoma l. californica* | 15 | 23 days | Pawlik, 1988a |
| (California to Panama) | 20 | 16 days | Pawlik, 1988a |
| | 17–18 | 34–39 days | Eckelbarger, 1977 |
| | 21–23 | 18–25 days | Eckelbarger, 1977 |
| | ?[a] | 2–5 months | Barry, 1989 |
| *Sabellaria alveolata* | 15 | 25 days | Pawlik, 1988a |
| (North Sea to Mediterranean) | 20 | 14 days | Pawlik, 1988a |
| | 15 | 6–32 weeks | Wilson, 1968 |
| | ? | 12 weeks | Cazaux, 1964 |
| *Sabellaria floridensis* | 15 | >40 days | Pawlik, 1988b |
| (Gulf of Mexico, Florida) | 20 | 17 days | Pawlik, 1988b |
| | 21–23 | 18–27 days | Eckelbarger, 1977 |
| *Sabellaria cementarium* | 15 | 25 days | Pawlik and Chia, 1991 |
| (North Pacific) | 20 | 27 days | Pawlik and Chia, 1991 |
| | 10–14 | 5–8 weeks | Smith and Chia, 1985 |

[a]Field population.

Convergence of the Brazil Current and the Falkland Current. The former, southward-flowing current may supply the Brazilian coastline with larvae from colonies further north, and its deflection to the east by the northward-flowing Falkland Current marks the range limit. The same can be said for *P. l. lapidosa* on the northern end of its range; the deflection of the Florida Current eastward to form the Gulf Stream appears to limit its distribution. Small colonies of *P. l. lapidosa* have occasionally been found along the coast of North Carolina (A. McCrary, pers. comm.), perhaps as a result of larval supply from meanders and filaments of Gulf Stream surface water that traveled onto the continental shelf (Bane et al., 1981; Atkinson et al., 1982).

The distribution of *Phragmatopoma* on the Pacific coast of North and South America is less readily explained. The northern limit, off central California, may result from a lack of larval supply from the southward-flowing California Current. Larvae are likely entrained in the currents of the California Bight, as indicated by the large populations of adults off southern California. Strangely, the southern distribution of *P. moerchi/P. virgini* extends to the tip of South America (Pawlik and Faulkner, 1988), despite the Peru Current flowing from the south. It remains unclear how larvae are transported to the southernmost regions of their range. Perhaps localized, near-shore countercurrents are important in maintaining this distribution.

Smaller-scale transport processes may also affect sabellariid distributions. For example, *Sabellaria alveolata*, a gregarious species found in the Northeast Atlantic and Mediterranean, forms large reefs in bays and estuaries (Horne, 1982). Hydrodynamics appear to play a partic-

ularly important role in the formation of the large, intertidal reef at the mouth of Mont Saint-Michel Bay in France (Gruet, 1986).

Entrainment may also explain the formation of reefs by otherwise nongregarious sabellariids. *Sabellaria cementarium*, for example, is found from Alaska to northern California. Larvae of this species show no settlement preferences for conspecific tube sand in laboratory experiments (Pawlik and Chia, 1991) and, not surprisingly, are found in single or paired tubes over most of their range. Yet, a large reef of aggregated *S. cementarium* has been reported in an embayment near Coos Bay, Oregon (Posey et al., 1984), and its formation is likely the result of larval entrainment and concentration at the time of settlement. Similarly, *Sabellaria vulgaris*, found along the east coast of North America, forms aggregations only in one area of Delaware Bay between Cape Henlopen and the Mispillion River Jetty (Wells, 1970; Curtis, 1978), again suggesting that larvae are entrained in this shallow, semienclosed region (Galperin and Mellor, 1990).

## Food Availability and Ontogenetic Plasticity

Development rates of invertebrate larvae can be influenced by temperature (e.g., Pechenik et al., 1990), but for most planktotrophic species, nutrition appears to play a more important role (Paulay et al., 1985; Olson and Olson, 1989). Of the invertebrate species studied to date, larvae of crustaceans are generally unable to survive after extended periods of low food availability (Lang and Marcy, 1982; Anger, 1987), while molluscan and echinoderm larvae simply slow their rates of growth (Paulay et al., 1985; Boidron-Metairon, 1988; Pechenik et al., 1990).

