

Ecology and Burrowing Behavior of *Ascobulla ulla* (Opisthobranchia: Ascoglossa)

by

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Abstract. A population of *Ascobulla ulla*, a tectibranch ascoglossan (=sacoglossan), was sampled on a high-energy jetty environment at Fort Pierce Inlet, Florida. The highest densities of *A. ulla* occurred during warm summer months when the surf was calm and the alga *Caulerpa racemosa* was more abundant. The habitat requirements for *A. ulla* appear to be narrow, resulting in seasonal fluctuations in population size. The ability to burrow in the more protected microhabitats where *C. racemosa* occurs is an important specialization that also adapts *A. ulla* for life in its high-energy habitat. The unusual burrowing behavior of *A. ulla*, involving the bilobed cephalic shield and a rotational twisting and periodic flexion of the thin shell, is described from field and laboratory observations.

INTRODUCTION

Ascobulla, *Volvatella*, and *Cylindrobulla* represent a phylogenetic link between the burrowing cephalaspideform opisthobranchs and the more advanced epifaunal tectibranch Ascoglossa (THOMPSON, 1979; CLARK, 1982). Information about *Ascobulla ulla* has been limited to taxonomic descriptions (MARCUS & MARCUS, 1956, 1970; MARCUS, 1972) and some brief ecological observations (CLARK & JENSEN, 1981; JENSEN & CLARK, 1983). *Ascobulla ulla* has been reported from "muddy algae" at the Enseada of Guarujá, east of Santos, Brazil (MARCUS & MARCUS, 1956); in association with mangroves at Key Biscayne, Florida (MARCUS, 1972); on the rhizoids of the alga *Caulerpa paspaloides* (Bory) Grev. at Key Largo, Florida (JENSEN & CLARK, 1983); in association with mangroves at Twin Cays, Belize, Central America (Clark and De Freese, unpublished data); and on the rhizoids of *C. racemosa* (Forsskål) J. Ag. at Crawl Key, Florida (personal observation) and at Fort Pierce Inlet, Florida (JENSEN & CLARK, 1983).

The inlet at Fort Pierce represents the northernmost record for *Ascobulla ulla* and is close to the northern limits of the tropical siphonate algal community (JENSEN & CLARK, 1983). Although high-energy habitats are often overlooked as suitable collecting sites for ascoglossans, 13 ascoglossan species have been collected from this habitat type (JENSEN & CLARK, 1983). The aim of this paper is to describe aspects of the behavior and population biology of *A. ulla*, emphasizing the burrowing behavior, habitat

selection, and effects of environmental stress on the population at Fort Pierce Inlet, Florida.

STATION DESCRIPTION

Fort Pierce Inlet (27°28'N, 80°18'W) connects the Indian River Lagoon system to Florida's Atlantic Coast (Figure 1). The inlet is defined by two man-made rock jetties that extend into the Atlantic Ocean. *Ascobulla ulla* predominantly inhabits the tidepools and the leeward side of boulders along the north face of the north jetty and is associated with algal mats of *Caulerpa racemosa*. These microenvironments are often subjected to severe wave disturbance, especially during late summer and fall (tropical disturbances) and during the winter (northern cold fronts). The inlet is also affected by upwelling events that occur each summer along the east coast of Florida (GREEN, 1944; SMITH, 1982).

MATERIALS AND METHODS

The population of *Ascobulla ulla* at Fort Pierce Inlet was sampled monthly from May 1984 to September 1985. Initially, samples were taken along two transects parallel to the jetty. One transect was positioned along the northern edge of the jetty where the rocks outcrop on the sandy beach. This transect included *Caulerpa racemosa* patches. The other transect, established 2 m to the north, was located in an area of bare sand only. *Ascobulla ulla* occurred only in association with *C. racemosa*. This alga was re-

