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Author(s): Carole S. Hickman and Stephanie S. Porter

Source: *Invertebrate Biology*, Vol. 126, No. 1 (2007), pp. 10-17

Published by: Wiley on behalf of American Microscopical Society

Stable URL: <http://www.jstor.org/stable/4621885>

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Nocturnal swimming, aggregation at light traps, and mass spawning of scissurellid gastropods (Mollusca: Vetigastropoda)

Carole S. Hickman^{1,a} and Stephanie S. Porter²

¹ Department of Integrative Biology, University of California, Berkeley, California 94720, USA

² Population Biology Graduate Group, University of California, Davis, California 95616, USA

Abstract. Thousands of minute scissurellid gastropods (Vetigastropoda: Scissurellidae) were observed and collected at floating light traps in Moorea, French Polynesia, where a mass spawning event occurred on November 11, 2002. More than 20,000 live snails were recovered from the traps, and epidemic spawning continued in the laboratory, where clouds of white sperm and red-orange eggs were broadcast into the water. No aggregations of this magnitude have been reported previously in vetigastropods, nor is the capacity for sustained swimming known from other vetigastropod taxa. Snails had emerged from a local benthic habitat of coral sand and swum through ≥ 2 m of water to reach the traps. Scanning electron micrographs of the ornate shells confirm the identity of the most abundant species as *Scissurella spinosa*, with lesser numbers of *Sinezona plicata*. Our observations indicate that scissurellids are not exclusively benthic and that they are not rare, even though they have seldom been collected and studied alive. Because little is known about the basic biology and anatomy of scissurellids and because their position within the basal Gastropoda is poorly resolved, we include information on the design and construction of inexpensive light traps to promote comparative investigation of other poorly known species.

Additional key words: locomotion, reproduction, gamete release, dispersal, microgastropods

A spectacular swarming of swimming scissurellid snails and their entry into floating light traps was accompanied by an epidemic nocturnal spawning event in a shallow back-reef lagoon in Moorea, French Polynesia. The minute snails were first observed as a red-orange glowing cloud surrounding the traps before recovery. When the traps were pulled from the water, thousands of individual snails were attached to the exterior surface and thousands of individuals had entered the traps. Sustained swimming and epidemic spawning add a new dimension to the already impressive diversity of behavior and reproductive modes at the “archeogastropod” grade of complexity (see Hickman 1992 for a review).

Although scissurellids are known primarily from empty shells in museum collections, they are noted for the translucency and intricacy of surface ornamentation on the crossed-lamellar aragonitic shell, and the hallmark slit (or closed foramen) and selenizone that identifies them as members of a basal group

of vetigastropods with a long geologic history and poorly resolved phylogenetic relationships.

Early studies documented the primitive anatomical features of several scissurellid species (Pelseneer 1899; Bourne 1910). There are now ~200 described living and fossil species under 25 genus-level names, and there is detailed scanning electron microscopy (SEM) documentation of shells and radulae in regional taxonomic revisions of scissurellids from the Red Sea (Yaron 1983), Southern Africa (Herbert 1986), New Zealand (Marshall 2002), and Australia (Geiger & Jansen 2004a,b). Interest in the group has grown with the discovery and documentation of new taxa at deep-sea hydrothermal vents (Haszprunar 1989; McLean 1989) and in submarine caves (Kase & Kano 2002). Other important articles include a review of the systematics of fossil and living scissurellids (Bandel 1998), the first formal delineation of shell and radular characters, and the first formal phylogenetic analysis of intra-generic relationships (Geiger 2003). Molecular data from Geiger & Thacker (2005) challenge the traditional view of scissurellid monophyly, and Geiger & Jansen (2004b) recognize Anatomidae as a separate family, not sister to Scissurellidae.

^a Author for correspondence.

E-mail: caroleh@socrates.berkeley.edu

There are several multispecies complexes within the more restricted family Scissurellidae that are poorly delineated. There are few scissurellid specimens from French Polynesia in museum collections. Initially we were able to identify only the rarer of the two Moorean species as one described originally from Australia and represented by distinctive shells in collections at the Australian Museum, Sydney (C.S. Hickman, unpubl. data). Although the more abundant of the two Moorean species was undescribed at the time of the mass aggregation, it has been described subsequently (Geiger & Jansen 2004b), also from Australia. In their thorough review of the Australian and Indo-Malayan scissurellid species, Geiger & Jansen (2004b) recognized both of the Moorean species in museum collections from French Polynesia.

Our primary purpose is to describe the aggregation and synchronized spawning, and to present images of spawning animals that clarify several heretofore unknown aspects of their reproductive biology. Scanning electron micrographs illustrate diagnostic features of the shells, which serve as the traditional basis for scissurellid species identification. The design

of the light traps is outlined as an aid to future investigation of the phenomena described below.