Larvae of sabellariid polychaetes appear to display the same food-dependent developmental plasticity found in some echinoderms (Paulay et al., 1985; Boidron-Metairon, 1988). Comparisons of the minimum developmental periods reported for five sabellariid species cultured in the laboratory revealed highly variable growth rates for different investigators (Table 21.1). Culture conditions for each of these studies were largely similar, with the exception that different species and concentrations of phytoplankton were used. For *Sabellaria alveolata*, these nutritional differences resulted in development times ranging from 25 days (Pawlik, 1988a) to 6–32 weeks (Wilson, 1968) at 15°C. The latter figure, in fact, is closer to the only estimate available for the development of sabellariid larvae in the field: for *Phragmatopoma lapidosa californica*, Barry (1989) reported a 2–5-month lag between winter storms (which induce adult spawning as worm reefs are damaged) and recruitment of juvenile worms into the intertidal of southern California. It is not evident whether this period was required for larval maturation, or whether larvae matured much earlier, but remained competent in the plankton until they could be advected back to shore. In the laboratory, however, Pawlik (1988a) was able to culture larvae of *P. l. californica* to maturity in 16 days at 20°C and in 23 days at 15°C (Table 21.1).

Plasticity in larval development may go beyond the length of time required to attain metamorphic competence, however. One of us (J. R. P.) has determined that larvae of *Phragmatopoma lapidosa californica* will lose and regain their ability to metamorphose dependent on the availability of food in laboratory cultures (Table 21.2, Fig. 21.1). The response time was remarkably rapid: only 20 percent of larvae sampled from a culture that was denied phytoplankton for 4 days metamorphosed on conspecific tube sand, whereas 76 percent from the same population metamorphosed prior to starvation (Fig. 21.1a, day 23–27). When provided with food again, the ability to metamorphose rapidly returned in the starved population, as levels of metamorphosis similar to those of unstarved larvae reappeared in as few as 2 days (Fig. 21.1b, day 28–30). For one population of larvae, competence was restored three times after two bouts of starvation (Fig. 21.1a).

Table 21.2. Feeding schedule for each batch of larvae (1, 2, and 3) for both time courses A and B

(See Figure 21.1 and Materials and Methods for details.)

| | A | | | B | |
|---|---|---|---|---|---|
| Day | Feed | Starve | Day | Feed | Starve |
| 1 | 1,2,3 | | 1 | 1,2,3 | |
| 23 | 1 | 2,3 | 22 | 1 | 2,3 |
| 33 | 1,2 | 3 | 28 | 1,2 | 3 |
| 39 | 1 | 2,3 | 34 | 1 | 2,3 |
| 47 | 1,2,3 | | 46 | (larvae dying, | |
| 55 | | 1(2,3 exhausted) | | experiment ended) | |
| 61 | 1 | | | | |

The loss and restoration of metamorphic competence of larvae of *P. l. californica* as a function of food availability were coincident with dramatic changes in larval morphology (Figs. 21.1 and 21.2). The overall length of the larval body decreased over the starvation period, as did the energy content of the larvae. In addition, the larval tentacles decreased in length by about 20 percent during a 10-day period over which time metamorphosis dropped from 76 percent to 12 percent (Fig. 21.1a, day 23–33). As with metamorphic competence, larval morphology was also restored when phytoplankton were again available, and both body and tentacle lengths returned to the sizes of those of unstarved larvae (Fig. 21.1). Strangely, larval energy content did not rebound when starved larvae were fed in time course A, but did rebound in time course B (Fig. 21.1).

