



New techniques yield new insights on the basic biology of living microgastropods

CAROLE S. HICKMAN

University of California, Department of Integrative Biology, 3060 VLSB, Berkeley, CA 94720-3140, USA,

E-mail: caroleh@berkeley.edu

Abstract

Light traps, undisturbed sediment cores and emergence traps were used to pursue new knowledge of the biology of poorly-known microgastropods. These tools were used specifically to explore novel habitats, behavior and function. The most interesting discoveries include significant interstitial populations of species previously considered rare, including epipsammic browsers and taxa that emerge from the sediment at night. Diel activity patterns include movement between sediment and water column, movement between sediment and marine plants, vertical migrations on marine plants, and movement between plants and plant epiphytes. Unsuspected behavioral correlates include active swimming and mass spawning aggregations and drifting and floating using mucus threads to launch into the water column from marine plants or the sides of aquaria. Ciliary locomotion is a convergent theme in microgastropods, with new examples from vetigastropod and neritopsine species that also use mucus threads in drifting. At the sediment-water interface, upside-down ciliary locomotion in the surface tension may be combined with feeding on the rich microbial ecosystem concentrated at the air-water interface.

Key Words: light traps, emergence traps, infauna, interstitial fauna, stygofauna, rafting, drifting, diel vertical migrations, epipsammic browsing, ciliary locomotion

Introduction

“Prosobranch” gastropod diversity is concentrated at small shell and body sizes (< 5 mm) among the so-called microgastropods. Malacological studies have concentrated on conspicuous, large-shelled species that are easily collected. There is a gap in our knowledge of minute and cryptic species, especially those that are invisible in the field and require special collection and recovery techniques. Microgastropods are known primarily from empty shells recovered from beach sand and “shell grit” by collectors who have specialized in the activities of “sorting” and “picking” through bulk samples. In museum collections it is common to find the microgastropods sorted to higher taxonomic levels and placed in drawers at the end of a series of well-curated and well-identified large-shelled species. There is growing recognition that a major component of marine biodiversity is small (< 5 mm). Estimates of species richness have increased dramatically in studies that have made a special effort to sample micromolluscan diversity (Bouchet *et al.* 2002). New methods for collecting and sorting in heterogeneous habitats will continue to yield new micromollusc taxa and increase understanding of species richness.

Resurgence of interest in obtaining live micromolluscs is driven primarily by systematists working to recover phylogenetic relationships from molecular data or from comparative anatomical data that

require more than an empty shell. For anatomical and molecular studies, fixation and preservation are of immediate concern.

Collecting live animals offers another kind of opportunity: filling the knowledge gap in the basic biology of behavior, function, and ecology of micromolluscs. This paper emphasizes the challenge of understanding the living organism. Precious opportunity is lost when live animals are placed directly in alcohol for DNA extraction or fixed and preserved immediately for sectioning and anatomical reconstruction. The purpose of this paper is twofold: (1) to outline three methods that have recovered large numbers of live microgastropods, and (2) to demonstrate the fruitfulness of these methods in terms of novel biological phenomena they elucidate.

The methods involve devices that are easily constructed and modified and do not require expensive and inflexible off-the-shelf technology: light traps and various uses of light to attract animals at night, recovery of undisturbed sediment cores and samples of natural habitat, and emergence traps to recover animals that undergo diel migrations between sediment and water column and sediment and marine plants (Figs 1–3). Examples of phenomena revealed by these techniques include: sustained swimming, mass aggregation, and mass spawning in the water column; epipsammic browsing on sand grains; and mucous thread launching and upside-down locomotion in surface tension using ciliary locomotion.