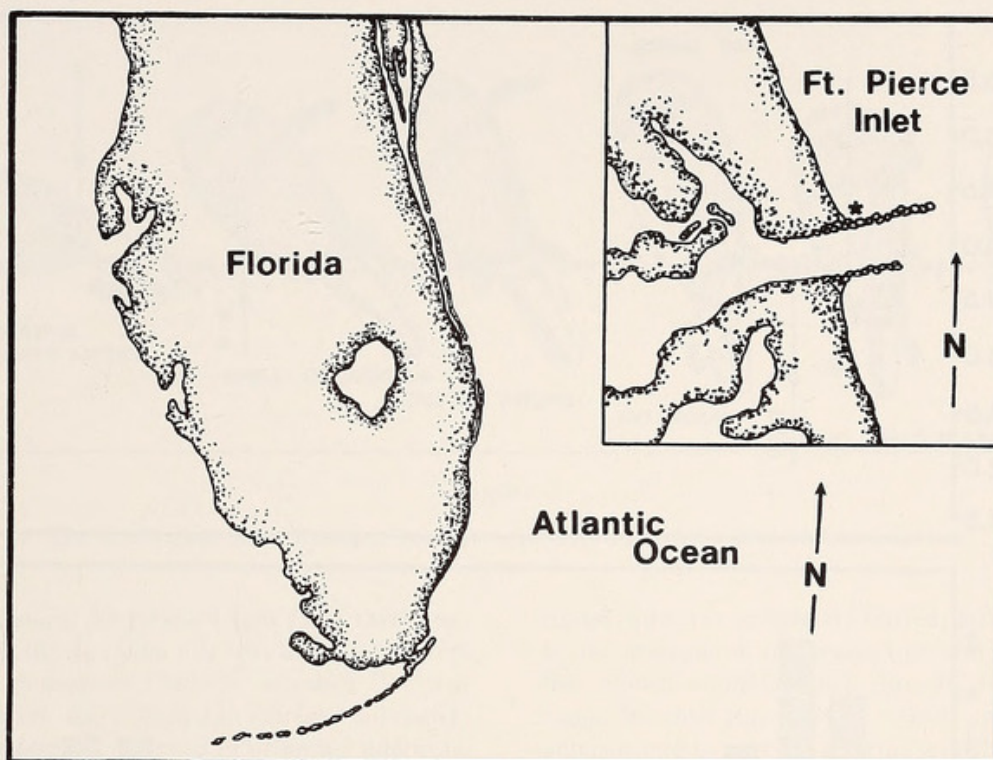


Figure 1

Location of the sampling site at Ft. Pierce Inlet, Florida. Site indicated by asterisk.

stricted to hard substrata and the areas of sand adjacent to boulders of the jetty. All subsequent samples were taken at sites having 100% algal cover. Because optimal habitats were chosen for sampling sites, the population density data are presented as "maximal density" (*i.e.*, the highest animal densities found for each monthly sampling date). Samples were taken using a 10-cm diameter PVC corer inserted to an approximate depth of 10 cm. Deeper cores (20 cm) were taken between December 1984 and March 1985, in an attempt to locate *A. ulla*. Sample sites were categorized as upper intertidal, midtidal, or subtidal habitats. Samples were washed through a 0.5-mm sieve and sorted in the field. Animals were transported live to the laboratory in 2-L plastic bottles containing seawater.

A midsummer (1985) sediment sample was collected from a site adjacent to the jetty where *Ascobulla ulla* was abundant. This sample was analyzed for particle size composition (median particle size = 0.22 mm, 2.2ϕ) (Wentworth classification). Based upon graphical analysis (BUCHANAN & KAIN, 1971) the sediment was poorly sorted ($\sigma_\phi = 1.23$), coarse skewed ($SK_\phi = 0.11$), and mesokurtic ($K_\phi = 1.10$). For consistency, this sediment sample was used for all burrowing trials.