Starvation also resulted in ultrastructural changes to the surfaces of the larval body and tentacles of *P. l. californica*, as revealed in the scanning electron micrographs (SEMs) shown in Figure 21.2. The dorsal hump and larval tentacles bear putative chemosensory ciliated structures (sensory tufts) that appear to mediate substratum selection and metamorphosis of this species (Eckelbarger, 1978; Amieva and Reed, 1987; Amieva et al., 1987). The numbers of cilia composing the sensory tufts were greatly reduced after 10 days of starvation (compare Figs. 21.2c and 21.2e with 21.2d and 21.2f), and the distal tips of the larval tentacles appeared to lose their ciliation almost completely. These ciliated structures were also restored when larvae were again provided with food, and SEMs of these larvae were indistinguishable from those of larvae that had never been starved (data not shown).

Larvae of *P. l. californica* were able to survive long periods of starvation, with subsequent loss of metamorphic competence, and then regain the ability to metamorphose when phytoplankton were again available (Fig. 21.1a). After 20 days of starvation, the number of larvae that metamorphosed fell to 3 percent. Larvae were then fed for 8 days, and metamorphosis rebounded to 65 percent. In addition, some larvae were fed and maintained in a competent state for 32 days before being starved, and these responded in much the same way as larvae that were starved immediately after attaining competence (Fig. 21.1a, days 55–67).

Is ontogenetic plasticity of sabellariid larvae important in nature? Given the difficulties in monitoring, sampling, and identifying populations of larvae in the field, the question is unlikely to be answered definitively (see review in Levin, 1990). But the fact that the single field estimate of a sabellariid larval life span (*P. l. californica*, 2–5 months; [Barry, 1989]) is considerably longer than the developmental rate of the same species in the laboratory (23 days at 15°C [Pawlik,
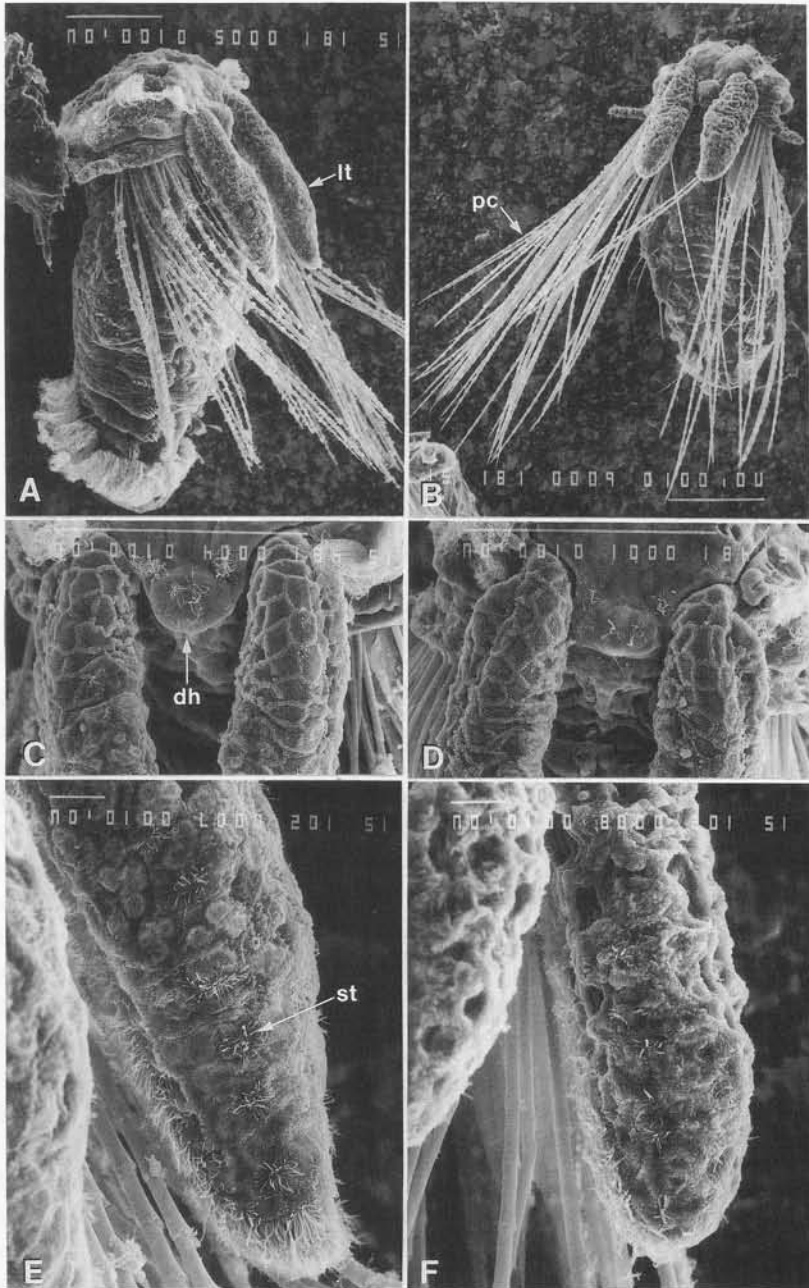
FIGURE 21.2. Scanning electron micrographs of representative larvae of *Phragmatopoma lapidosa californica* sampled from time course A, day 33. The larvae shown in A, C, and E were fed through day 33; those shown in B, D, and F were starved from day 23 through day 33. (scale bar = 100 μm for A–D, 10 μm for E and F.) A and B: full view of larva; note overall change in larval size from A to B (length of provisional chaetae remains constant). C and D: dorsal view, close-up of dorsal hump and proximal end of larval tentacles; note loss of ciliation from C to D. E and F: side view, distal end of larval tentacle; note loss of ciliation, particularly of sensory tufts (dh = dorsal hump, lt = larval tentacle, pc = provisional chaetae, st = sensory tuft). Compare with figures in Eckelbarger (1978); Amieva and Reed (1987); Amieva et al. (1987).