Methods

Light trap construction and deployment

Light traps were constructed from inexpensive and readily available materials (Fig. 1). The trap body consisted of a heavy-plastic, 9.45-L water container. Circular openings were cut into each of the four side panels of the container, and funnels were fitted into each of the openings after drilling eight small holes in each funnel and the corresponding face of the container. Funnels were sewed to the container with a fine-gauge fishing line and the stitches were covered with acetate-based silicon aquarium sealant. The outer funnel diameter was 65 mm and the inner funnel diameter, through which organisms entered the container, was 8 mm.

The collection catchment on the bottom face of the trap was constructed from a cylindrical wide-mouth Nalgene® bottle. The bottle was sawed twice: once to separate a basal section and a second time to remove

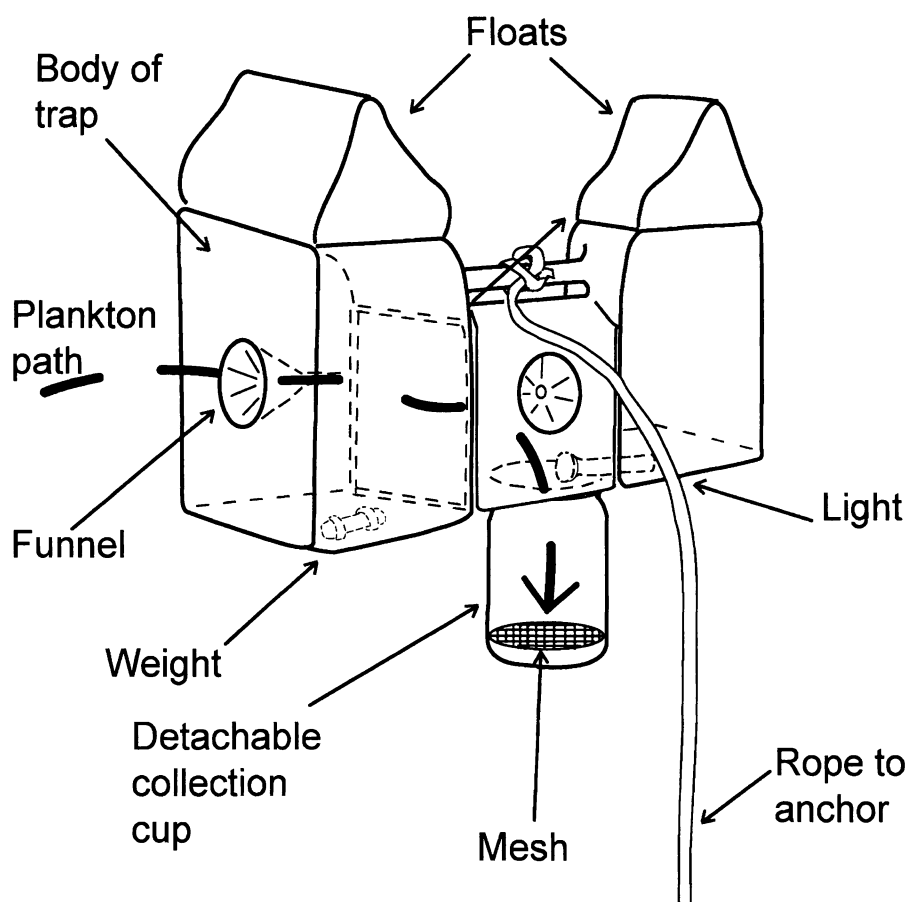


Fig. 1. Diagram of light trap. See text for construction details.

the bottom. The remaining cylinder and bottle were glued back together with a circle of 210- μ m-gauge plankton mesh between them. A large circular opening was cut in the lid of the bottle, and the lid was secured (via drilled holes, fishing line, and silicone sealant) to a corresponding circular opening cut in the bottom face of the trap. In this manner, the lid remained fixed to the trap so that the bottle could be freely detached after all the water had drained out of the trap, depositing trapped organisms on the mesh.

Weights and floats were fixed to the trap to ensure that it would float submerged at the surface in an upright position. Two 75-g lead weights were cable tied on diagonally opposite bottom corners of the trap, again via drilled holes, monofilament, and silicone sealant. Two foam floats were attached to the outside of the top face of the trap, one on either side of the pre-existing handle. A nylon rope was tied to the handle and anchored to a cinder block on the bottom. The trap was lit by a small hand-held dive light, cable tied to the interior wall, and powered by rechargeable batteries that lit the trap for 2.5-h sampling intervals.

Traps were deployed and collected from a two-person kayak. When traps were recovered and drained, the catchment bottles were removed and placed in seawater in heavy-duty zip-lock bags and returned to the lab for sorting.