Burrowing time was measured at 10, 15, 20, 26, and 30°C. Animals were allowed to adjust at experimental temperatures for approximately 30 min in fingerbowls containing seawater. After 30 min the animals were transferred to a fingerbowl containing the midsummer (1985)

sediment sample and seawater maintained at the experimental temperature. The "digging period," defined as the time elapsed between the first probing by the foot and the complete coverage of the shell by sand (TRUEMAN & ANSELL, 1969), was measured with a stopwatch.

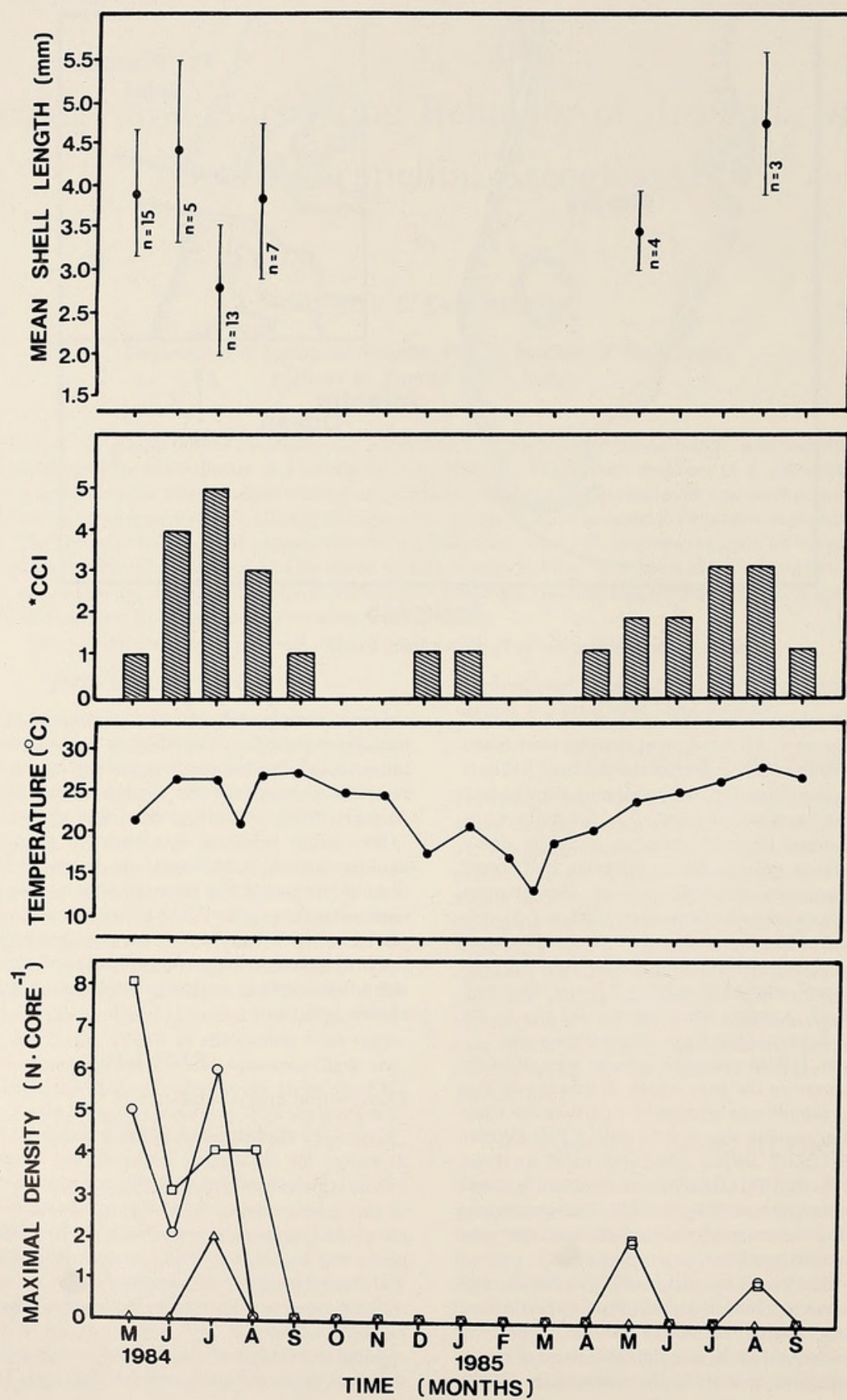
Burrowing behavior was observed in narrow, glass aquaria containing sediment and seawater. The mechanism of burrowing was recorded with a video camera and video cassette recorder (VCR). *Ascobulla ulla* was carefully placed on the substratum at the glass-sediment interface. Burrowing activity began immediately and often proceeded along this interface, enabling detailed observations of sub-surface behavior.