Light traps

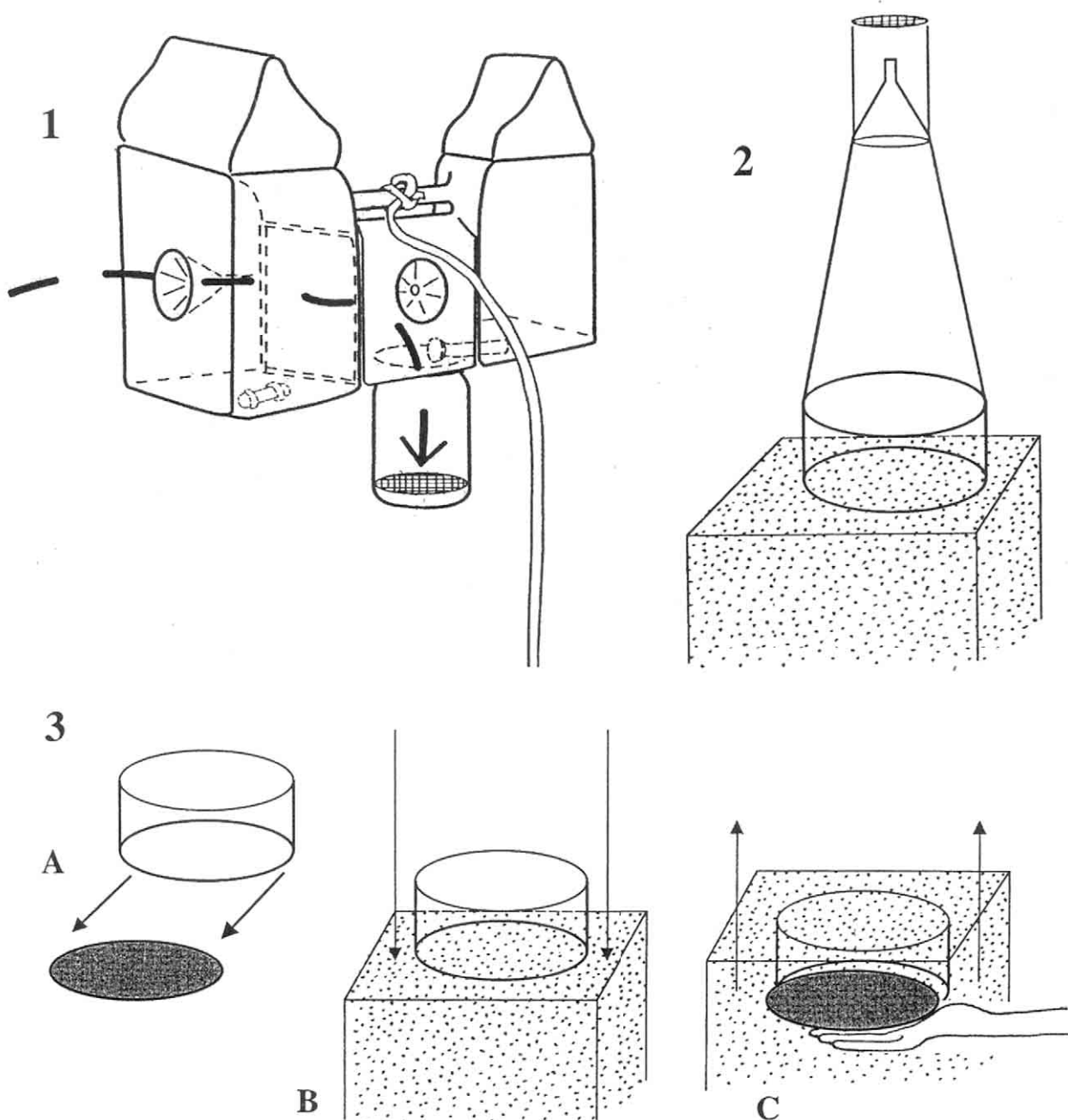
Rationale and Design. Light traps of different designs have been used for many years to attract and capture positively-phototropic aquatic organisms. The major target organisms have been larval and juvenile fishes in both freshwater (Marchetti *et al.* 2004) and marine environments (Doherty 1987) and marine zooplankton, especially copepods (Holmes & O'Connor 1988; Holmes 1998) and larval crustaceans (Porter *et al.* 2008). In order to be caught in a light trap, an organism must have the appropriate visual photosensitivity and the ability to swim to the trap and enter it. Light trap designs for fish larvae are often fairly elaborate: capable of recording depth and controlling angles, wavelength, and intensity of illumination. Battery-powered incandescent bulbs and chemical light sticks are the most common sources of illumination. Comparative studies of light trap designs have shown significant differences and biases in sampling studies (*e.g.*, Kissick 1993; Hernandez & Lindquist 1999; Meekan *et al.* 2001; Marchetti *et al.* 2004).

Although trap design may bias the size, the age, or the taxa that are captured, the physiological characteristics of the taxa may be equally important. For quantitative studies it is nearly impossible to determine the area that is being sampled (Hernandez & Lindquist 1999). None of these factors is particularly relevant to the potential use of light traps to attract, concentrate, and capture new or poorly known microgastropods. The simplest and least expensive homemade light traps are the best way for malacologists to experiment with the technique.

The light trap illustrated here (Fig. 1) is one of five that were constructed and deployed over the course of one tidal cycle to sample larval stomatopods in back-reef habitats on Moorea, French Polynesia (S.S. Porter unpubl. data). The trap was designed to hang in the water column immediately beneath the surface, attached to a cinder block on the bottom. It was lit by a small underwater flashlight for several hours shortly after sunset, and designed so that organisms would enter the PVC body of the trap via the wide end of one of four plastic funnels (see Hickman & Porter 2007 for design de-

tails). Subsequent design experiments have included smaller traps with a single funnel at one end and catchment at the other and lit by Cyalume® “light sticks.”

Results. Light traps deployed in a variety of marine environments in Western Australia, Hawaii, and Moorea (French Polynesia) have captured both larval and adult microgastropods and revealed some interesting biological phenomena. The most detailed account to date is of sustained swimming, mass aggregation at light traps, and epidemic spawning in two species of benthic scissurellid gastropods (Hickman & Porter 2007). The thousands of individuals recovered on one night in 2002 demonstrate that these cryptic microgastropods are not rare. An earlier observation of a “struggling mode of lo-



Figures 1–3. Basic design of three devices for collecting microgastropods. **1.** Light trap (modified from Hickman & Porter 2007). **2.** Emergence trap. **3.** Sediment corer. See text for details.

comotion” in a single scissurellid individual led Haszprunar (1988) to conclude that the behavior “cannot be used to traverse large distances.” Hasegawa (2004) reported mass swimming and spawning of scissurellids at an underwater fishing lure, also indicating a behavioral attraction to light. It is probable that other poorly-known groups of microgastropods that are rare in museum collections are not actually rare in nature and that aggregation can be induced.

A second significant microgastropod component in light trap assemblages is larval and early juvenile neritid gastropods (C.S. Hickman unpubl. data). In Moorea three morphologically distinct neritid larval forms have been recovered from light traps deployed at the surface in shallow water in both back-reef lagoons and at the mouths of estuaries at the heads of two major embayments. The appearance of small numbers of juveniles (< 5 mm) in the traps is more difficult to explain given the lack of any structural features to facilitate sustained swimming. However, laboratory observations of mucous thread production, drifting, and upside-down locomotion in surface tension by microneritids (C.S. Hickman unpubl. data) provide a potential explanation for their presence at the surface during the time intervals in which traps were deployed.

A morphological feature that scissurellid gastropods and neritid gastropod larvae share with larval fish, larval crustaceans, and many other forms in light trap assemblages is disproportionately large eyes (Figs 4–5). This is a convergent feature of organisms that are attracted to light and navigate by light and may serve as a predictor of other micromolluscs for which light traps may be appropriate collecting devices.

Undisturbed sediment cores

Rationale and design. Little is known of microgastropods that are infaunal, living at the sediment-water interface, or interstitial, living between grains in coarse sand and pebble- to cobble-sized sediment. “Shell grit” and biogenic sediment samples (“grunge”) have been important sources of empty shells of microgastropods, but the procedures have not concentrated on recovering live animals for study. Sediment samples that are washed in fresh water and air-dried for sorting and “picking” of microgastropods may add substantially to species richness in surveys, but study of the living animal requires different methods.