Sampling

Light traps were set at five stations on a transect across the back-reef northwest of Cook's Bay, Moorea, French Polynesia, adjacent to the Richard B. Gump South Pacific Research Station (17°29'15"S, 149°49'67"W). The traps were deployed as part of a project to evaluate patterns of diversity and abundance of stomatopod larvae over a lunar cycle (Porter 2002). The five back-reef stations were sampled on October 22, 26 and November 1, 9, 2002. Water depth at the scissurellid mass aggregation sites was ~2 m, over a bottom of calcareous sand and coral heads. The traps were lit for ~2.5 h, between 20:30 and 24:00 hours.

Sample treatment and preservation

Within 40 min of transport to the lab, scissurellids hosed with salt water from the catchment bottle, as well as the interior and exterior of the light traps, were observed under a dissecting microscope and photographed in the act of epidemic spawning. The entire unsorted sample was preserved in 70% ethanol and returned to Berkeley, where the scissurellids were

separated from other organisms for further examination and identification.

SEM

Animals were carefully removed from the shells selected for SEM. Shells were cleaned by sonication, air dried, and mounted on aluminum SEM stubs on a small drop of silver paste. Stubs were coated with gold/palladium alloy and examined with a Hitachi S-800 field-emission scanning electron microscope (Hitachi, Ltd., Tokyo, Japan) at the Biological Electron Microscopy Facility at the University of Hawaii Pacific Biomedical Research Center. They were viewed at an accelerating voltage of 10 kV. Digitally recorded images were imported as .tif files into Adobe Photoshop® and image adjustments were restricted to those allowed by standard darkroom technique.

Voucher specimens

Preserved wet specimens are deposited in the University of California Museum of Paleontology under locality numbers UCMP IP 100 and UCMP IP 101. Specimen numbers for illustrated shells are given in the caption for Fig. 3.

Results

Swarming observations

The scissurellid swimming and spawning event occurred on November 11, 2002, 5 d past new moon. No scissurellids were recovered from any of the traps on the other three sampling dates. The most spectacular aggregations occurred at two stations on either side of a deep channel through the reef flat. At the time of recovery, the lit traps were surrounded by a glowing, red-orange cloud. When the traps were pulled from the water, thousands of minute snails coated the inside and outside surfaces of the traps, and many were concentrated from the water in the traps into the catchment bottles when the traps drained. The source of the glow surrounding the floating traps and continued glow of the traps as they were pulled from the water proved to have been from red-orange eggs that were clearly visible through the thin translucent shells of females, and possibly from a cloud of gametes that had already been broadcast into the water. However, we have no direct evidence that epidemic spawning had begun before pulling of the traps.

In images taken through a dissecting microscope (Fig. 2A), pigmented females and unpigmented males are readily distinguished. The images show that

