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Growth Stasis and Limited Shell Calcification in Larvae of *Cymatium parthenopeum* During Trans-Atlantic Transport

Abstract. *Larvae of the shallow-water marine gastropod* Cymatium parthenopeum *show no appreciable shell calcification and no demonstrable growth as they disperse across the Atlantic Ocean. Evidence of what appears to be physiological specialization for prolonged delay of metamorphosis was found in larvae of this prosobranch gastropod.*

The larvae of at least 19 families of shallow-water prosobranch gastropods can be found in the open waters of the Atlantic and Pacific oceans (*1–4*). In the absence of the environmental cues to initiate metamorphosis, these long-distance (teleplanic) larvae (*2*) may remain planktonic for many months after first becoming competent to metamorphose (*2*). Such flexibility in the timing of metamorphosis permits widespread larval dispersal and may result in virtual panmixia within North Atlantic populations of species such as *Cymatium parthenopeum* (*5, 6*) (Fig. 1). In contrast, larvae of most invertebrate species that have been reared in the laboratory rarely delay metamorphosis for more than a few weeks, most individuals either dying or metamorphosing spontaneously after that time (*1, 7–12*).

The greater potential for delayed metamorphosis and for widespread dispersal of teleplanic larvae is presumed to have a physiological basis (*13*). In particular, metabolism of teleplanic larvae is thought to shift from a growth phase to an equilibrium condition of no-growth energy balance at the time the larvae become competent to metamorphose (*13*), and the shells of some teleplanic larvae in the family Cymatiidae are thought to be uncalcified (*2, 4*). These characteristics are regarded as adaptive because they would discourage weight gain during transoceanic transport (*13*). However, there has been no documentation of either reduced growth or reduced calcification in teleplanic larvae. For the few nonteleplanic prosobranch species that have been studied in the laboratory (*Crepidula fornicata* and *C. plana*), larval growth (size, weight, protein content) continues unabated during the period of delayed metamorphosis, and larval shells are calcified (*11, 14, 15*). Growth stasis has been shown only for larvae of opisthobranch gastropods (*16, 17*).

An inverse relation between rate of development and ability to postpone metamorphosis has recently been shown for larvae of *Crepidula fornicata* and *C. plana* (*14, 15*). It appears that the maximum length of time that metamorphosis can be delayed by feeding (planktotrophic) larvae may be related to the rate at which such larvae develop toward a genetically determined end for maintaining larval form and function (*11, 14*). Because the presumed cessation of growth by teleplanic larvae may be related to their ability to delay metamorphosis, it is important to know whether their growth actually does cease during transoceanic transport. We report that teleplanic larvae of the prosobranch gastropod *Cymatium parthenopeum* are physiologically different from species with a more restricted range and a shorter maximum planktonic duration. In particular, we show that larvae of *C. parthenopeum* do not grow during transport across the Atlantic Ocean and that the larval shells are not significantly calcified.

Larvae of *C. parthenopeum* were obtained from plankton tows made between 1964 and 1966 along a west-east transect (Fig. 1). Larvae were killed in buffered Formalin (pH ~ 8.0) and later transferred to 80 percent ethanol buffered to pH ~ 8.0 with sodium borate. Other larvae were obtained from coastal plankton samples (13°21′N, 61°28′W) collected in 1982 by S. Humphries and preserved in Formalin buffered to a pH of approximately 8.0 with sodium borate. Larval shell lengths were measured with a dissecting microscope (×40) equipped with an ocular micrometer. Total dry weights (n = 150) and ash-free dry weights (n = 53) of individual larvae were then determined by standard techniques (*11, 18*). In addition, empty shells of eight individuals that had died and decomposed after being cultured for up to several months after their collection were dried, weighed, and reduced to ash in order to look at ash content of the shell. For comparison, total dry weight and ash content were determined for competent larvae (approximately 1200 μm in shell length) of nonteleplanic prosobranch species *Crepidula fornicata* and *C. plana*.