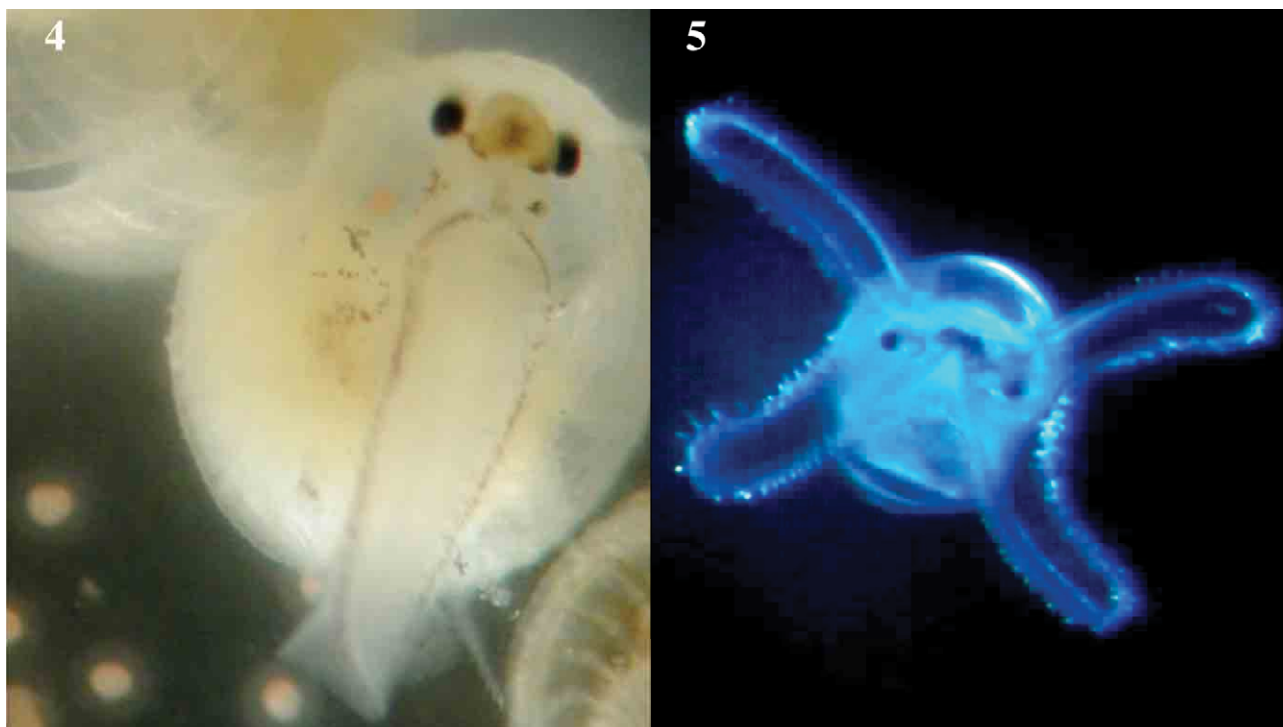
Sediment can be screen-washed either in the field or the lab to recover live infaunal or interstitial microgastropods. However, observations of live animals crawling on glass or plastic after they have been separated from sediment do not get at animal-sediment interactions. A simple device for removing sediment and live animals without mixing can be constructed by carefully removing the bottom from a large plastic ice-cream container (Fig. 3). The sharp bottom edges of the container can be carefully rocked down into sediment. Along one side of the container, the piece of flat plastic that was removed from the bottom (or a slightly larger piece of thin, flexible, flat plastic) can be carefully and slowly worked down and under the corer. The core can then be gently lifted from the sediment and placed in the bottom of a larger container such as a bucket. If the bottom of the original container is used, the “core” can be lowered and nested into an identical ice-cream container from which the bottom has not been removed. Replenishing the seawater should be done carefully to avoid disturbance of the core.

Results. Sediment cores have been particularly useful for studying microgastropods in the vetigastropod subfamily Umboniinae. Umboniines are infaunal, and the best-known species are facultative

suspension feeders (Hickman 1985, 1993, 1988, 2003a; Hickman & McLean 1990). Most of the diversity within the family is in microumboniid genera and species for which there are almost no published observations of living animals. A study of *Isanda coronata* (H. & A. Adams, 1854) has shown that the animal behaves differently when removed from its substrate (Hickman 2003a). Observations of the animal emerging from an undisturbed sediment sample, burrowing, and re-establishing itself in filter-feeding position at the sediment-water interface were crucial to behavioral documentation. *Isanda coronata* occurs in large numbers (as high as 1,500/m²) in dirty sandflats on the tropical Australian coast and is infaunal rather than interstitial.

Three other microumboniid genera are either interstitial or associated with unusual benthic substrates, and benthic coring has revealed some unusual biological behaviors. The genera are *Vanitrochus* Iredale, 1929, *Parminolia* Iredale, 1929, and *Conotalopia* Iredale, 1929. In undisturbed sediment cores of coarse-grained skeletal carbonate substrates in tropical Western Australia, an undescribed species of *Vanitrochus* lives semi-interstitially amongst skeletal grains of various sizes (Fig. 6). Individuals appeared and disappeared from view at the sediment surface, but when visible they were observed selecting grains with the translucent semitubular proboscis. The grain was subsequently rolled around within the proboscis while the radula was applied to it. The grain was then spit out and the process repeated with another grain. Epipsammic browsing (removing the microbial coating on grains as a source of nutrition) is a recurring mode of feeding in invertebrates in the meiobenthos, although it has not been noted previously in microgastropods.