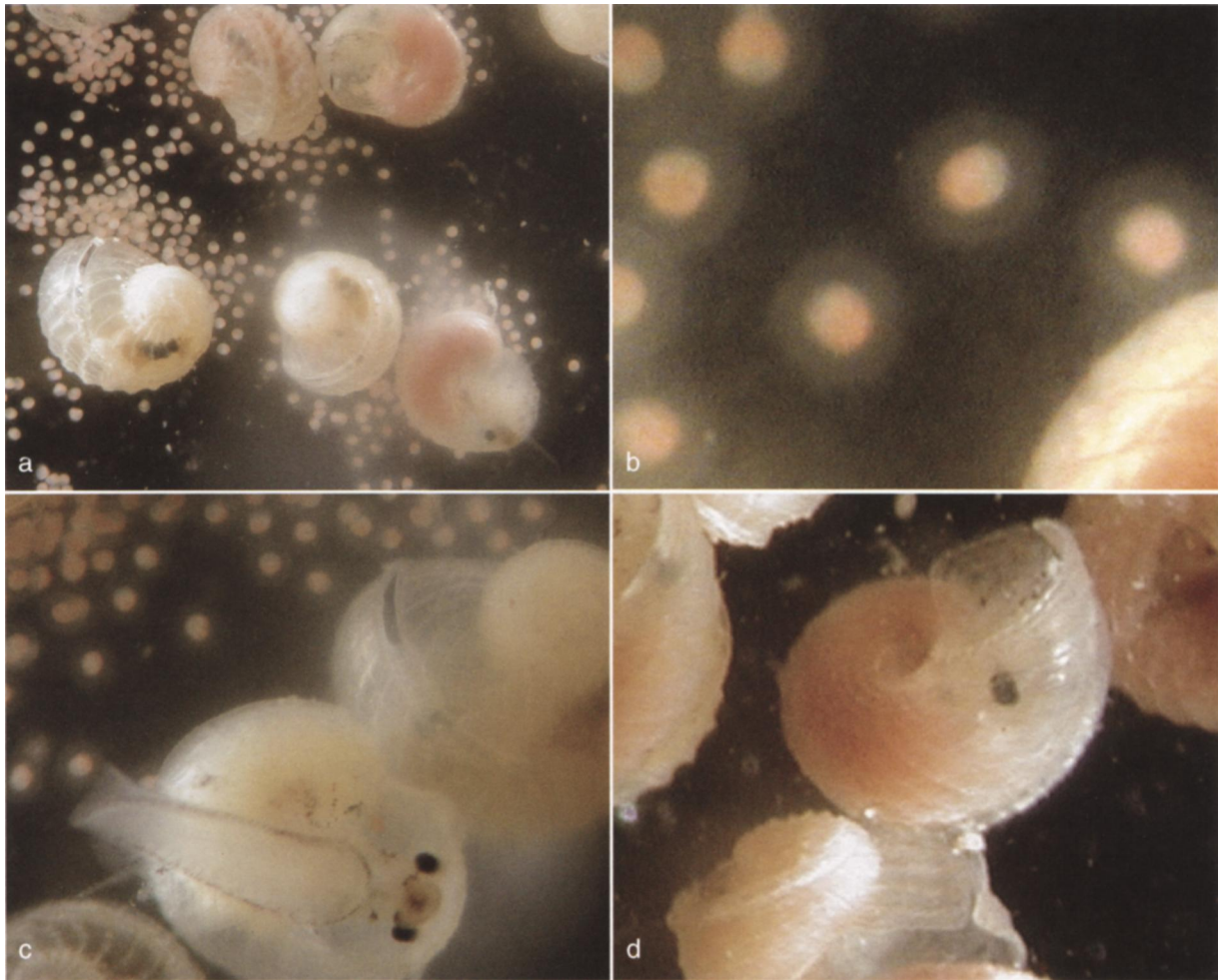


Fig. 2. *Scissurella spinosa*; spawning males and females. Shell diameters range 1.2–1.5 mm. **A.** Reddish-orange eggs in water and visible through shells of females. Female and eggs in lower right enveloped in a cloud of sperm from adjacent male. **B.** Eggs with surrounding translucent jelly coating. **C.** Male with dorsal fin at the posterior end of the expanded sole of the foot, and large black eyes on either side of the circular oral disc. **D.** Retracted female with the left eye clearly visible through the transparent shell.

male gametes emerge in diffuse, pale-white clouds both from the slit in the shell and at the margin of the aperture. Eggs, however, appear to emerge only at the apertural margin. Spawned red-orange eggs are surrounded by an unpigmented jelly coat (Fig. 2B).

The head and foot of the animal are white, in striking contrast to the extraordinarily large black-pigmented eyes on short stalks at the base of the cephalic tentacles (Fig. 2C). The eye is clearly visible even through the translucent shell of a retracted animal (Fig. 2D), and may register light intensity while an animal is inactive. The sole of the foot is long and narrow, and bordered by a fine line of purplish-black pigment granules (Fig. 2C). The most striking feature of the foot is the lateral compression of the posterior

metapodium into a prominent “fin” (Fig. 2C) that is moved rapidly back and forth to generate the swimming locomotion.

In the course of sorting the preserved samples, 3000 individuals of *Scissurella spinosa* GEIGER & JANSEN 2004 were counted. The counted volume was then used to estimate that there are ~20,000 individuals in the archived lots of voucher specimens. This number represents an unknown fraction of the number swarming in the water column that did not enter the light traps, and the number that were hosed off the surfaces of the traps and not preserved. Fifty-one individuals of a second scissurellid species, *Sinezona plicata* HEDLEY 1899, were also recovered in the course of sorting the samples.