The mean ash content of intact teleplanic larvae was 4.8 percent [standard error of the mean (S.E.M.) = 0.3 percent, n = 38] for larvae preserved in alcohol and 6.5 percent (S.E.M. = 0.4 percent, n = 15) for those preserved in buffered Formalin. These differences are small but statistically significant

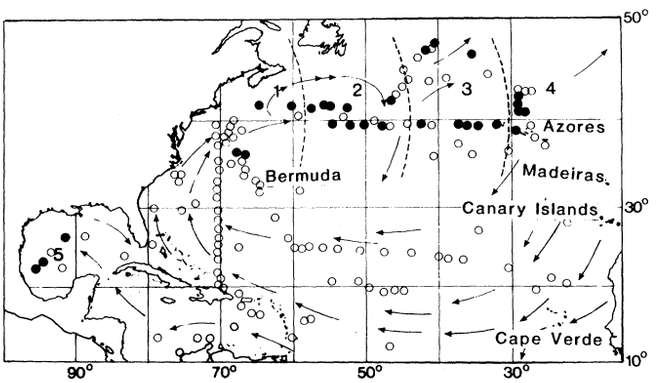

Fig. 1. Distribution of veliger larvae of *Cymatium parthenopeum* in the North Atlantic Ocean. Closed circles denote sites where larvae were obtained; open circles show other locations where larvae of this species have been found. Zones 1 through 4 (see Table 1) are delineated by dashed lines. Arrows indicate surface circulation of the North Atlantic gyre.

Table 1. Shell length and total nonlipid dry weight of *Cymatium parthenopeum* larvae collected from different areas in the Atlantic Ocean.

Zone	Position (West longitude)	Mean shell length (mm ± S.E.M)	Mean dry weight (μg ± S.E.M)	*n*
1	68°–60°	2.313 ± 0.009	480.6 ± 5.3	44
2	59°–45°	2.315 ± 0.017	490.6 ± 14.2	15
3	44°–31°	2.308 ± 0.024	468.6 ± 8.7	16
4	30°–28°	2.267 ± 0.007	470.4 ± 7.5	20
5	Gulf of Mexico	2.272 ± 0.014	463.3 ± 9.8	11

[$F(1,49) = 21.0$, $P < 0.05$). Ash content of empty shells was only 0.55 percent of total dry weight. Thus, most of the ash content of intact larvae was from the tissue component rather than the shell material. In contrast, inorganic constituents made up about 45 percent of the total dry weights of the more typical prosobranch larvae of *C. fornicata*, even though shells of these larvae are as transparent as those of *C. parthenopeum*. Treatment with standard decalcifying agents (19) did not decrease birefringence of *C. parthenopeum* shells and did not visibly alter shell morphology or sculpture. Observations of the *C. parthenopeum* shell external surface at high magnification with scanning electron microscopy did not reveal the presence of any obvious calcareous concretions. Moreover, shells shrunk substantially in length (7.2 percent, S.E.M. = 0.4 percent, $n = 18$) and width (12.7 percent, S.E.M. = 0.7 percent, $n = 8$) when allowed to air-dry, a result consistent with a lack of pronounced shell calcification.

Electron probe x-ray microanalyses of the elemental composition of four shells (two from alcohol and two from Formalin-preserved samples) also revealed little calcium (*20*). The x-ray spectra for all four shells had distinct aluminum, sulfur, chlorine, and calcium (K_α and K_β) peaks (Fig. 2A). However, the calcium peaks were very low compared with those from larval shells of different gastropod species present in the same preserved plankton samples. For example, the mean number of counts (calcium, K_α peaks) produced during a 30-second analysis was 101 (S.E.M. = 26, $n = 9$) for *C. parthenopeum* compared with 4,658 ($n = 3$) and 4,038 ($n = 2$) for the shells of two other prosobranchs, *Thais haemostoma* and *Bursa thomae*. Lack of significant calcium in *C. parthenopeum* shells is therefore not an artifact of preservation. We cannot explain the large aluminum peak seen for larval shells of *C. parthenopeum* and other species collected at the same time; probes of the double-sided tape used between the shell and the stub did not produce aluminum peaks (*21*).