RESULTS

Distribution and Abundance

Densities of *Ascobulla ulla* were generally low (Figure 2) except for population peaks during May (1984 and 1985), which coincided with the presence of stable stands of *Caulerpa racemosa*. Animal lengths and densities fluctuated during the summer months. In July 1984, the populations of both *A. ulla* and *C. racemosa* appeared to decline with lower temperatures accompanying an apparent upwelling event, and by August both populations were significantly reduced.

Most individuals of *Ascobulla ulla* were collected in the sediment layer associated with the algal mat. The sediment



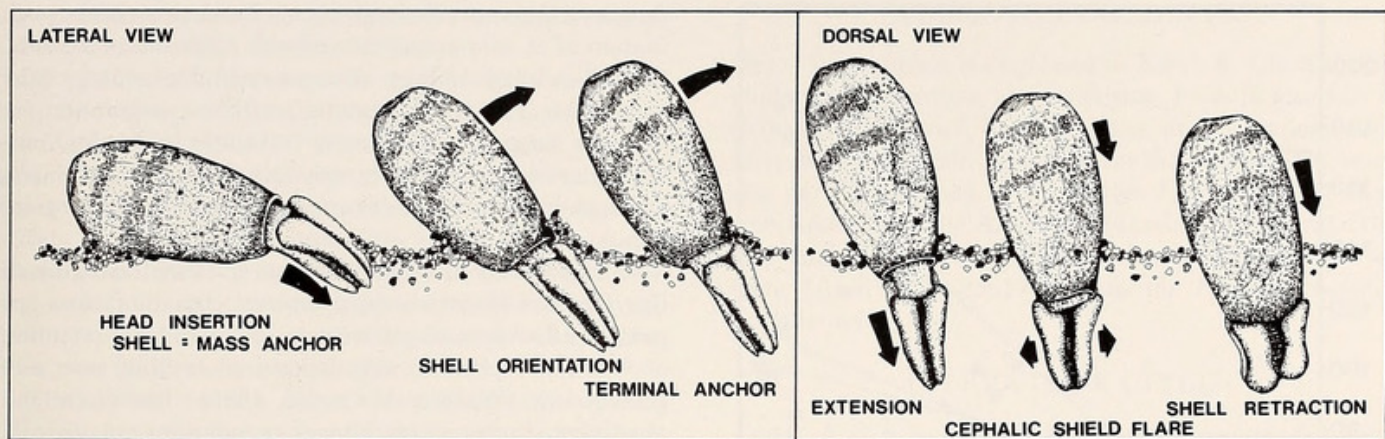


Figure 3

The mechanism of burrowing in *Ascobulla ulla*. Sequence from lateral and dorsal views.

that accumulated along the leeward rock faces rarely exceeded 1 cm in depth. *Ascobulla ulla* was usually in direct contact with the rhizoids of *Caulerpa racemosa* (0–3 cm depth). Animals were also collected in the sand surrounding anchored clumps of *C. racemosa* in protected tidepools. Under these protected conditions, *A. ulla* occasionally emerged from the sediment and crawled up the assimilators of the alga for egg deposition and feeding. This behavior has also been observed in the laboratory and at other field collection sites (Belize, Central America; Crawl Key, Florida Keys).