A second phenomenon, less easily explained, occurs in an undescribed species of *Conotalopia* from Shark Bay, Western Australia. This species occurs on and within a dense mat of living and empty shells of the photosymbiotic bivalve *Fragum erugatum* (Tate, 1889). An undisturbed sediment core of the *Fragum* mat was taken in order to observe the unusual concentration of living bivalves (Hick-



Figures 4–5. Examples of microgastropods captured in light traps, illustrating the large eyes that are typical of phototropic aquatic organisms. **4.** A scissurellid gastropod. **5.** A neritid gastropod veliger larva.

man 2003b), and the microumboniid gastropods were not discovered until the surface of the core was observed under a dissecting microscope that evening (Fig. 7). The gastropods were actively crawling over the exposed mantle tissue and siphons of live individuals of *F. erugatum* on the surface of the mat. The nature of this association merits further investigation. Subsequent recovery of a second unidentified microumboniine gastropod from exposed tridacnid mantle tissue at the Waikiki Aquarium in Honolulu suggests that the tridacnid-microumboniine association may be more widespread (C.S. Hickman unpubl. data).

Emergence traps

Rationale and design. Emergence traps have been used to capture demersal zooplankton that emerge from the sediment and move up into the water column at night and return to the sediment to spend the day. These diel vertical migrations are a prominent feature of nearshore communities (Alldredge & King 1977, 1980). Animals that live in or on the sediment by day emerge between sunset and sunrise on different seasonal and lunar patterns and return to the substratum before dawn on different schedules (Jacoby & Greenwood 1988). Diel migrations have been studied in many different environments, ranging from tropical coral reefs (Alldredge & King 1977) to temperate seagrass flats (Robertson & Howard 1978) and kelp forests (Hammer 1981).

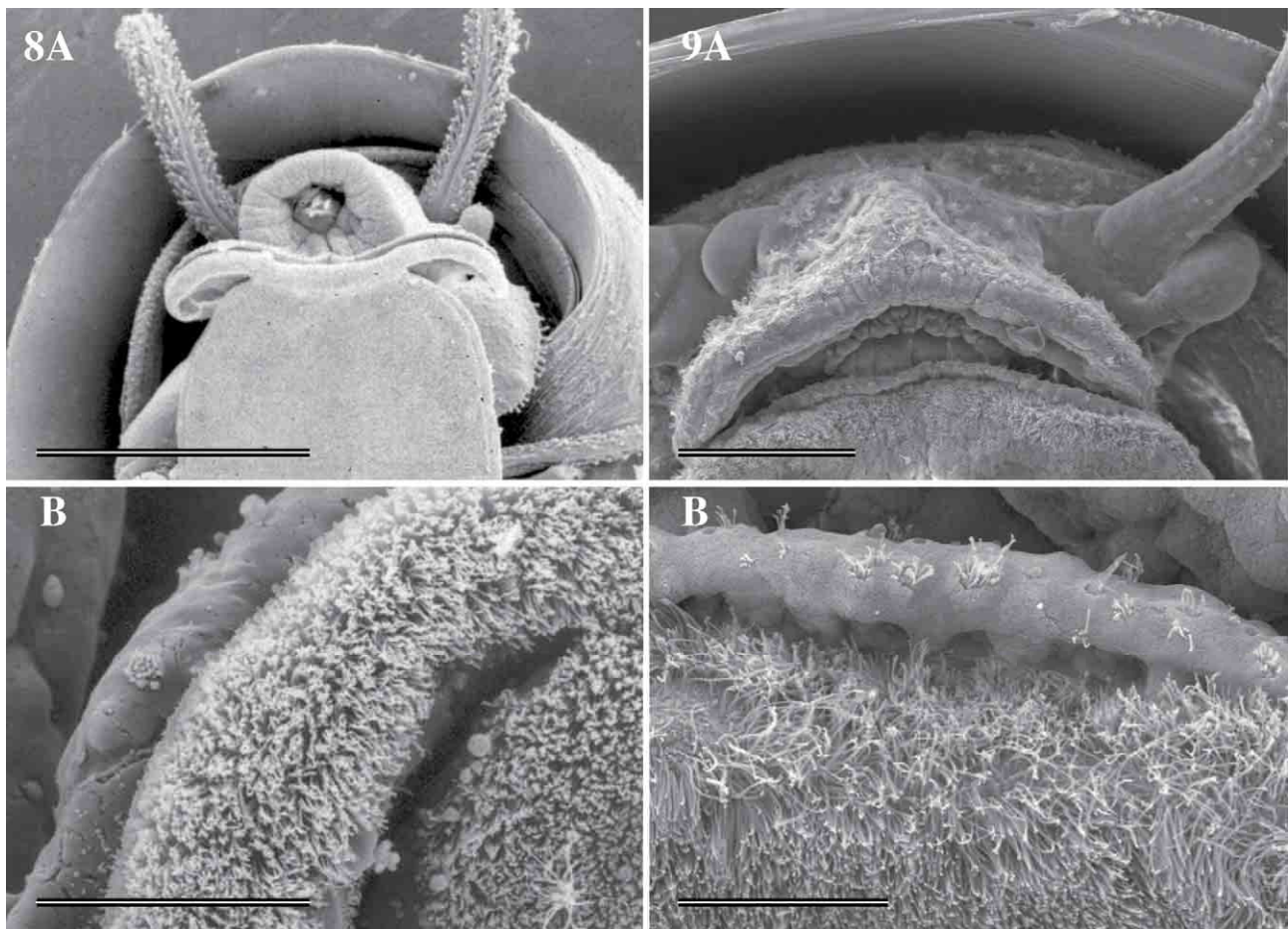
There are various designs for emergence and reentry traps (Alldredge & King 1977, 1980; Jacoby & Greenwood 1988), but the basic elements (Fig. 2) are a cone or pyramid of plankton mesh or plastic with a broad base at the sediment-water interface, tapering to a funnel and catch-bottle at the cod end. As with light traps, foam floats can be added to provide buoyancy at the cod end. The catch bottle should be covered with mesh at the open end to permit water circulation. At the substrate, the plankton mesh or plastic can be weighted in a variety of ways to secure it.