Because ash content was only about 5 percent of dry weight for larvae of *C. parthenopeum*, biomass was estimated as total dry weight. Total dry weight of alcohol-preserved larvae increases as a linear function of shell length for larvae of this species (Fig. 2B): $y = 314.5x - 250.27$, $r = 0.55$, $n = 119$; the slope (314.5 ± 45.7) is significantly different from zero ($P < 0.05$, F test). Thus, shell length can be used as an index of biomass in larval *C. parthenopeum*. As expected, Formalin-preserved larvae show greater biomass for individuals of given shell length: $y = 645.5x - 883.7$ ($r = 0.90$, $n = 16$). Because larvae of *C. parthenopeum* are released in shallow coastal waters, larval age increases with distance from shore, along the axis of the North Atlantic Drift (Fig. 1). The extent of larval growth during transoceanic transport can therefore be inferred from the relation between either shell length or total dry weight as a function of the distance from shore that larvae were collected. In both cases, the slopes of the lines (Fig. 2, C and D) are not significantly different from zero (*t*-test, $P > 0.10$) (*22*) suggesting no significant change either in biomass or in shell length as larvae drift across the ocean. Larval growth was also examined in five longitudinal zones in the Atlantic Ocean (Fig. 1); mean shell lengths and mean dry weights of larvae were compared among zones (Table 1). Larvae from the different zones did not differ significantly in tissue weight [$P > 0.10$, $F(4,100) = 1.25$]. Shell lengths were marginally different for larvae captured from the different zones [$P > 0.05$; $F(4,100) = 2.7$] because zone 4 contained larvae whose shell lengths were slightly less than those in the other zones [$P < 0.05$, Fisher's test of least significant difference (*23*)]. The opposite result should have been obtained if larvae were growing during transport. Azorean populations probably contributed to larvae in zone 4.

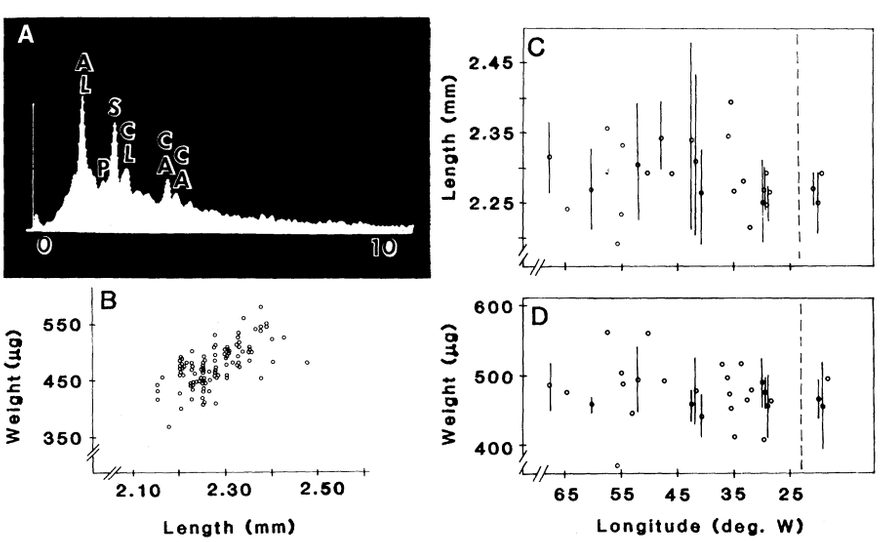

Fig. 2. Data obtained from preserved samples indicated in Fig. 1. (A) Typical elemental spectrum from shell, surface probe, showing extremely low calcium peaks (K_α and K_β); x-ray energy in kiloelectron volts on *x*-axis. (B) Relation between shell length and total dry weight. (C) Relation between larval shell length and site of collection. (D) Relation between larval dry weight and site of collection. Vertical bars (C and D) indicate 1 σ about the mean.

Our evidence indicates that larvae of *C. parthenopeum* have poorly calcified shells throughout larval life; to our knowledge this is the first demonstration of such limited shell calcification in larval prosobranchs. Larvae of *C. parthenopeum* may strengthen their shells by tanning of shell proteins, as in molluscan periostracum (*24*), instead of through deposition of $CaCO_3$ and other salts in an organic matrix, as occurs in other species (*25*). The adaptive value of reduced shell calcification is unclear, since shells account for a high percentage of total dry weight of the larvae (*26*). In addition, we found that larval biomass did not differ significantly among longitudinal zones and that changes in shell length were less than 2 percent (zone 2 versus zone 4); growth apparently ceases during trans-Atlantic transport in this species. Our samples do not allow examination of changes in lipid levels that may occur

during larval life, since much of the initial lipid is likely to have been lost during storage in alcohol.

The apparent cessation of growth by larval *C. parthenopeum* is in contrast to the increases in size and biomass of nonteleplanic prosobranch larvae (*Bittium alternatum, Ilyanassa obsoleta, C. fornicata*, and *C. plana*) after they become competent to metamorphose; these increases are apparent whether the larvae are preserved in alcohol or Formalin (*11, 14, 15*). Lack of growth during long-distance oceanic transport of *C. parthenopeum* larvae may be due either to shifts in metabolism (*11*) or to food limitation in the open ocean (*2*). Larvae must be laboratory-reared to distinguish between these possibilities. Laboratory studies may also help in determining whether larvae retain the capacity for successful metamorphosis after transoceanic transport and in assessing the relation between rate of growth and rate of differentiation.