Maximal animal size and density occurred during the warm summer months, when surf conditions were generally calm. *Caulerpa racemosa* was most abundant along the shallow areas of the jetty. In deeper water (2–3 m), well-developed stands of another alga, *Halimeda discoidea* (Decaisne), predominated, and *C. racemosa* was uncommon at these depths. A decrease in the *C. racemosa* population was observed after upwelling events, coastal storms, and heavy rainfall. During the fall and winter months, no specimens of *Ascobulla ulla* were collected, and *C. racemosa* was observed only occasionally.

The Mechanism of Burrowing

The mechanism of burrowing in *Ascobulla ulla* is illustrated in Figure 3, and described using the burrowing terminology of TRUEMAN & ANSELL (1969).

When *Ascobulla ulla* is placed on the sandy substratum, the animal begins burrowing almost immediately and con-

tinues until it is completely buried. Burrowing is initiated by the insertion of the propodium and the anterior end of the bilobed cephalic shield into the substratum. At this stage, the shell functions as a mass anchor, enabling the anterior end to take on a vermiform shape, which probes and wedges into the substratum. This penetration phase is accompanied by slight side-to-side movement. After the head is inserted into the substratum, it functions as a terminal anchor, facilitating shell orientation and increasing the angle of penetration. During the shell-orientation phase, the head and propodium continue to extend deeper into the sediment. As the shell approaches a vertical position in relation to the substratum, the cephalic shield flares, laterally compresses the sediment, and thus firmly establishes the terminal anchor. The shell is then slowly pulled into the substratum until it contacts the median furrow at the posterior end of the cephalic shield. Shell insertion is accompanied by the rhythmic pumping and rotational twisting of the shell as it "augers in." The shell apex bears a spiral slit that physically separates the whorls (MARCUS & MARCUS, 1956), thus permitting the periodic contraction and expansion of the shell. This allows the shell to function as a penetration anchor during the expansion phase (when mantle musculature relaxes), and presents minimal cross-sectional area during retraction (terminal anchoring by head). When observed from the apical view, the shell appears as a spring that coils and uncoils. The rotational twisting of the shell has not been reported for other infaunal opisthobranchs and appears to facilitate shell retraction. The animal repeats this

Figure 2

Composite figure of seasonal data taken at Ft. Pierce Inlet. Mean Shell Length: ● = mean; vertical lines = standard deviation. *Caulerpa* Coverage Index (*CCI): 0 = no *Caulerpa*, 1 = sparse coverage, 2 = short growth + clumped distribution, 3 = well-developed growth + clumped distribution, 4 = well-developed growth + broad coverage, 5 = dense growth + broad coverage. Temperature: ● = water temperature in °C. Maximal Animal Density: Δ = upper intertidal zone, ○ = midtidal zone, □ = subtidal zone.