Figures 6–7. Umbonine microgastropods at the sediment-water interface of undisturbed sediment cores. **6.** *Conotalopia* n. sp. engaged in epipsammic browsing at the surface of a coarse coral sand. Scale bar = 3 mm. **7.** *Vanitrochus* n. sp. crawling on the exposed mantle tissue of the tridacnid bivalve *Fragum erugatum* in a mat of live animals and dead shells. Scale bar = 2.5 cm.

The reasons for experimenting with the use of emergence traps to collect micromolluscs were four-fold. The first was an extension of the use of light traps to determine whether taxa attracted to artificial light at night could be captured as a consequence of a natural diel rhythm. The second was to determine whether there are micromolluscs that live interstitially by day and emerge from sediment at night. The third was to minimize disturbance of more invasive procedures for separating microgastropods from sediment. The fourth was to follow-up on previous observations (Hickman 2005, unpubl. data) of diel migrations of phytal microgastropods between sediment and marine plants, diel vertical migrations on marine plants, and the ability to use pedal mucus threads to launch from plants into the water column.

Results. Emergence traps deployed in the water column over bare sediment have thus far failed to recover large numbers of micromolluscs. Although there may be significant patterns of diel migration between sediment and marine algae and seagrasses, there is no evidence of a hidden diversity of microgastropods that swim at night. This is perhaps no surprise, although the sustained night swimming of scissurellids (Hickman & Porter 2007) was unsuspected.



Figures 8–9. Mesopodia and details of cilia in two microgastropods that engage in ciliary locomotion and excursions into the water column using mucus threads. **8A.** Anterior ventral view of a relaxed individual of *Alcyna ocellata*, with two prominent anterior “horns.” Scale bar = 600 μm . **8B.** Detail of the sole and dense cilia on the right foot horn and edge of foot. Scale bar = 30 μm . **9A.** Anterior ventral view of a relaxed individual of *Smaragdia bryanae*. Scale bar = 100 μm . **9B.** Detail of the anterior margin of the foot with dense cilia. Scale bar = 20 μm .

However, emergence traps placed over marine algae and seagrasses have captured live microtrochids of the genus *Alcyna* A. Adams, 1860, and microneritids of the genus *Smaragdia* Issel, 1869, in Western Australia and French Polynesia (C.S. Hickman unpubl. data). Further observations of species in these two genera in Hawaii, *Alcyna ocellata* (A. Adams, 1861) and *Smaragdia bryanae* Pilsbry, 1917, show that both secrete long threads of pedal mucus that they use to launch from the substrate into the water column (C.S. Hickman unpubl. data). The elasticity of the mucus threads of *S. bryanae* is sufficiently great that individuals can be removed from water into air by the thread before it breaks (C.S. Hickman & C.R.C. Unabia unpubl. data).

An especially interesting feature of phytal microgastropods is their propensity to leave their host plants and drift in the water column during laboratory observations, especially at night (C.S. Hickman unpubl. data). They are most often observed floating upside-down at the air-water interface, locked into the surface tension at the boundary and apparently engaged in feeding – protracting and retracting the radula. Although animals move unidirectionally at the interface, there is no evidence of muscularly-generated pedal waves. This led to the prediction that these microgastropods were engaged in ciliary locomotion. Scanning electron micrographs of the sole of the foot of relaxed, fixed, and critical point dried specimens of *A. ocellata* and *S. bryanae* (Figs 8, 9) confirm that the sole of the foot is covered with cilia.

Discussion

Gastropods in the microbenthos. Although a major part of animal production of the sea floor is attributed to the interstitial fauna of marine sand (Fenchel 1978), molluscs are not generally recognized as a significant faunal element. In a review of interstitial marine gastropods, Arnaud *et al.* (1986: 158–159) recognized Caecidae as the only obligately interstitial prosobranch family and stated that “only 45 prosobranchs out of 20,000 are interstitial.” Other treatments of infaunal micromolluscs have emphasized the “vermiformity” of interstitial solenogasters and polyplacophorans (Salvini-Plawen 1986) and a suite of anatomical and ecological peculiarities of interstitial opisthobranchs (Swedmark 1968). The size of the interstices in most marine sand restricts body size of < 3 mm (Swedmark 1968). However, interstices in coarse sand, coral rubble, and cobbles offer a range of unique interstitial space that is less well explored. An interstitial gastropod microfauna, including an undescribed neritiliid gastropod, was documented from a lower intertidal habitat where brackish water is discharged into rubble and boulders imbedded in coarse-grained sand (Kano *et al.* 2003). Novel habitats are an important source of insight into microgastropod biodiversity.

Phytal microgastropods. Microgastropods are an important component of macroalgal and seagrass beds, but sampling in these habitats tends to under-represent both their biodiversity and their contribution to productivity. The traditional techniques for collecting phytal microgastropods involve rapid physical defaunation by vigorously “washing” marine plants in buckets of seawater, plastic bags, or lidded containers or hosing plant material over a sieve. Alternative methods involve heat or chemical inducements to encouraging the snails to “let go.” The physiologically stressed or dead results are unfit for functional and behavioral observation.

Two important considerations in collecting phytal taxa for biological observation are retention of the snail in association with its algal or seagrass host plant and the time of day and season. Field collections are typically made during the daylight hours. However floating plants in dishpans in camp

or the lab for observation at night can be rewarding because snails will often move vertically and concentrate on the uppermost surfaces where they can be gently removed along with part of the plant for observation. Ecological studies of the mobile epifauna of marine plants have shown that densities may fluctuate dramatically with season (Edgar 1983, 1990; Toyohara *et al.* 2004; Kanamori *et al.* 2004). Phytal microgastropods are often food limited and show dramatic seasonal increases in recruitment and density associated with rapid increases in growth of host plants and their epiphytes.

Several studies of seasonal variation in phytal communities have focused on micromollusc populations in seagrass beds (Arroyo *et al.* 2006) and macroalgal beds (Rueda & Salas 2003).