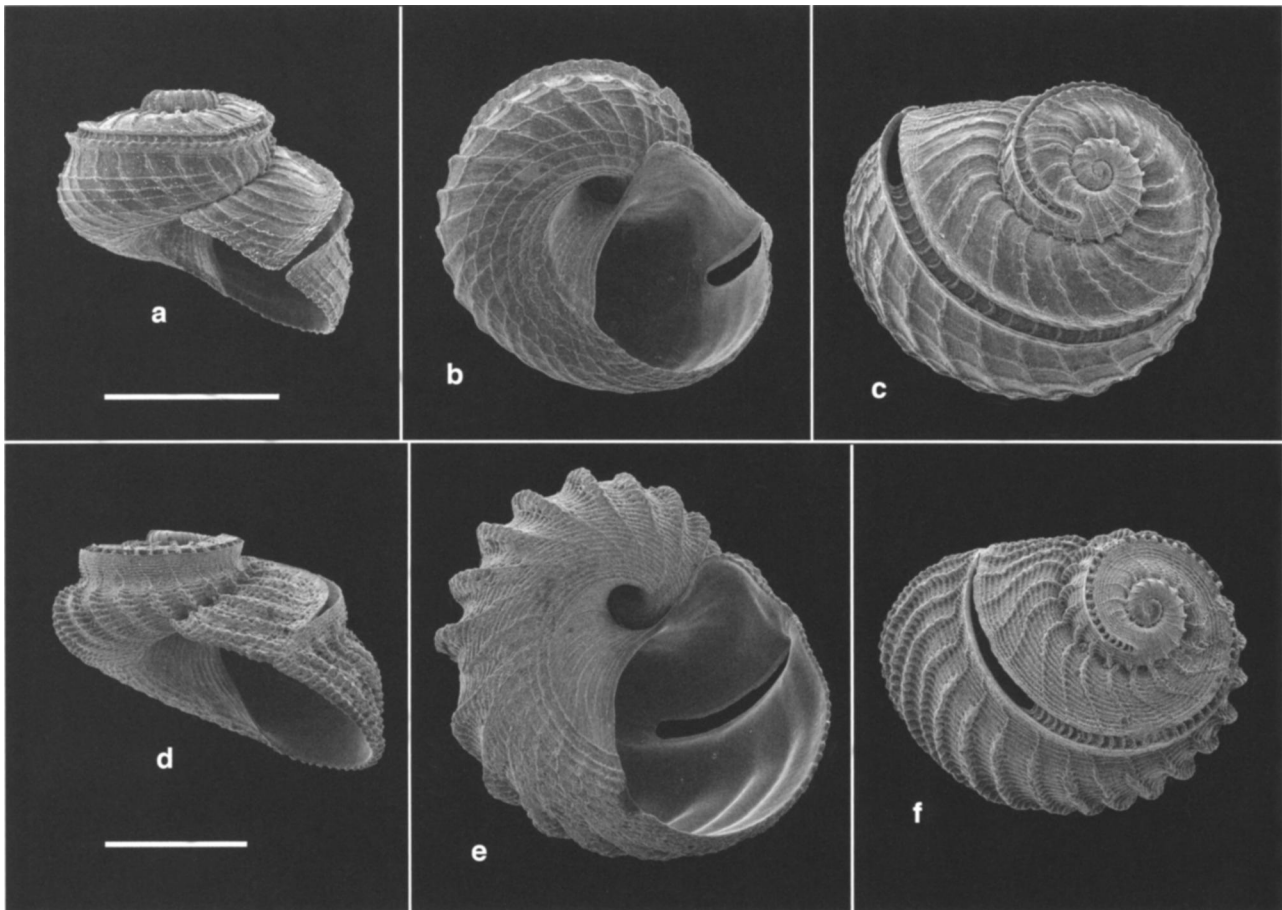


Fig. 3. Representative shells of the two scissurellid gastropod species. **A–C:** *Scissurella spinosa*. Scale bar, 750 μ m. **A.** Semi-apertural view (UCMP 50043). **B.** Umbilical view (UCMP 50044). **C.** Apical view (UCMP 50045). **D–F.** *Sinezona plicata*. Scale bar, 750 μ m. **D.** Semi-apertural view (UCMP 5046). **E.** Umbilical view (UCMP 5047). **F.** Apical view (UCMP 5048).

Taxonomic notes

Scissurella spinosa, the more abundant of the two species, had not yet been named and described at the time of our original observations. We initially assigned our specimens to *S. coronata* WATSON (1886), a name that has been applied to museum specimens showing considerable phenotypic variation in sculpture and protoconch morphology. Watson (1886) gave the type locality simply as “Tahiti,” and the type material in the British Museum of Natural History has subsequently disintegrated (Geiger & Thacker 2005). *Scissurella coronata* now appears to be a complex of species in at least three distinct groups (Geiger & Thacker 2005). Described from the Australian Great Barrier Reef, *S. spinosa* is characterized by distinctive details of shell sculpture (Geiger & Jansen 2004b). As in all species of *Scissurella*, the slit is open.

Sinezona plicata is readily distinguished from *S. spinosa* by its larger size (slightly >2 mm) and

the strong axial ribs on the shell (Fig. 3D–F). The slit is closed at the apertural margin, forming a foramen. Shell morphology and radular morphology are clearly delineated by Geiger & Jansen (2004b), who also provide detailed distributional data and specimen records. Moorea and the Tuamotus in French Polynesia are at the eastern end of the longitudinal range, which extends westward as far as the Seychelles.

Discussion

Scissurellid swimming behavior

This is not the first observation of modification of the scissurellid metapodium into a fin, nor is it the first observation of its use in locomotion. Haszprunar (1988) described 5–6 s bursts of what he called a “struggling mode of locomotion” in a species of *Sukashitrochus* HABE & KOSUGE 1964. He concluded that it could not be used to traverse large distances and was most likely an escape response used in

predator avoidance. Foot thrashing, as a means of traversing short distances, has been documented in two subfamilies of trochoidean gastropods: Umboniinae and Solariellinae. In *Umbonium vestiarium* LINNAEUS 1758, foot thrashing, resulting in swimming for short distances, is a response to predators (Hickman 1985; Kikuchi & Doi 1987). In *Isanda coronata* A. ADAMS 1854, swimming is triggered both by contact with potential predators in the field and by mechanical disturbance in the laboratory (Hickman 2003). Herbert (1987) describes swimming behavior in all of the solarielline species that he observed alive in Southern Africa, and suggests that it is an escape response.