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19. The decalcifying agents used were 5 percent HCl for 2 hours, 10 m*M* EGTA for 1 hour, or 5 percent EDTA for 12 hours.
20. Shells were rinsed in several changes of distilled water and air dried onto double-stick tape on standard aluminum-scanning electron microscope stubs. Analyses were conducted with an AMR 1000A scanning electron microscope equipped with a Kevex detector and a Tracor Northern energy dispersive x-ray analyzer. For all analyses, the stub was set at an angle of 45° to the detector, and an accelerating voltage of 20 kV was used. The bremsstrahlung background was subtracted, and the total number of counts in each major peak was integrated by computer.
21. Aluminum has been detected as a minor element during probes of other mollusc shells [M. R. Carriker, C. P. Swann, L. W. Ewart, *Mar. Biol.* **69**, 235 (1982); L. S. Eyster, unpublished observation].
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26. Lengths of the eight empty shells in the collection were measured, and the total biomass expected for intact larvae of equivalent size was calculated. Empty shells weighed 63 percent (standard deviation = 4.5 percent, $n = 7$) of the total dry weight expected for intact larvae of equivalent size.
27. Contribution 5458, Woods Hole Oceanographic Institution, and contribution 120, Marine Science and Maritime Studies Center.

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The Appearance of Sustained Equatorial Surface Westerlies During the 1982 Pacific Warm Event

Abstract. *In June 1982 a band of anomalous southerly surface wind, extending from the equator as far south as the Tasman Sea, formed east of Australia (150°E to 160°E). This flow crossed the equator just before the appearance of sustained westerly winds on the equator somewhat west of the date line. Because these westerly winds induced the initial strong equatorial warming of the ocean east of the date line during the 1982 El Niño–Southern Oscillation (ENSO) event, the southerly jet appears to be an important atmospheric component leading to the onset of the vigorous phase of this event. Some historical evidence suggests that anomalous southerly winds in the same region occurred prior to the appearance of sustained equatorial westerly winds in the major ENSO events of 1957, 1965, and 1972.*

Although an El Niño–Southern Oscillation (ENSO) event is a coupled ocean-atmosphere phenomenon (*1*), some stages of ENSO events can be examined usefully if one imposes the behavior of one fluid and examines the response of the other. The onset of strong equatorial warming east of the date line in the 1982 Pacific warm event appears to be such an instance. Prior to June 1982, there were only weak anomalies in the monthly mean surface zonal wind (*2*) (< 1 m/sec) along the equator west of the date line, and there was at most weak equatorial warming (anomalous sea-surface temperature < 1°C). However, westerly surface winds appeared west of the date line in late June 1982 and persisted for several months, and rapid equatorial surface warming east of the date line began subsequent to the onset of these westerlies (*3, 4*). Harrison and Schopf have shown that the ocean surface warming between July and October 1982 can be substantially accounted for as the oceanic response to these winds (*5*). Of course, the initial warming is but part of the 1982 ENSO event; ocean and atmosphere anomalies continued to evolve after October 1982.

Because the equatorial surface westerlies that began in June 1982 can be linked to the first substantial oceanic signal of the 1982 event, it is important to understand the origin of these winds. I show here that they did not originate in the eastern Indian Ocean or far western Pacific (*6*), or as a large-scale weakening of the mid-Pacific southeast trades (*7*). Rather, they were associated with the breakdown of a jet of strongly anomalous southerly winds east of Australia between 150°E to 160°E and 40°S to 5°N. This result is based on an examination of monthly average and 10-day average winds at a nominal height of 19.5 m, produced from the U.S. Navy NOGAPS operational analysis program (*8*), and is consistent in its major features with available ship wind data and other meteorological products.

Because Fleet Numerical Ocean Central (FNOC) began operational use of the NOGAPS during 1981 and because its winds can be substantially different from those of earlier FNOC programs, no consistent climatological record is available with which to directly assess the anomalous character of the 1982 NOGAPS 19.5-m winds. However, a high-spatial-resolution global climatological wind record of merchant ship observations (*9*) provides a useful alternative and permits the detection of strongly anomalous conditions.

The region of particular interest is 150°E to 170°E and 10°N to 50°S, although data over a much larger area have been examined. The large-scale patterns of the NOGAPS winds from January