1988a]) suggests that sabellariid growth can be food limited and larvae are probably not developing at an optimum rate in nature. A similar conclusion was reached by Paulay et al. (1985) after rearing larvae of the serpulid polychaete, *Serpula vermicularis*, in natural sea water and sea water augmented with cultured algae. Suboptimal larval growth may permit normal development when food is limiting (as opposed to death, as for many crustacean larvae), but a decrease in growth rate does not ensure survival to recruitment, because the probability of mortality by predation increases with the length of time spent in the plankton (reviewed in Rumrill, 1990).

How might sabellariid larvae survive extended development? Larvae of sabellariid polychaetes are unusual among invertebrate larvae in having been shown to deter planktonic predators with a physical defense mechanism (Wilson, 1929; Pennington and Chia, 1984). When disturbed, a sabellariid larva (greater than 2 to 5 days old) contracts its body longitudinally, thereby erecting two bundles of barbed, provisional chaetae around itself (see Fig. 21.2a and 21.2b, and Fig. 1 in Pennington and Chia [1984]). Larvae of *Sabellaria cementarium* bearing provisional chaetae were eaten significantly less often than nonmotile eggs or larvae that had not yet developed chaetae in laboratory assays with four planktonic predators: a ctenophore, hydromedusa, brachyuran megalopa, and a juvenile fish (Pennington and Chia, 1984). The physical defense afforded by provisional chaetae probably enhances survivorship of sabellariid larvae in the plankton.

Although field evidence for food-dependent ontogenetic plasticity of sabellariid larvae has yet to be obtained, the advantages of the strategy seem apparent. Larvae advected to offshore, oligotrophic regions would slow their development, or reverse it, until transport processes brought them back into more productive near-shore waters where suitable adult habitat might be found. Competent larvae may revert to precompetence in a near-shore area experiencing a periodic oligotrophic condition, such as an upwelling of phytoplankton-poor water (Attwood and Peterson, 1989), thereby forestalling metamorphosis until food is available for early juvenile development. In areas of high phytoplankton abundance, larvae are likely to attain competence quickly and delay metamorphosis until they encounter a suitable substratum. For *Phragmatopoma lapidosa californica*, if not for all gregarious sabellariids, larval survival to recruitment is probably greatly enhanced by the combination of developmental responses to food supply and physical defense and by larval responses to hydrodynamic conditions and the presence of adult conspecifics (Pawlik and Butman, 1993).

## Acknowledgments

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