Our observations in *Moorea* provide evidence of sustained swimming through ≥ 2 m of water, with the possibility that animals attracted to light traversed significantly greater distances between the substratum and the light traps (1000–2000 body lengths). The red-orange glowing “halo” of snails surrounding the traps indicates that animals continued to swim for an unspecified interval of time after reaching the light source. Swimming clearly results in aggregation and culminates in epidemic broadcast spawning. Although we had direct evidence of spawning only after animals were collected, broadcast gametes likely contributed to the halo surrounding the traps.

Subsequent to our observations, an abstract by Hasegawa (2004) reports swimming and spawning by three scissurellid species attracted to an underwater light for luring fish. One of the three species was *Sinezona plicata*, and the other two were species of *Scissurella*, subsequently described as new by Geiger & Jansen (2004b).

Because there is no prior literature on nocturnal surface spawning aggregations in benthic molluscs, it is difficult to suggest what cues and responses might be involved without looking to more distantly related taxa. Swarming at the surface should increase the probability of fertilization success in free-spawning taxa, but it requires proficient swimming, in addition to precise behavioral responses to cues, to insure coordination. The formation of enormous nocturnal spawning aggregations at the surface is well known in many polychaetes, with a remarkable array of lunar periodicities and phototactic responses to light intensity or change in light intensity (for review see Evans 1971). The best examples of nocturnal surface swarming and coordinated mass spawning are in species of palolo worms (Korringa 1947). The classic description of their “nuptial dances” (Fage & Legendre 1923) is in fact based on observations from a small boat by the light of a submerged lantern. Clark & Hess (1940) subsequently showed that these worms are positive to light only at very low

intensities, becoming negative as intensity increases. Pertinent to our observation of aggregation closely following the new moon, several polychaete species that undergo surface mass spawning do so during this portion of the lunar cycle (Korringa 1947).

We urge caution against assuming that the light trap provided the initial stimulus for scissurellid swimming. However, a low-intensity light could have served to concentrate animals that were already actively swimming at the surface.

Swimming, broadcast spawning, and a period of planktonic larval development of unknown duration may have significant implications for dispersal and geographic ranges of scissurellid species. Planktonic larval stages are regarded as the primary mode of dispersal in marine invertebrates (Strathmann 1974). However, a different paradigm may hold for microgastropods. If swimming scissurellids can launch themselves into the water column, especially in a strong current, passive dispersal may occur over significant distances. Launching by means of mucous threads has been observed in microgastropods (<5 mm) in both Turbinidae and Trochidae (C.S. Hickman, unpubl. data). Floating behavior in the microgastropod *Hydrobia ventricosa* MONTAGU 1803 in Denmark has been interpreted as a mechanism for emigration of snails when population densities are elevated (Levinton 1979). Martel & Chia (1991) used off-bottom collectors to document the arrival of small or juvenile bivalves and gastropods from the water column, and suggested that drifting excursions may favor long-distance dispersal.

Scissurellid habitat and microhabitat

Why are scissurellids so seldom seen alive, and why are they so rare in museum collections? D.L. Geiger (pers. comm., 2003) estimates that the modal number of specimens in a museum lot is 1, a figure based on examination of >4000 samples. Aggregation and concentration are partially responsible for the numbers of specimens that we recovered, but we suggest that there is a need for careful examination of the habitats and microhabitats in which these microgastropods occur.

Sources of scissurellid specimens range from marine macrophytes to coral sand and rubble, and most individuals collected alive in shallow water have been recovered from algal washings (C.S. Hickman, unpubl. data). Edgar & Robertson (1992) made the interesting observation that individuals of *Sinezona* sp., in a seagrass bed in Western Australia, occurred on seagrass epiphytes during the day, but moved out to graze on microbial films on the seagrass blades at

night. We suggest that diel migration may also take place between the sediment and marine macrophytes, with animals emerging from a diurnal interstitial habitat to move up onto algae and seagrasses at night. It is also possible that some scissurellid species are exclusively interstitial epipsammic browsers, feeding by removing microbial coatings from sand grains. Epipsammic browsing is characteristic of several trochoid microgastropods (Hickman 2003, unpubl. data).

Scissurellid reproduction and development

There are no comprehensive literature accounts of reproduction and development in scissurellid gastropods. Our observation of broadcast spawning joins earlier reports of alternative reproductive modes. Bandel (1982:17) reported spawning of eggs in benthic jelly masses, attached primarily to algae, by *Scissurella costata* D'ORBIGNY 1824 in the Mediterranean. Marshall (1993) documented sexual dimorphism and brooding of young in a specialized subpallial chamber, bounded by a unique internal septum, behind the modified inner lip of the female shell in New Zealand species of *Larochea* FINLAY 1927. Marshall (1993) reported sexual dimorphism in shell size in his description of the genus *Larocheopsis* MARSHALL 1993, and Hickman (1999) reported small males stereotypically attached to larger females in an unidentified species of *Incisura* HEDLEY 1904 (as "*Sinezona* sp.") subsequently described by Geiger & Jansen (2004b) as *I. auriformis*.