Diel migration. Discovery of nocturnal swimming in scissurellids (Hasegawa 2004; Hickman & Porter 2007) highlights the possibility of other kinds of activity differences between day and night. There are at least three kinds of diel activity that merit further study: migration from sediment to marine plants, vertical migration on plants from basal to the more vegetated upper portions, and movement from the plant to the water column (Greening & Livingston 1982). A subtle diel migration has been observed in an Australian scissurellid that occurs in seagrass epiphytes by day and moves onto seagrass blades at night to graze on microbial films (Edgar & Robertson 1992). Evidence for migrations that increase the presence of motile epifauna on plants at night has been recorded in the diets of fish that are herbivores by day and carnivores by night (Robertson & Klumpp 1983).

Diel migration between sediment and water column is a distinct possibility in the microumboniid taxa that are capable of swimming (Hickman 2003a). In a study of demersal zooplankton at Lizard Island, Australia, Alldredge & King (1977: 326) reported that *Vanitrochus semiustus* (Fischer, 1896) emerged at night in large numbers (70/m²). They concluded that it “entered the traps as a demersal, actively swimming form.”

Ciliary locomotion. The original classifications of gastropod locomotion (Vlès 1907; Parker 1911) were based on patterns of waves of musculature contraction. Ciliary locomotion was first proposed based on observation of rapid progression in the microgastropod *Hyalina avena* (Kiener, 1834 *ex Valenciennes*, ms) in the absence of any rhythmic pedal movement (Olmsted 1917). Olmsted's (1917: 232) inference of ciliary locomotion was based on microscopic observation of “long and vigorously beating cilia” covering the entire sole (mesopodium) of the foot. A subsequent study of the behavior of pedal cilia in two nassariid gastropods (Copeland 1919) established the connection between backward-beating cilia and forward progression.

Although ciliary locomotion is now recognized as common in small caenogastropods (e.g., hydrobiids, skeneopsids and rissoideans) (Fretter & Graham 1994), it is remarkable that it has not been recognized heretofore in more microgastropods, and particularly in the more basal “prosobranch” microgastropods within the Vetigastropoda and Neritopsina. The original function of pedal ciliation may not have been locomotory. Pedal ciliation in swimming veliger larvae appears to function in cleansing and selective rejection of particles that are captured in the metatroch but not ingested (C.S. Hickman unpubl. obs.). Post-metamorphic retention of cilia may be a widespread phenomenon, and their exaptation for benthic locomotion merits further consideration as a convergent evolutionary phenomenon in microgastropods.

The presence of a mesopodial mucous gland and secretion of mucus threads also merits further comparative study in microgastropods and is discussed further below.

Microgastropod drifting, flotation, and mucus thread “kiting”. Planktonic drifting in the water column and flotation at the air-water interface have been reported from a broad range of prosobranch families in species including Littorinidae (Martel & Chia 1991a,b), Calyptraeidae (Cañete *et al.* 2007), Vermetidae (Strathmann & Strathmann 2006), Hydrobiidae (Newall 1962; Meireles & Queiroga 2004) and Muricidae (DiSalvo 1988). In some instances it is restricted to early post-metamorphic juveniles. Drifting has been associated with a raising the posterior part of the foot (metapodium) prior to lifting off on a mucus thread (Martel & Chia 1991b) and also with flotation at the air-water interface with the aid of a gas bubble in the mantle cavity (Cañete *et al.* 2007; DiSalvo 1988).

Drifting and flotation have been regarded in the ecological literature as a dispersal mechanism (Highsmith 1985; Martel & Chia 1991a) or strategy (Cañete *et al.* 2007). The littorinid microgastropod *Lacuna vincta* (Montagu, 1803) produces mucous threads up to 106 times the length of a 2 mm snail (Martel & Chia 1991b). Mucous thread production is also reported as a mechanism for drifting in minute tellinid bivalves (Sorlin 1988; Beukema & Vlas 1989) and small adults of freshwater corbiculid bivalves (Prezant & Charlermwat 1984).

Capture of drifting micromolluscs deserves more intense effort and may be accomplished more effectively using other collecting devices. For example, suspended PVC pipe wrapped with hoghair air conditioning filter, routinely used in the capture of crab megalope (van Montfrans *et al.* 1995), has been used to demonstrate a semilunar pattern of drifting in *Hydrobia ulvae* (Pennant, 1777) (Meireles & Queiroga 2004). Thousands of juveniles of the calyptraeid gastropod *Trochita calyptraeaformis* Born, 1788, have been recovered from nylon mesh collector bags and suspended colorless acrylic plates (Cañete *et al.* 2007). Drifting juveniles were primarily in the 1–2 mm size range and offshore capture indicated drifting distances up to several kilometers.

New methods of collecting and observing live animals are essential to filling the microgastropod knowledge gap. Discovery of microgastropod diversity in unexpected and poorly explored habitats and microhabitats provides rewarding evidence of unusual or unsuspected behaviors and functional traits. This paper highlights only three of many possible ways to probe the basic biology of microgastropods and emphasizes the key role that field studies and observational biology play in understanding molluscan biodiversity.