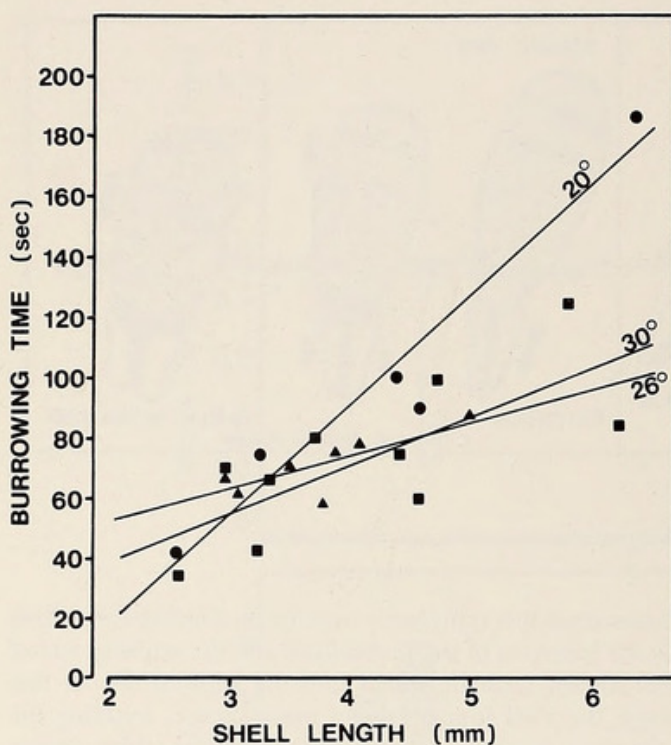


Figure 4

Rate of burrowing versus shell length of *Ascobulla ulla*, at three temperatures. ● = 20°C: ($Y = 36.86X - 56.80$, $r = 0.9659$, $n = 5$). ▲ = 26°C: ($Y = 11.45X + 28.65$, $r = 0.7912$, $n = 7$). ■ = 30°C: ($Y = 16.43X + 5.25$, $r = 0.7462$, $n = 10$).

sequence of penetration, shell orientation, head extension, cephalic shield flare, and shell retraction until burial is complete. Mucus secreted at the anterior end of the shell appears to prevent the movement of substratum particles into the mantle cavity. Slight disturbances such as water currents or rough handling resulted in a rapid, copious discharge of dilute, milky white mucus from the posterior region of the shell. Animals anchor to the algae or sediment by viscous mucous threads *in situ* if exposed during wave surge.

Burrowing Rate

Figure 4 shows the effects of animal size and water temperature on the burial rate of *Ascobulla ulla*. At 10°C, *A. ulla* was immobilized; no movements or attempts at burrowing were observed. At 15°C, the experimental animals slowly twisted their head and attempted to probe the substratum. After 10 minutes, several animals had achieved head penetration, although burial was clearly impaired. At 20, 26, and 30°C, burrowing time generally increased with increasing animal size.

DISCUSSION

Peak population densities of *Ascobulla ulla* coincide with the presence of well-developed mats of the alga *Caulerpa*

racemosa, their specific food source. Reductions in the population of *A. ulla* appear to coincide with thermal stress, rainfall-induced salinity changes, and high-energy surf conditions. The great magnitude of these population reductions suggests that climatic variations in the high-energy intertidal zone heavily constrain populations of *A. ulla* and such high-energy areas appear to represent a marginal habitat.

In *Elysia tuca* Marcus, 1967, an epifaunal ascoglossan that feeds on *Halimeda* spp., seasonal climatic factors appear to affect several parameters, including the retention of functional plastids, egg deposition, feeding rate, and growth rate (WAUGH & CLARK, 1986). The biotic and abiotic constraints on ascoglossan populations are not fully understood, providing a fertile area for additional research.

A variety of environmental factors appear to have important effects on the stability of the *Caulerpa racemosa* population. Changes in the quality or quantity of the food alga may have a direct effect on the animal population owing to the stenophagous nature of *Ascobulla ulla*. The algal population appears to decline at lower temperatures associated with summer upwelling events. In addition, *C. racemosa* may be adversely affected by high summer temperatures, which often exceeded 30°C in the shallow intertidal pools. This was especially evident when low tides prevented an open exchange of seawater.

The apparent disappearance of *Ascobulla ulla* during the fall and winter months coincides with a seasonal transition to rougher surf conditions, increased turbidity, and decreasing water temperatures. The effects of these factors and others, such as photoperiod and irradiance, are not known. *Ascobulla ulla* appears to be capable of maintaining its position on the assimilators of the alga in a moving current or a light surge, but the animals are easily displaced from the alga by moderate shaking of the thallus, which indicates a vulnerability to high surf or heavy surge conditions during emergence. *Ascobulla ulla* may also emerge at high tide, when depth could provide some protection from surface waves. *Ascobulla ulla* may burrow more deeply into the sediment during fall and winter. Although deeper core samples were taken during the winter months when *A. ulla* was uncommon or absent, no evidence was found to confirm this hypothesis. *Ascobulla ulla* has direct development (CLARK & JENSEN, 1981); therefore, a winter burrowing response or undiscovered, subtidal, winter habitats could account for the rapid spring colonization observed at the sampling site. The disappearance of *A. ulla* from the jetty habitat during the winter suggests that vernal recolonization occurs from deep-water populations inhabiting reefs adjacent to the jetty. Direct development presents some advantages to the colonization of high-energy beaches because juveniles are presumably able to burrow immediately and faster if juvenile size approximates sediment grain size, and the efficient recruitment associated with direct development should enable a rapid increase in the population. The coincidence of low tides and freezing temperatures observed during the winter of 1985 might