We saw no obvious size dimorphism in the shells of spawning individuals of *S. spinosa*, and the numbers of individuals spawning eggs and sperm were roughly equal. Further quantitative documentation in large populations will be accomplished most easily in samples of live snails, while sex is easily determined by gonad color through the translucent shell.

There are currently no data on how long scissurellids live or on any other life-history parameter. Our observations provide only a weak indication that spawning may be tied to lunar periodicity, as the phenomenon occurred only once at stations that were sampled on four dates during a single lunar cycle.

Scissurellid systematics and evolution

Intensive comparative study of shell and radular morphology, phylogenetic assessment of supraspecific scissurellid taxa, and naming and characterization of new taxa (Geiger 2003; Geiger & Jansen 2004a,b; Geiger & Thacker 2005) dramatically alter even the most recent summary views (e.g., Bandel 1998; Hickman 1998) of scissurellids and their relationship with

other basal gastropod groups. Molecular data will undoubtedly assist in establishing relationships. Pleas for more comparative anatomical, ecological, and behavioral data (Herbert 1986; Hickman 1999; Geiger 2003) are even more relevant with the discovery of unsuspected and fundamental aspects of their basic biology. We hope that this article will encourage further field studies of these remarkable minute snails and facilitate the collection of live animals for comparative study.

Acknowledgments. We thank the Richard B. Gump South Pacific Research Station for field and laboratory support in Moorea. S.S.P. gratefully acknowledges Ginny Eckert for introduction to light trap design and construction. Daniel Geiger, Santa Barbara Museum of Natural History, confirmed species identifications and generously shared preprints and communications about his ongoing scissurellid research. SEM was performed at the Biological Electron Microscope Facility of the Pacific Biomedical Research Center at the University of Hawaii, and C.S.H. gratefully acknowledges advice from Tina Carvalho as well as assistance with image manipulations in Photoshop®. We thank Christine Huffard for realization of the light trap diagram, and Daniel Geiger and an anonymous reviewer for helpful comments on the manuscript. Financial assistance was provided to C.S.H. from the University of California Committee on Research and the University of California Museum of Paleontology. This is UCMP contribution no. 1823 and contribution no. 138 of the Richard B. Gump South Pacific Research Station.

References

- Bandel K 1982. Morphologie und Bildung der frühontogenetischen Gehäuse bei conchiferen Mollusken. *Facies* 7: 1–198.
- 1998. Scissurellidae als Modell für die Variationsbreite einer natürlichen Einheit der Schlitzbandschnecken (Mollusca, Archaeogastropoda). *Mitt. Geol. Paläontol. Inst. Univ. Hamburg* 81: 1–120.
- Bourne GC 1910. On the anatomy and systematic position of *Incisura* (*Scissurella*) *lytteltonensis*. *Q. J. Microsc. Sci.* 55: 1–47.
- Clark LB & Hess WN 1940. Reactions of the Atlantic palolo, *Leodice fucata*, to light. *Carnegie Inst. Washington Papers Tortugas Lab.* 33: 73–81.
- Edgar GJ & Robertson AI 1992. The influence of seagrass structure on the distribution and abundance of mobile epifauna: pattern and process in a Western Australian *Amphibolis* bed. *J. Exp. Mar. Biol. Ecol.* 160: 13–31.
- Evans SM 1971. Behavior in polychaetes. *Q. Rev. Biol.* 46: 379–405.
- Fage L & Legendre R 1923. Les danses nuptiales de quelques neréidiens. *C. R. Acad. Seances Paris* 177: 1150–1152.