References

- Allredge, A.L. & King, J.M. (1977) Distribution, abundance, and substrate preferences of demersal zooplankton at Lizard Island Lagoon, Great Barrier Reef. *Marine Biology*, 41, 317–333.
- Allredge, A.L. & King, J.M. (1980) Effects of moonlight on the vertical migration patterns of demersal zooplankton. *Journal of Experimental Marine Biology and Ecology*, 44, 133–156.
- Arroyo, M.dC., Salas, C., Rueda, J., & Gofas, S. (2006) Temporal changes of mollusc populations from a *Zostera marina* bed in southern Spain (Alboran Sea), with biogeographic considerations. *Marine Ecology*, 27, 417–430.
- Arnaud, P.M., Poizat, C.L. & Salvini-Plawen, L.v. (1986) Marine interstitial Gastropoda. In: Botosaneanu, L. (Ed.), *Stygofauna Mundi: A Faunistic, Distributional, and Ecological Synthesis of the World Fauna Inhabiting Subterranean Waters (Including Marine Interstitial)*. E.J. Brill, Leiden, pp. 153–176.
- Beukema, J.J. & Vlas, J.de (1989) Tidal-current transport of thread-drifting postlarval juveniles of the bivalve *Macoma balthica* from the Wadden Sea to the North Sea. *Marine Ecology Progress Series*, 52, 193–200.
- Bouchet, P., Lozouet, P., Maestrati, P. & Héros, V. (2002) Assessing the magnitude of species richness in tropical marine environments: exceptionally high numbers of molluscs at a New Caledonia site. *Biological Journal of the Linnean Society*, 75, 421–436.

- Cañete, J.I., Gallardo, C.S., Romero, M. & Ambler, R. 2007. Planktonic drifting dispersal of early juvenile *Trochita calyptraeaformis* Born 1788 (Gastropoda: Calyptraeidae). *Journal of Experimental Marine Biology and Ecology*, 346, 1–7.
- Copeland, M. (1919) Locomotion in two species of the gastropod genus *Alectrion*, with some observations on the behavior of pedal cilia. *Biological Bulletin*, 37, 126–138.
- DiSalvo, L.H. (1988) Observations on the larval and postmetamorphic life of *Concholepas concholepas* (Brugière, 1789) in laboratory culture. *The Veliger*, 30, 358–368.
- Doherty, P.J. (1987) Light traps: selective but useful devices for quantifying the distribution and abundances of larval fishes. *Bulletin of Marine Science*, 41, 423–431.
- Edgar, G.J. (1983) The ecology of south-east Tasmanian phytal animal communities. II. Seasonal change in plant and animal populations. *Journal of Experimental Marine Biology and Ecology*, 70, 181–203.
- Edgar, G.J. (1990) Population regulation, population dynamics and competition amongst mobile epifauna associated with seagrass. *Journal of Experimental Marine Biology and Ecology*, 144, 205–234.
- Edgar, G.J. & Robertson, A.I. (1992) The influence of seagrass structure on the distribution and abundance of mobile epifauna: pattern and process in a Western Australian Amphibolis bed. *Journal of Experimental Marine Biology and Ecology*, 160, 13–31.
- Fenchel, T.M. (1978) The ecology of micro- and meiobenthos. *Annual Reviews of Ecology and Systematics*, 9, 99–121.
- Fretter, V. & Graham, A. (1994) *British Prosobranch Molluscs. Their Functional Anatomy and Ecology*, 2nd Edition. Ray Society Publications, London. 820 pp.
- Greening, H.S. & Livingston, R.J. (1982) Diel variation in the structure of seagrass-associated epibenthic macroinvertebrate communities. *Marine Ecology Progress Series*, 7, 147–156.
- Hammer, R.M. (1981) Day-night differences in the emergence of demersal zooplankton from a sand substrate in a kelp forest. *Marine Biology*, 62, 275–280.
- Hasegawa, K. (2004) Swimming behavior of scissurellids (Gastropoda: Scissurellidae) and its taxonomic significance. In: Wells, F.E. (Ed.), *Molluscan Megadiversity: Sea, Land and Freshwater. World Congress of Malacology Perth, WA, July 11–16, 2004*, p. 62.
- Haszprunar, G. (1988) *Sukashitrochus* sp., a scissurellid with heteropod-like locomotion (Mollusca: Archaeogastropoda). *Annalen des Naturhistorischen Museums Wien*, 90/B, 367–371.
- Hernandez, F.J. & Lindquist, D.G. (1999) A comparison of two light trap designs for sampling larval and presettlement fish above a reef in Oslow Bay, North Carolina. *Bulletin of Marine Science*, 64, 173–184.
- Hickman, C.S. (1985) Comparative morphology and ecology of free-living suspension-feeding gastropods from Hong Kong. In: Morton, B. & Dudgeon, D. (Eds), *The Malacofauna of Hong Kong and of Southern China*, Hong Kong University Press, pp. 217–134.
- Hickman, C.S. (1993) Theoretical design space: a new program for the analysis of structural diversity. *Neues Jahrbuch für Paläontologie und Geologie*, 190, 5–18.
- Hickman, C.S. (1998) Subfamily Umboniinae. In: Beesley, P.L., Ross, G.J.B. & Wells, A. (Eds): *Mollusca: the Southern Synthesis*, CSIRO Publishing, Melbourne, pp. 689–690.
- Hickman, C.S. (2003a) Functional morphology and mode of life of *Isanda coronata* (Gastropoda: Trochidae) in an Australian macrotidal sandflat. In: Wells, F.E., Walker, D.I. & Jones, D.S. (Eds), *The Marine Flora and Fauna of Dampier, Western Australia*, Western Australian Museum, Perth, pp. 69–88.
- Hickman, C.S. (2003b) Mollusc-microbe mutualisms extend the potential for life in hypersaline systems. *Astrobiology*, 3, 631–644.
- Hickman, C.S. (2005) Seagrass fauna of the temperate southern coast of Australia I. The cantharidine trochid gastropods. In: Wells, F.E., Walker, D.I. & Kendrick, G.A. (Eds.), *The Marine Fauna and Flora of Esperance, Western Australia*. Australian Museum, Perth, pp. 199–220.
- Hickman, C.S. & McLean, J.H. (1990) Systematic revision and suprageneric classification of trochacean gastropods, *Natural History Museum of Los Angeles County Science Series*, 35, 1-169.
- Hickman, C.S. & Porter, S.S. (2007) Nocturnal swimming, aggregation at light traps, and mass spawning of scissurellid gastropods (Mollusca: Vetigastropoda). *Invertebrate Biology*, 126, 10–17.