also explain the slow rate of vegetative recolonization of *Caulerpa racemosa* in the intertidal areas.

The habitat requirements for *Ascobulla ulla* appear to be quite narrow, resulting in seasonal fluctuations in population stability. Data on population dynamics, zoogeographic distribution, and the effects of temperature on burrowing rates support a hypothesis that *A. ulla* is relatively stenothermal. Because Fort Pierce represents the distributional limit of several tropical and subtropical ascoglossan and siphonate species (JENSEN & CLARK, 1983), minor climatological conditions may have important effects on floral and faunal distributions.

The bilobed cephalic shield characteristic of *Ascobulla ulla* enhances the burrowing capability of this primitive ascoglossan and may function as a more efficient terminal anchor than the single broad cephalic shield of most primitive infaunal cephalaspids. The distinctive apical spiral slit of the thin shell permits cross-sectional changes that may aid the flow of water through the mantle cavity as well as provide a more efficient penetration anchor during burrowing. Contraction and passive relaxation of the shell adductor muscle control the rhythmic pumping of the shell (MARCUS & MARCUS, 1956). A detailed analysis of muscular structure, similar to BRACE's (1977) anatomical study of some tectibranch opisthobranchs, would further clarify the burrowing mechanics of *A. ulla*.

The burrowing sequence in *Ascobulla ulla* diverges from the behavior of the cephalaspid *Haminea antillarum* (d'Orbigny, 1842). *Haminea antillarum* has a single broad cephalic shield, which is used to plow slowly into the sediment at a shallow angle of penetration (TRUEMAN & ANSELL, 1969; De Freese, personal observations).

Ascobulla ulla shares some similarities with the oxynocean *Volvatella laguncula* (Sowerby, 1894), which also exhibits adduction movements of its flexible shell (THOMPSON, 1979). Because there was no obvious exclusion of particulate matter, THOMPSON (1979) suggested that *V. laguncula* pumped a suspension of fine sediment through its mantle cavity. An alternate hypothesis, by CLARK (1982), suggests that shell adduction in *V. laguncula* may assist burrowing in compacted sand, by loosening the sediment surrounding the shell, and coincidentally increasing the availability of interstitial water for respiratory needs.

Ascobulla ulla burrows at considerably slower rates than more typical, infaunal, high-energy beach organisms: *Macra odorina* burrows in 1.5 sec (ANSELL & TREVALLION, 1969) and the burrowing rate of *Donax denticulatus* declines from 2.9 sec at 32°C to 8.15 sec at 24°C (TRUEMAN, 1983).

Data on burrowing rates, habitat preference, and seasonal population stability suggest that *Ascobulla ulla* should not be strictly viewed as a high-energy beach organism. However, burrowing is an important capability that allows *A. ulla* to exploit the high-energy habitat at Fort Pierce Inlet, Florida.

ACKNOWLEDGMENTS

Great appreciation is expressed to Kerry B. Clark for his guidance, suggestions, and criticisms. I would also like to thank R. L. Turner, W. G. Nelson, and two anonymous reviewers for critically reviewing the manuscript. The work was partly supported by the Lerner-Gray Fund for Marine Research of the American Museum of Natural History and by a Doctoral Dissertation Research Improvement Grant OCE-8501715 from the National Science Foundation.

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