- Geiger DL 2003. Phylogenetic assessment of characters proposed for the generic classification of Recent Scissurellidae (Gastropoda: Vetigastropoda) with a description of one new genus and six new species from Easter Island and Australia. *Mollus. Res.* 23: 1–62.
- Geiger DL & Jansen P 2004a. Revision of the Australian species of Anatomidae (Mollusca: Gastropoda: Vetigastropoda). *Zootaxa* 415: 1–35.
- 2004b. New species of Australian Scissurellidae (Mollusca: Gastropoda: Vetigastropoda) with remarks on Australian and Indo-Malayan species. *Zootaxa* 714: 1–72.
- Geiger DL & Thacker C 2005. Molecular phylogeny of Vetigastropoda reveals non-monophyletic Scissurellidae, Trochoidea, and Fissurelloidea. *Mollus. Res.* 25: 47–55.
- Hasegawa K 2004. Swimming behavior of scissurellids (Gastropoda: Scissurellidae) and its taxonomical significance. In: *Molluscan Megadiversity: Sea, Land and Freshwater*. World Congress of Malacology Perth, WA, July 11–16, 2004. Wells FE, ed. Western Australian Museum, Perth. p. 62.
- Haszprunar G 1988. *Sukashitrochus* sp., a scissurellid with heteropod-like locomotion (Mollusca, Archaeogastropoda). *Ann. Naturhist. Mus. Wien. Ser. B* 90: 367–371.
- 1989. New slit-limpets (Scissurellacea and Fissurellacea) from hydrothermal vents. Part 2. Anatomy and relationships. *Contrib. Sci. Los Angeles County Mus. Nat. Hist.* 408: 1–17.
- Herbert DG 1986. A revision of the southern African Scissurellidae (Mollusca: Gastropoda: Prosobranchia). *Ann. Natal Mus.* 27: 601–632.
- 1987. Revision of the Solariellinae (Mollusca: Prosobranchia: Trochidae) in southern Africa. *Ann. Natal Mus.* 28: 283–382.
- Hickman CS 1985. Comparative morphology and ecology of free-living suspension-feeding gastropods from Hong Kong. In: *Proceedings of the Second International Workshop on the Malacofauna of Hong Kong and Southern China, 1983*. Morton B & Dudgeon D, eds., pp. 217–234. Hong Kong University Press, Hong Kong.
- 1992. Reproduction and development of trochacean gastropods. *Veliger* 35: 245–272.
- 1998. Superfamily Pleurotomarioidea. In: *Mollusca: The Southern Synthesis Part B*. Beesley PL, Ross GJB, & Wells A, eds., pp. 664–669. CSIRO Publishing, Melbourne.
- 1999. Sexual dimorphism and contact pairing in *Sinezona* sp. (Vetigastropoda: Scissurellidae). In: *The Seagrass Flora and Fauna of Rottnest Island, Western Australia*. Walker DI & Wells FE, eds., pp. 129–135. Western Australian Museum, Perth.
- 2003. Functional morphology and mode of life of *Isanda coronata* (Gastropoda: Trochidae) in an Australian macrotidal sandflat. In: *The Marine Flora and Fauna of Dampier, Western Australia*. Wells FE, Walker DI, & Jones DS, eds., pp. 69–88. Western Australian Museum, Perth.
- Kase T & Kano Y 2002. *Trogloconcha*, a new genus of larochene Scissurellidae (Gastropoda: Vetigastropoda) from tropical Indo-Pacific submarine caves. *Veliger* 45: 25–32.
- Korringa P 1947. Relations between the moon and periodicity in the breeding of marine animals. *Ecol. Monogr.* 17: 347–381.
- Kikuchi T & Doi T 1987. Defensive escape response of two trochid sand snail species of the genus *Umbonium*: the effect of species-specific response to asteroid predators. *Publ. Amakusa Mar. Biol. Lab.* 9: 47–65.
- Levinton JS 1979. The effect of density on deposit-feeding populations: movement, feeding and floating of *Hydrobia ventricosa* Montagu (Gastropoda: Prosobranchia). *Oecologia* 43: 27–39.
- Marshall BA 1993. The systematic position of *Larochaea* Finlay, 1927, and introduction of a new genus and two new species (Gastropoda: Scissurellidae). *J. Mollus. Stud.* 59: 285–294.
- Marshall BA 2002. Some recent scissurellids from the New Zealand region, and remarks on some scissurellid genus group names (Mollusca: Gastropoda). *Mollus. Res.* 22: 165–181.
- Martel A & Chia F-S 1991. Drifting and dispersal of small bivalves and gastropods with direct development. *J. Exp. Mar. Biol. Ecol.* 150: 131–147.
- McLean JH. 1989. New slit-limpets (Scissurellacea and Fissurellacea) from hydrothermal vents. Part 1. Systematic descriptions and comparisons based on shell and radular characters. *Contributions in Science, Natural History Museum of Los Angeles County*, no. 407, pp. 1–29.
- Pelseneer P 1899. Recherches morphologiques et phylogénétiques sur les mollusques archaïques. *Mém. Couronnés Mémoires Savants Étrangers Acad. Roy. Sci. Lettres Beaux-Arts Belgique* 57: 1–113.
- Porter SS 2002. A light trap survey of stomatopod larvae at Cook's Bay, Moorea. *Biology and Geomorphology of Tropical Islands, Moorea Student Research Papers* 11, pp. 135–152.
- Strathmann RR 1974. The spread of sibling larvae of sedentary marine invertebrates. *Am. Nat.* 108: 29–44.
- Watson RB 1886. Report on the Scaphopoda and Gastropoda collected by H.M.S. Challenger during the years 1873–1876. Report on the Scientific Results of the Voyage of H.M.S. Challenger. *Zoology* 15: 1–680.
- Yaron I 1983. A review of the Scissurellidae (Mollusca: Gastropoda) of the Red Sea. *Ann. Naturhist. Mus. Wien. Ser. B* 84: 263–279.