- Highsmith, R.C. (1985) Floating and algal rafting as potential dispersal mechanisms in brooding invertebrates. *Marine Ecology Progress Series*, 25, 169–179.
- Holmes, J.M.C. (1998) Phenetic relationships among some free-living siphonostomatoid copepods from southwest Ireland, and the description of *Glannapoiticus maculatus* gen. et sp. nov. *Journal of Marine Systems*, 15, 220–241.
- Holmes, J.M.C. & O'Connor, J.P. (1988) A portable light trap for collecting marine crustaceans. *Journal of the Marine Biological Association of the United Kingdom*, 68, 235–238.
- Jacoby, C.A. & Greenwood, J.G. (1988) Spatial, temporal, and behavioral patterns in emergence of zooplankton in the lagoon of Heron Reef, Great Barrier Reef, Australia. *Marine Biology*, 97, 309–328.
- Kanamori, M., Goshima, S. & Mukai, H. (2004) Seasonal variation in host utilization of epiphytic *Lacuna* species in mixed algal and surfgrass stands in Japan. *Marine Ecology*, 25, 51–69.
- Kano, Y., Kase, T. & Kubo, H. (2003) The unique interstitial habitat of a new neritiliid gastropod, *Neritilia littoralis*. *Journal of the Marine Biological Association of the United Kingdom*, 83, 835–840.
- Kissick, L.A. (1993) Comparison of traps lighted by photochemical or electric bulbs for sampling warmwater populations of young fish. *North American Journal of Fisheries Management*, 13, 864–867.
- Marchetti, M.P., Esteban, E., Limm, M. & Kurth, R. (2004) Evaluating aspects of light trap bias and specificity in the northern Sacramento River system: Do size and color matter. *American Fisheries Society Symposium*, 39, 269–279.
- Martel, A. & Chia F.S. (1991a) Drifting and dispersal of small bivalves and gastropods with direct development. *Journal of Experimental Marine Biology and Ecology*, 150, 131–147.
- Martel, A. & Chia F.S. (1991b) Foot-raising behaviour and active participation in the initial phase of post-metamorphic drifting in the gastropod *Lacuna* spp. *Marine Ecology Progress Series*, 72, 247–254.
- Meekan, M.G., Wilson, S.G. & Retzel, A. (2001) A comparison of catches of fishes and invertebrates by two light trap designs, in tropical NW Australia. *Marine Biology*, 139, 373–381.
- Meireles, S. & Queiroga, H. (2004) Use of artificial collectors shows semilunar rhythm of planktonic dispersal in juvenile *Hydrobia ulvae* (Gastropoda: Prosobranchia). *Journal of the Marine Biological Association of the United Kingdom*, 84, 761–766.
- Montfrans, J., van Epifanio, C.E., Knott, D.M., Lipcius, R.N., Mense, D.J., Metcalf, K.S., Olmi, E.J.III., Orth, R.J., Posey, M.H., Wenner, E.L. & West, T.L. (1995) Settlement of blue crab postlarvae in Western North Atlantic estuaries. *Bulletin of Marine Science*, 57, 834–854.
- Newell, R. (1962) Behavioural aspects of the ecology of *Peringa* (= *Hydrobia*) *ulvae* (Pennant) (Gastropoda, Prosobranchia). *Proceedings of the Zoological Society of London*, 138, 49–75.
- Olmstead, J.M.D. (1917) Notes on the locomotion of certain Bermudian mollusks. *Journal of Experimental Zoology*, 24, 223–236.
- Parker, G.H. (1911) The mechanism of locomotion in gastropods. *Journal of Morphology*, 22, 155–170.
- Porter, S.S., Eckert, G.L., Byron, C.J. & Fisher, J.L. (2008) Comparison of light traps and plankton tows for sampling brachyuran crab larvae in an Alaskan fjord. *Journal of Crustacean Biology*, 28, 175–179.
- Prezant, R.S. & Charlermwat, K. (1984) Flotation of the bivalve *Corbicula fluminea* as a means of dispersal. *Science*, 225, 1491–1493.
- Robertson, A.I. & Howard, R.K. (1978) Diel trophic interactions between vertically migrating zooplankton and their fish predators in an eelgrass community. *Marine Biology*, 48, 207–213.
- Robertson, A.I. & Klumpp, R.K. (1983) Feeding habits of the southern Australia garfish *Hypporhamphus melanochir*: a diurnal herbivore and nocturnal carnivore. *Marine Ecology Progress Series*, 10, 197–201.
- Rueda, J.L. & Salas, C. (2003) Seasonal variation of a molluscan assemblage living in a *Caulerpa prolifera* meadow within the inner Bay of Cádiz (SW Spain). *Estuarine, Coastal and Shelf Science*, 57, 909–918.
- Salvini-Plawen, L.v. (1986) Lower Mollusca. In: Botosaneanu, L. (Ed.): *Stygofauna Mundi: A Faunistic, Distributional, and Ecological Synthesis of the World Fauna Inhabiting Subterranean Waters (Including Marine Interstitial)*. E.J. Brill, Leiden, pp. 148–152.
- Sorlin, T. (1988) Floating behavior in the tellinid bivalve *Macoma baltica* (L.). *Oecologia*, 77, 273–277.
- Strathmann, M.F. & Strathmann, R.R. (2006) A vermetid gastropod with complex intracapsular cannibalism of nurse eggs and sibling larvae and a high potential for invasion. *Pacific Science*, 60, 97–108.
- Swedmark, B. (1968) The biology of interstitial Mollusca. *Symposia of the Zoological Society of London*, 22, 115–149.

- Toyohara, T., Nakaoka, M. & Aioi, K. (1999) Population dynamics and reproductive traits of phytal gastropods in sea-grass bed in Otsuchi Bay, northeastern Japan. *Marine Ecology*, 20, 273–289.
- Vlès, F. (1907) Sur les ondes pédieuses des mollusques repatateurs. *Comptes Rendus de l'Académie des Sciences, Paris*, 145, 276–278.

